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SUBSTRATES USED FOR THE CULTIVATION OF SHIITAKE MUSHROOMS (LENTINULA EDODES): A REVIEW

Stephanie Nabhan^{1*}, Zeina El Sebaaly², Maria Lacheva¹, Nicolas Bitar²,
Youssef Najib Sassine², Teodor Nedelin³

¹Agricultural University - Plovdiv, Bulgaria

²Lebanese University, Beirut, Lebanon

³University of Forestry, Sofia, Bulgaria

*E-mail: stephanie.nabhan@st.ul.edu.lb

Abstract

Lignocellulosic materials are the main substrates used in shiitake (*Lentinula edodes*) cultivation. Their physicochemical composition in terms of sawdust size, cellulose, hemicellulose, lignin, carbon, and nitrogen contents influences the mycelia run and mushroom yield and quality. The highest number of studies on shiitake have been focusing on its medicinal properties and biotechnological applications; however, a good number of them investigated the effect of substrate composition on the mushroom's productive and qualitative traits. This review is a first report summarizing findings from earlier studies that investigated a variety of substrates (supplemented or not), including hardwood sawdust (maple, eucalyptus), and agro-industrial byproducts (vine, olive, corn cobs, sunflower seed husk...). Results demonstrate that the substrate selection containing a single type or a combination of different types of hardwood had varying effects on the shiitake mycelial colonization rate, fruit initiation, yield, and nutritional composition of mushrooms. Most studies emphasized that mixing hardwood sawdust (vineyard residues, hazelnuts, and corn residues) with oak residues (sawdust or acorns), and supplementing shiitake substrates with wheat bran or rice bran as nitrogen sources, enhances both the yield and quality of shiitake mushrooms. The current review provides researchers and farmers with insights into optimal substrate choices for improving shiitake production under diverse cultivation systems.

Keywords: Agro-industrial byproducts, Biological yield, Hardwood sawdust, Lignocellulosic material, Shiitake strain, Substrate selection

Introduction

Shiitake mushroom, known as “*Lentinula edodes*”, is a Japanese mushroom with a light to dark brown convex cap, creamy white gills, and a light brown stipe (Annepu et al., 2019). The word “Shii” refers to the hardwood of *Castanopsis* spp.,

and “take” refers to the word mushroom (Chen, 2001); also it belongs to the genus of *Lentinula* and the order of *Agaricales* (Chen, 2005). Shiitake mushroom is currently the second most cultivated mushroom in the world, accounts for 25% of global mushroom production and is well-known for its nutritional and medicinal properties (Lindquist, 2024). It is rich in vitamins (B1, B2, and B3), minerals (calcium, magnesium, and iron) (Zhao et al., 2019), has antimicrobial and anticarcinogenic properties (Raghoonundon et al., 2021), and is distinguished by its “umami” taste that is becoming more popular, especially in the Asian cuisine (Ahmad et al., 2023).

The life cycle of *shiitake* is divided into two phases: the vegetative phase in which the mycelium grows into a hyphal network, and the reproductive phase in which fruiting bodies are formed. During the vegetative phase, dark and warm conditions with moderate humidity are essential, whereas the reproductive phase requires light, lower temperatures, and high humidity. (Annepu et al., 2019; Meyer et al., 2020). Over time, the cultivation method of shiitake has changed from inoculating natural wood logs to a more controlled method using sawdust blocks. This transition occurred because the availability of oak wood logs in many countries represents a limiting factor, and cutting oak trees increases the risk of extinction of such species (Gaitán-Hernández et al., 2014). On the other hand, shiitake is a versatile white rot fungus that can colonize a large variety of lignocellulosic substrates (Sattar et al., 2021), and thrives on substrates with a pH of 5.5–6.5 and a carbon-to-nitrogen (C/N) ratio between 25:1 and 55:1, with 40:1 being the optimal (Chen, 2005; Zied et al., 2011). Consequently, conventional substrates can be replaced or supplemented with locally available agro-industrial and forest residues (Fan & Soccol, 2005; Eira et al., 2010). Early studies showed that *L. edodes* can be cultivated on natural hardwood logs or synthetic sawdust substrates such as oak, willow, poplar, alder, maple, beech, sweetgum; and various agro-industrial residues such as coffee residues, sugarcