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Substrate Management Affecting Yield and Quality Formation of Shiitake Mushroom (*Lentinula edodes*)

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Abstract Shiitake mushroom (*Lentinula edodes*) is one of the important edible and medicinal mushrooms, and substrate management is a key factor affecting production stability, yield formation, and quality improvement. This review analyzes the effects of different substrate materials, including sawdust and agricultural and forestry residues, as well as nutrient supplementation, carbon-to-nitrogen ratio, moisture conditions, and physical properties of substrates on mycelial growth, bag maturation, fruiting process, and fruit body quality formation. A high-quality substrate should not only provide sufficient carbon and nitrogen sources but also maintain good aeration, water-holding capacity, and an appropriate nutrient release rate. Hardwood sawdust remains the main basic material in current production; however, with increasing resource costs, alternative materials such as fruit tree branches, crop straw, and forestry residues have received increasing attention. Appropriate supplementation with nutrients such as wheat bran and rice bran, together with optimization of the carbon-to-nitrogen ratio, can promote mycelial growth, improve substrate bag maturity, and enhance yield stability. Meanwhile, substrate composition also affects cap color, commercial appearance, nutritional components, and flavor compound accumulation of shiitake mushrooms. Based on production practices in major cultivation regions, including Qingyuan in Zhejiang Province and Xixia in Henan Province, this review discusses regional differences in substrate management strategies and industrial development characteristics. In the future, shiitake mushroom production should further promote the recycling utilization of agricultural and forestry residues, precise substrate management, and quality-oriented production to achieve resource conservation, cost reduction, and sustainable development of the shiitake mushroom industry.

Keywords Shiitake mushroom (*Lentinula edodes*); Substrate management; Lignocellulosic materials; Agricultural and forestry residues; Bag cultivation; Yield; Quality formation

1 Introduction

Shiitake mushroom (*Lentinula edodes*) is one of the most important edible and medicinal mushrooms worldwide. It has attracted extensive attention due to its unique flavor, desirable texture, and rich nutritional and functional components. The fruiting bodies contain abundant proteins, polysaccharides, vitamins, minerals, and various bioactive compounds, providing both food value and health benefits. A mature shiitake mushroom industry has been established in many Asian countries, including China, Japan, and South Korea (Asdullah et al., 2025). Shiitake cultivation has gradually developed from traditional log cultivation to synthetic log cultivation, sawdust-based bag cultivation, and the use of mixed substrates containing various agricultural and forestry by-products. Modern production increasingly focuses on shortening production cycles, improving resource utilization efficiency, and maintaining stable product quality.

Shiitake mushroom is a typical white-rot fungus capable of degrading lignocellulosic materials, and its growth largely depends on complex carbon sources such as cellulose, hemicellulose, and lignin in the substrate. *L. edodes* possesses a strong lignocellulose-degrading enzyme system, which provides the biological ability to utilize various plant residues for growth and development (Chen et al., 2016). Substrate management not only determines nutrient availability for mycelial growth but also directly affects mycelial colonization, bag maturation, fruiting body development, and final yield and quality. With increasing pressure on sawdust resources, the utilization of agricultural and forestry residues and the optimization of mixed substrates have become important research directions. The goal of substrate management has gradually shifted from simply increasing yield to improving resource efficiency, production stability, and product quality.

However, current substrate management in shiitake production still faces several challenges. Traditional hardwood sawdust resources are limited by supply availability and increasing costs, making the development of suitable alternative materials an important requirement for sustainable industry development. Nevertheless, agricultural and forestry residues differ greatly in fiber structure, nutrient composition, and degradation characteristics, and direct replacement of traditional sawdust often fails to achieve consistent production performance. Therefore, this review systematically summarizes the effects of substrate composition, wood-based materials, nutrient supplementation strategies, carbon-to-nitrogen balance, and physical properties of substrates on mycelial growth, bag development, yield formation, and quality formation. By combining production practices from major shiitake cultivation regions in China, this study further discusses current substrate management models and future development directions. The aim is to provide theoretical support and practical references for the recycling utilization of agricultural and forestry by-products, the development of low-cost and efficient cultivation substrates, and the production of high-quality shiitake mushrooms.

2 Construction of High-Quality Substrate Systems for Shiitake Mushroom Production

2.1 Principles for developing high-quality substrate systems

Shiitake mushroom is a typical wood-decaying edible fungus, and its growth mainly depends on lignocellulosic materials in the substrate as nutrient sources. *Lentinula edodes* has strong lignocellulose-degrading ability and can utilize materials such as sawdust, branches, and some agricultural residues for mycelial growth and fruiting body formation (Chen et al., 2016). However, in practical production, not all plant materials are suitable for shiitake cultivation. Different raw materials vary in their chemical composition and physical characteristics, which can affect mycelial growth rate, bag maturation period, fruiting performance, and final product quality.

A suitable shiitake substrate mainly needs to solve two basic problems: whether the mycelium has sufficient nutrients and whether the substrate environment is suitable for mycelial development. Wood-based materials such as sawdust mainly provide a stable carbon source and help maintain proper substrate looseness, allowing normal mycelial growth. Hardwood sawdust remains the main substrate material in current shiitake production because it decomposes at a moderate rate and can provide nutrients for a relatively long period. However, with the expansion of the shiitake industry, dependence on high-quality sawdust has resulted in increasing costs and resource shortages. Therefore, more studies have focused on using agricultural and forestry residues as alternative or supplementary materials.

For example, fruit tree pruning branches, forestry residues, and some crop residues have potential as substrate resources. However, these materials cannot directly replace sawdust without proper adjustment. Their characteristics need to be considered during formulation to avoid negative effects on mycelial growth and later fruiting performance. Nabhan et al. (2025) reported that different substrate materials influence mycelial growth, yield, and fruiting body quality, indicating that substrate selection should consider both raw material properties and production objectives.

2.2 Selection of wood-based substrate materials

Under natural conditions, shiitake mushrooms mainly grow on hardwood materials. Therefore, hardwood sawdust has been the most commonly used substrate material in commercial cultivation for many years. Compared with some softwood materials, hardwood sawdust generally has a more stable structure and a suitable nutrient release rate, providing a relatively long growth period for shiitake mycelia.

In practical production, however, not all types of sawdust perform equally. The tree species used as raw materials can influence mycelial growth, fruiting performance, and product quality. Thakur et al. (2024) compared the effects of different wood substrates on shiitake production and nutritional composition, and found that wood sources caused differences in yield performance and accumulation of functional components. Among them, hardwood materials such as *Populus ciliata* and *Mangifera indica* supported better production performance. In addition, different wood substrates affected ergosterol accumulation and the potential formation of vitamin D_2.

Using only one type of sawdust does not always result in the best production performance. Reasonable mixing of different wood materials can improve substrate properties. A mixture of oak and eucalyptus substrates increased the biological efficiency of shiitake cultivation, and the combination of oak, eucalyptus, and wheat bran showed better production performance (El Sebaaly et al., 2024).

With the continuous expansion of shiitake production, the supply pressure of high-quality traditional sawdust resources has gradually increased. Agricultural and forestry residues have therefore attracted increasing attention as alternative substrate materials. Sassine et al. (2024) evaluated the application of woody residues, including acorns, grape branches, and olive branches, in shiitake substrates. The results showed that some properly formulated alternative materials could achieve production performance close to that of traditional oak sawdust.

2.3 Nutrient supplementation strategies

Using sawdust alone often results in insufficient nutrient supply, especially due to low nitrogen and mineral contents, which cannot fully support long-term mycelial growth and fruiting body development. Therefore, adding appropriate nutrient supplements to sawdust-based substrates is an important strategy for improving shiitake production performance.

Currently, wheat bran and rice bran are the most widely used nutrient supplements in shiitake cultivation. These cereal by-products contain relatively high levels of proteins, minerals, and vitamins, which can improve substrate nutrition, promote mycelial expansion, and enhance later fruiting. Paswal et al. (2024) conducted a study in the Jammu region of India and found that a substrate containing wheat straw combined with wheat bran showed better nutritional characteristics than sawdust alone. The contents of crude protein, crude fat, crude fiber, and total carbohydrates reached 22.44%, 3.97%, 7.69%, and 63.50%, respectively.

Different types of supplements also show different effects on shiitake production. Shanmugaraj et al. (2025) compared several nutrient supplements and found that wheat bran treatment resulted in higher fruit body weight and biological efficiency, followed by rice bran, while some other supplements showed relatively lower effects.

Desisa et al. (2023) investigated the effects of different nutrient supplementation strategies in agricultural waste-based substrates. The S4 treatment, based on sugarcane bagasse supplemented with 20% poultry manure, showed the best performance, with a fresh mushroom yield of 434.33 g per 500 g substrate, a biological efficiency of 86.83%, and continuous production of five flushes. This treatment also resulted in higher protein, fiber, and fat contents of the fruiting bodies (Desisa et al., 2024) (Figure 1).

2.4 Carbon-nitrogen balance and substrate performance

During cultivation, carbon in the substrate is mainly used for mycelial growth and energy supply, while nitrogen participates in mycelial formation, enzyme synthesis, and fruiting body development. The balance between carbon and nitrogen directly affects mycelial growth rate, bag maturation time, and later fruiting performance. However, a higher C/N ratio or increased nitrogen content does not always lead to better production. An appropriate balance is required. Nutrient supplements such as wheat bran and rice bran not only provide additional nutrients but also help regulate the C/N ratio, creating a more suitable environment for long-term shiitake growth.

Different substrate systems may require different C/N conditions. In agricultural waste-based substrates, crop residues usually contain high carbon levels but relatively low nitrogen levels, and additional nitrogen sources are often needed to improve nutrient utilization efficiency. However, the relationship between C/N ratio and shiitake yield is not simply linear. Chen et al. (2022) studied the effects of hardwood substrates and different nitrogen supplementation levels on shiitake production and found that nitrogen supply significantly influenced lignocellulose degradation and yield formation. Although substrates without nitrogen supplementation showed faster mycelial expansion, the highest yield was not obtained in this treatment but occurred after adding an appropriate amount of whey nitrogen source.

Figure 1 Improvement of the nutritional composition of *Lentinula edodes* using different cultivation substrates (Adapted from Desisa et al., 2024)

The utilization of substrate nutrients also changes during different growth stages of shiitake mushrooms. During the mycelial colonization stage, shiitake preferentially utilizes relatively easily degradable components such as hemicellulose. After entering primordium formation and fruiting body development stages, the fungus further utilizes more complex components such as cellulose and lignin (Atila, 2019).

2.5 Moisture content and physical structure of substrates

For family farms and small-scale producers, a good substrate should not only provide sufficient nutrients but also create suitable environmental conditions for mycelial growth. Mycelia require adequate moisture, oxygen supply, and appropriate physical structure for effective colonization. In practice, different particle sizes of sawdust are often mixed to ensure that the substrate maintains both water retention capacity and good aeration. Substrate particle size, pore structure, and raw material composition jointly influence mycelial expansion, nutrient utilization, and final production performance, indicating that physical structure is an important factor in substrate design rather than a secondary consideration (Nabhan et al., 2025).

The moisture content of substrates should be adjusted according to the characteristics of raw materials. Desisa et al. (2023) controlled the moisture content of agricultural waste-based shiitake substrates at 60%–65% and added gypsum and calcium carbonate to improve substrate stability. Gypsum provides minerals such as calcium and sulfur while improving substrate structure, whereas calcium carbonate helps regulate substrate pH conditions.

Different agricultural residues show considerable differences in water retention, air permeability, and mycelial colonization ability due to their structural characteristics. Baktemur et al. (2022) compared several agricultural by-products as shiitake substrate materials and found significant differences in mycelial growth rates among different formulations, with large variation between the fastest and slowest treatments. These differences were not only related to nutrient composition but also associated with fiber structure, aeration capacity, and water-holding ability of the materials.

3 Substrate Management During Shiitake Mushroom Bag Production

3.1 Substrate preparation, bag filling, and sterilization management

Shiitake mushroom bag production usually uses lignocellulosic materials such as sawdust or agricultural and forestry residues as the basic substrate components. Nutrient supplements, including wheat bran, grain powder, and mineral elements, are added according to the nutritional requirements of mycelial growth. The substrate preparation process generally includes raw material crushing, mixing, moisture adjustment, supplementation with additives, bag filling, and sterilization. The main purpose of these steps is to create suitable nutritional and physical conditions for shiitake mycelial growth.

Insufficient moisture can restrict mycelial expansion, while excessive moisture may reduce aeration and increase the risk of contamination. In most bag cultivation systems, raw materials need to be fully moistened and adjusted before bag filling to maintain an appropriate moisture level. Shanmugaraj et al. (2024) evaluated different agricultural by-product substrates for shiitake cultivation in West Bengal, India. The tested materials included sawdust, rice straw, wheat straw, corn cob, sugarcane bagasse, and bean shells. After soaking, the moisture content was adjusted to 60%-65%, and wheat bran and $CaCO_3$ were added for nutritional and structural regulation, forming a typical substrate preparation process based on agricultural residues. Kumar et al. (2022) also applied a combination of moisture adjustment, mineral supplementation, and sterilization in agricultural waste-based substrates, indicating that whether traditional sawdust systems or alternative agricultural residue systems are used, maintaining substrate stability and reducing contamination risks are essential foundations for successful bag cultivation (Figure 2).

In commercial production, high-temperature sterilization is commonly used to treat substrates by reducing competition from bacteria, molds, and other microorganisms, thereby improving bag cultivation success rates. Because different substrate materials vary in structure and moisture status, sterilization efficiency depends not only on temperature and treatment duration but also on substrate density, particle size, and bag compaction level.

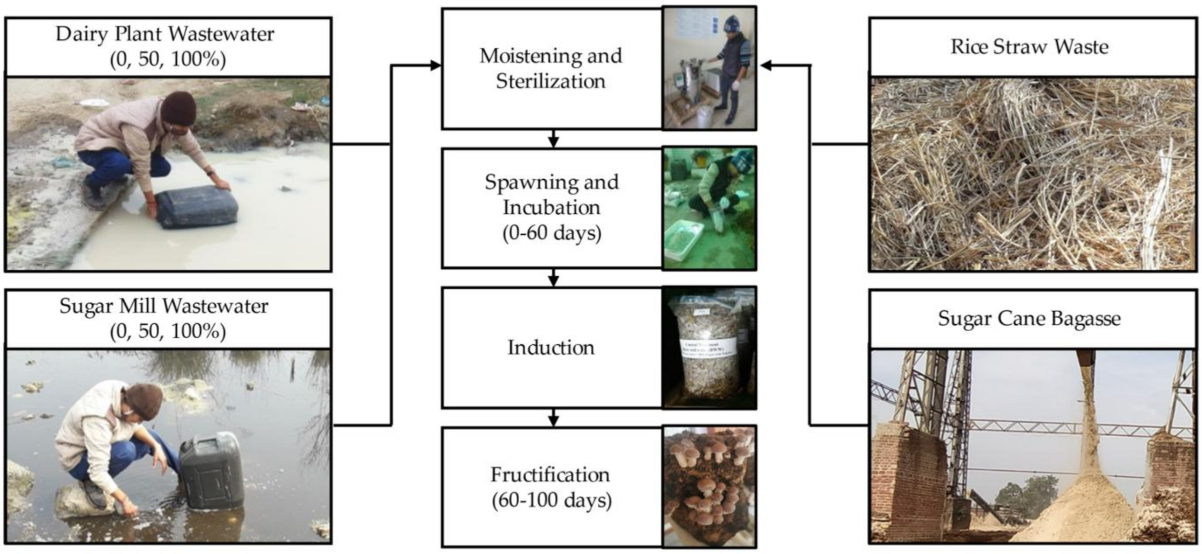

Figure 2 Experimental steps for Shiitake mushroom cultivation using agro-industrial wastes (Adopted from Kumar et al., 2022)

3.2 Mycelial colonization and bag maturation management

After inoculation, shiitake mushroom bags first enter the vegetative growth stage. The mycelia begin to utilize lignocellulosic materials and nutrient supplements in the substrate and gradually complete the maturation process, including substrate colonization, mycelial film formation, mycelial knot development, browning, and formation of the outer protective mycelial layer. For growers, a fully colonized bag does not necessarily indicate that cultivation is complete. Only when the mycelia have sufficiently transformed substrate nutrients and reached a stable mature state can the bags support subsequent primordium formation and continuous fruiting. Different substrate formulations can influence the maturation speed of cultivation bags. Significant differences in mycelial expansion rates have been observed among agricultural by-product-based substrates, and different combinations of plant residues can alter the colonization process and maturation rhythm of shiitake bags.

The maturation process of shiitake bags is influenced not only by substrate nutrient composition but also by cultivation environmental conditions. Shiitake mycelia are considered mesophilic fungi, and most studies indicate that 24 ℃~25 ℃ is suitable for vegetative growth, while a pH range of 5.0-6.0 promotes mycelial expansion (Trang et al., 2023). However, under practical production conditions, there is a clear interaction between substrate characteristics and environmental factors.

3.3 Fruiting induction and bag management

After the substrate bags reach maturity, shiitake mycelia gradually transition from vegetative growth to reproductive growth. At this stage, external environmental stimulation and management practices are required to induce primordium formation and fruiting body development. Common induction measures include temperature changes, soaking treatment, humidity adjustment, light regulation, and gas exchange control. These measures do not directly produce mushrooms but promote the transition from vegetative growth to reproductive growth after the substrate bags have completed nutrient accumulation and physiological maturation.

In practical production, soaking and temperature variation are among the most commonly used induction methods in shiitake bag cultivation. Studies on different bag-opening methods and stimulation treatments have shown that bag management approaches can influence the location and number of primordia formed (Yamauchi et al., 2009). Traditional bag-opening methods may cause primordia to form simultaneously on multiple surfaces of the substrate block, increasing the need for spraying and water management to prevent dehydration. By adjusting stimulation timing and water supply methods, primordium formation can be more concentrated, improving subsequent management efficiency. Therefore, fruiting induction is not only a process of environmental regulation but also a management approach for optimizing the spatial distribution of fruiting bodies.

4 Effects of Substrate Management on Shiitake Mushroom Yield

4.1 Effects of substrate on fruiting initiation and production cycle

The production cycle of shiitake mushrooms mainly includes mycelial expansion, bag maturation, primordium formation, and fruit body harvesting. Among these stages, substrate composition is an important factor affecting the transition speed between different growth stages. Because different woody materials vary in lignin, cellulose, and hemicellulose contents, as well as their degradation rates, shiitake mycelia show different utilization efficiencies for different substrates.

El Sebaaly et al. (2024) used oak, eucalyptus, mixed sawdust, and wheat bran-supplemented substrates to evaluate substrate suitability by comparing mycelial colonization time, fruiting initiation time, and first harvest time under different formulations. The oak + wheat bran treatment showed faster bag maturation, with a full colonization time of 72.2 days, first fruiting at 75.5 days, and harvest readiness at only 79.5 days. In contrast, the eucalyptus + maple wood + wheat bran treatment required 88.3, 87.5, and 92.0 days for full colonization, fruiting initiation, and harvest, respectively. The difference in production cycle between the two substrates exceeded 10 days, indicating that different combinations of woody materials can significantly influence the transition from vegetative growth to reproductive growth in shiitake mushrooms.

Sassine et al. (2024) selected oak acorns (OA), vine pruning residues (VIP), and olive pruning residues (OLPR) as alternative materials to replace oak sawdust and evaluated the effects of different mixing ratios on mycelial maturation and fruiting time (Figure 3). Substrates containing oak acorns showed better production adaptability. The OA treatment and OA combined with vine pruning residues shortened mycelial maturation and first harvest time by approximately 9 days compared with the oak sawdust control. However, when vine pruning residues or olive pruning residues were used alone, the production cycle was significantly extended.

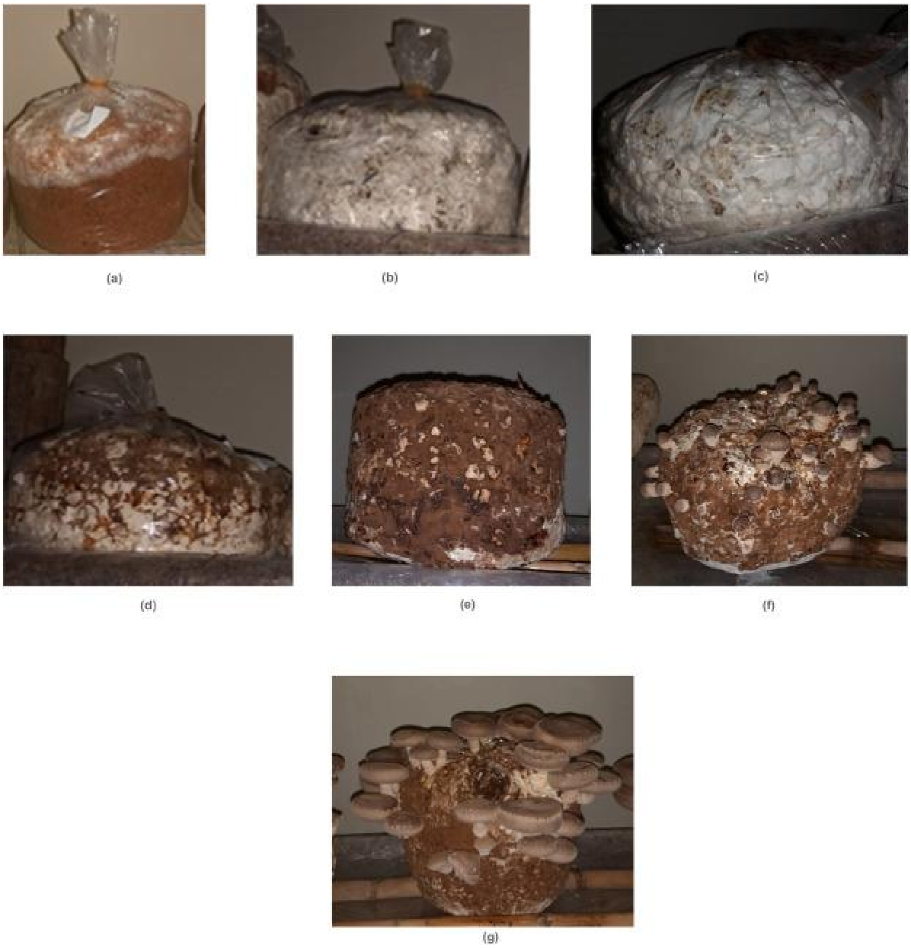

Figure 3 a Substrate blocks at stage 1: mycelial run. b Substrate blocks at stage 2: coat formation. c Substrate blocks at stage 3: bump formation. d Substrate blocks at stage 4: pigmentation. e Substrate blocks at stage 5: coat hardening. f Substrate blocks at pin head formation stage. g Substrate blocks at fruit development stage (Adopted from Sassine et al., 2024)

4.2 Effects of substrate on biological efficiency and yield stability

Biological efficiency (BE) is an important indicator for evaluating the conversion capacity of shiitake cultivation substrates. It reflects the ability of a substrate to produce fresh mushrooms per unit weight of dry substrate. The type of substrate materials, nutrient supplementation strategies, and carbon-to-nitrogen balance are major factors determining BE.

Studies evaluating different substrate components have shown that oak sawdust substrates achieved a BE of 92.35%, together with higher mushroom numbers and a shorter mycelial growth period (Ranjbar and Olfati, 2017). High-quality woody materials can provide suitable physical structure and continuous nutrient supply, and therefore still have important value in some commercial production systems.

However, for agricultural by-product-based substrates, nutrient supplementation strategies often determine substrate conversion efficiency. Improving the utilization efficiency of agricultural residues requires not only replacing sawdust but also adjusting nutrient balance through appropriate nitrogen supplementation. The performance across multiple flushes often provides a better indication of substrate quality than the highest yield from a single flush. Under a fixed substrate system, optimization of inoculum composition can improve overall production performance across two flushes, suggesting that stable shiitake production is influenced not only by substrate composition but also by the establishment process of mycelial growth.

Increasing nutrient supplementation does not always improve yield. Different nitrogen addition levels can significantly affect fresh mushroom production, and moderate nitrogen supplementation generally performs better than insufficient or excessive nitrogen supply. This indicates that shiitake substrates require an appropriate nutrient balance rather than simply increasing nitrogen availability.

4.3 Substrate regulation of fruiting body formation

Fruiting body formation in shiitake mushrooms represents the transition from vegetative growth to reproductive growth after sufficient nutrient accumulation by the mycelia. This process is jointly regulated by nutrient supply, physical structure, and moisture conditions of the substrate. Therefore, substrate evaluation should not only focus on the number of fruiting bodies but also consider its effects on fruiting patterns and morphological characteristics.

For fresh-market shiitake production, large fruiting bodies with thick flesh generally have higher commercial value. Therefore, substrates should support sufficient nutrient accumulation and fruit body development. In contrast, processing-oriented production may place greater emphasis on mushroom number and total yield per cultivation area.

Bansal and Ravi (2024) used different woody agricultural residues as main substrate materials and supplemented them with rice bran and wheat bran. They evaluated substrate performance by comparing mycelial growth, primordium appearance time, cap diameter, stipe length, and final yield under different treatments. The eucalyptus + poplar + rice bran + wheat bran combination promoted rapid mycelial expansion and earlier formation of mycelial films and primordia, showing faster reproductive transition. However, although the poplar + mango + rice bran + wheat bran treatment did not form primordia the earliest, it produced larger fruiting bodies, with a total yield of 666.03 g and a biological efficiency of 66.63%.

In addition to basic woody materials, supplementary additives can also modify fruiting body development patterns. Zied et al. (2024) investigated the effects of different charcoal powder addition levels and compared the responses of different strains in terms of yield, mushroom number, and individual mushroom weight. Charcoal supplementation showed clear regulatory effects on fruiting body formation, and the 4% addition level had the most obvious influence on yield and morphological traits. The study also found a negative relationship between mushroom number and individual fruit body weight. Some treatments promoted the formation of more fruiting bodies but resulted in smaller individual mushrooms, whereas other treatments reduced mushroom number but increased individual mushroom weight.

5 Quality Formation of Shiitake Mushroom and Substrate Management

5.1 Formation of commercial appearance quality

The commercial value of shiitake mushrooms is mainly determined by fruiting body appearance, including cap color, cap thickness, individual mushroom weight, stipe characteristics, and overall uniformity. Although these traits are expressed during the fruiting stage, their formation is closely related to nutrient supply and physical properties of the substrate. The composition of lignocellulosic materials, particle size, and nutrient release rate in the substrate influence mycelial growth status and primordium development, thereby affecting final commercial appearance.

Changes in the proportion of woody materials in the substrate can significantly modify shiitake appearance characteristics. Replacing hardwood sawdust with 50% or 100% bamboo sawdust resulted in lighter cap color and reduced melanin and chitin contents (Xu et al., 2026). Among these treatments, the 50% replacement treatment did not reduce fruiting body weight, whereas complete replacement decreased individual mushroom weight. This indicates that an appropriate replacement level is needed to balance substrate substitution, commercial quality, and yield performance.

In different sawdust mixture systems, individual mushroom weight varied significantly between the first and second flushes, suggesting that substrate composition influences nutrient distribution among different fruiting stages. Plant residues such as mugwort and stevia can improve both yield and nutritional quality when used as suitable partial substitutes for sawdust (Asdullah et al., 2025) (Figure 4).

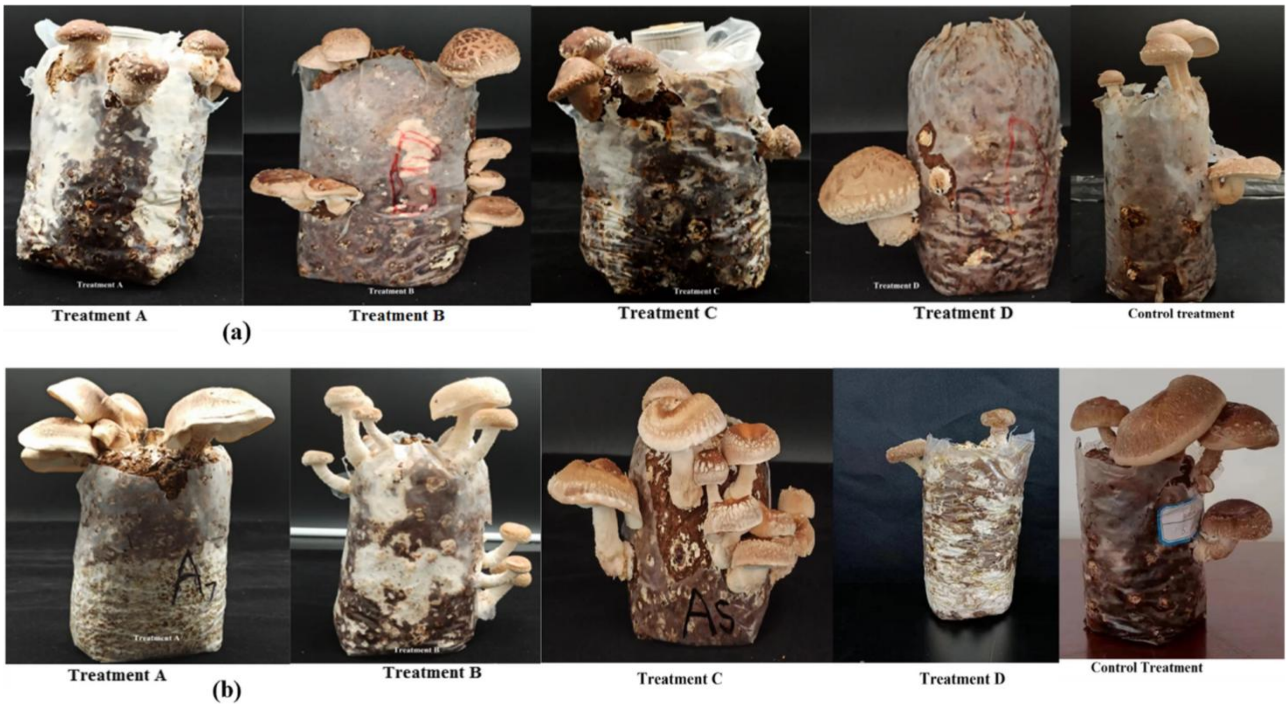

Figure 4 Emergence of mushrooms on different wormwood (*A. argyi*) (A). & stevia (*S. rebaudiana*) (B) formulations (Adopted from Asdullah et al., 2025)

5.2 Formation of nutritional quality

Nutrients in shiitake fruiting bodies, including proteins, amino acids, polysaccharides, minerals, and lipids, mainly originate from the absorption and transformation of carbon sources, nitrogen sources, and mineral elements by fungal mycelia. In practical production, substrates influence not only whether mushrooms can successfully form fruiting bodies but also the nutritional value of the final products. The type of woody materials, carbon-to-nitrogen ratio, and nutrient supplement composition all affect the accumulation of nutritional components in shiitake mushrooms.

Bach et al. (2018) compared the nutritional differences between log cultivation and sterile bag substrate cultivation of shiitake mushrooms and found clear differences in nutrient composition between fruiting bodies produced under different cultivation systems. Shiitake cultivated on sterile substrates showed higher levels of proteins, minerals, and lipids. The lower lignin content and more suitable carbon-to-nitrogen conditions of the substrate may have promoted nutrient utilization by fungal mycelia.

For family farms and growers, substrate optimization should not focus only on yield but also consider nutritional characteristics of the products. With increasing consumer demand for functional foods, bioactive components such as polysaccharides, vitamins, and minerals in shiitake mushrooms have attracted more attention. Different cultivation systems and substrate conditions can affect the composition of micronutrients, including vitamin and mineral levels (Farhan and Chechan, 2023).

5.3 Formation of flavor precursors and sensory quality

The aroma of shiitake mushrooms mainly originates from volatile compounds, sulfur-containing compounds, free amino acids, organic acids, and flavor-related nucleotides. Although these flavor compounds undergo further release and transformation during drying and processing, their formation is closely associated with the nutritional environment provided by the substrate during cultivation.

Different substrate materials can alter the accumulation of flavor-related metabolites in shiitake fruiting bodies. Xu et al. (2025) investigated the effects of agricultural and forestry residue-based mixed substrates on shiitake quality and found that different plant residues could regulate the levels of several flavor precursor compounds. Among them, the treatment containing 20% *Caragana korshinskii* residues increased sweet taste-related compounds and aromatic amino acid levels, whereas the treatment with 10% wolfberry branch residues significantly increased methionine content.

The characteristic aroma of shiitake mushrooms is mainly associated with the formation of specific volatile compounds. 1-octen-3-ol is an important contributor to the typical mushroom aroma of fresh shiitake, while sulfur-containing compounds such as lenthionine are key substances responsible for the characteristic aroma of dried shiitake mushrooms (Qin et al., 2020; Zhang et al., 2021). The formation of these volatile compounds is closely related to lipid, amino acid, and sulfur metabolism in fruiting bodies, and substrate nutrient conditions can influence the accumulation of these precursor substances.

6 Case Studies of Substrate Management Models in Major Shiitake Production Regions in China

6.1 Qingyuan, Zhejiang: forest-mushroom co-development system

Qingyuan County in Zhejiang Province is one of the important origins of artificial shiitake cultivation in China and represents a typical region where traditional log cultivation has gradually shifted toward modern bag-based cultivation systems. Relying on abundant forest resources in mountainous areas, Qingyuan has developed a “forest-mushroom co-development” model that integrates forest resource utilization with shiitake production. In 2022, the “Qingyuan Forest-Mushroom Co-development System in Zhejiang Province” was recognized by the Food and Agriculture Organization of the United Nations (FAO) as a Globally Important Agricultural Heritage System, reflecting the long-term interaction between shiitake production and ecological resource utilization in the region.

The development of the shiitake industry in Qingyuan has also been a process of continuous adjustment in substrate resource utilization. Early log cultivation mainly depended on natural wood resources. However, with increasing requirements for forest resource protection and production efficiency, shiitake cultivation gradually shifted toward sawdust-based bag cultivation systems. In modern substrate systems, hardwood sawdust remains an important structural material. Its abundant lignocellulosic components provide continuous carbon sources for mycelial growth and help maintain suitable substrate porosity and water-holding capacity.

With the expansion of the shiitake industry, several challenges have emerged, including insufficient supply of high-quality sawdust, increasing raw material costs, and differences in sawdust quality from different sources. Therefore, shiitake production in Qingyuan has gradually shifted from simple dependence on woody resources toward more efficient resource utilization strategies, including improving sawdust utilization efficiency, exploring agricultural and forestry residues as supplementary materials, and promoting recycling of spent mushroom substrates.

6.2 Xixia, Henan: large-scale standardized production

Xixia County in Henan Province is one of the major shiitake production areas in China. Its industrial development reflects the transition from production expansion toward standardized management and quality improvement. After years of development, Xixia has established an integrated industrial system covering substrate material supply, mushroom bag production, cultivation bases, processing, and marketing. The local shiitake industry has developed from traditional log cultivation and bag cultivation toward standardized production, characterized by large-scale cultivation, standardized management, and industrialized operation.

The shiitake production system in Xixia has implemented standardized management for mushroom substrate materials, auxiliary ingredients, and bag production processes. During production, particular attention is given to quality control of major substrate materials such as sawdust. At the same time, supplementary materials including wheat bran, gypsum, and cultivation bags are supplied under standardized systems to reduce variation among different production units.

Xixia has promoted the standardization of mushroom bag production by regulating bag preparation procedures, optimizing production parameters, and strengthening process management. Related technical practices emphasize precise control of substrate moisture content, pH, sterilization procedures, and mycelial cultivation stages to ensure stable bag maturation and improve subsequent fruiting management efficiency.

7 Future Development Directions of Substrate Management

7.1 Sustainable and circular substrate systems

An important future direction for shiitake substrate development is the transition from traditional dependence on woody resources toward regional and circular resource utilization systems. Hardwood sawdust has long been a fundamental material for shiitake production because of its stable lignocellulosic structure and good compatibility with shiitake mycelial growth. However, with the continuous expansion of the shiitake industry, pressure on high-quality sawdust supply has increased, and some regions have experienced rising costs and unstable raw material availability. Therefore, increasing the utilization of agricultural and forestry by-products while maintaining substrate performance will become an important strategy for future industry development.

Future resource utilization should also extend to the recycling of spent mushroom substrates after production. Large amounts of spent mushroom substrate generated during shiitake cultivation still contain partially degraded cellulose, lignin, and mineral nutrients. Direct disposal not only increases environmental pressure but also causes resource waste. Spent shiitake substrate can be used as an important raw material for preparing nitrogen-doped biochar, which has potential applications in environmental remediation, indicating its high value for resource utilization (Grimm et al., 2023). Spent substrate can also be used for organic fertilizer production, soil improvement, and agricultural recycling.

Therefore, future development of the shiitake industry should expand from focusing only on “substrate input” toward whole-life-cycle management, establishing a circular system of “agricultural residues → cultivation substrate → shiitake production → spent substrate utilization.”

7.2 Precision substrate management and digital optimization

Another important future direction of shiitake substrate management is the transition from experience-based decisions toward data-driven management. Currently, many small-scale producers still rely on visual observation of mycelial color, bag hardness, and fruiting status to determine production conditions. Although this approach is based on practical experience, it has limitations, including strong subjectivity, poor reproducibility, and insufficient consistency among production batches. With the development of large-scale cultivation, substrate management requires more accurate recording and analysis of relationships among different factors.

In recent years, artificial intelligence and predictive modeling technologies have begun to be applied to shiitake substrate optimization. Safaie et al. (2024) used a multilayer perceptron combined with a genetic algorithm to predict mycelial growth performance under different substrate combinations. The model achieved prediction accuracies of 92% and 97% for mycelial running length and growth speed, respectively. In the future, substrate screening may gradually shift from traditional large-scale experimental comparisons toward model-assisted decision-making based on production data.

7.3 Integration of substrate management with quality-oriented production

An important trend in future shiitake industry development is the shift of substrate management objectives from simply pursuing high yield toward balancing yield, quality, and market value. Future substrate optimization should move from identifying the “highest-yield formula” toward developing “quality-oriented substrate formulas.”

Different markets have different requirements for shiitake quality. Fresh mushroom markets mainly focus on cap color, morphological integrity, flesh thickness, and product uniformity. In contrast, dried mushroom markets place greater emphasis on aroma formation, rehydration performance, nutrient retention, and processing stability. Therefore, future substrate design should determine optimization targets according to product positioning rather than evaluating substrate performance only based on yield.

The establishment of quality-oriented substrate systems requires comprehensive consideration of raw material characteristics, production costs, yield stability, nutritional quality, and market demand. By integrating substrate management with quality evaluation systems, the shiitake industry can achieve a transition from production-scale expansion toward high-quality development.

Author Contributions

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Conflict of Interest Disclosure

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

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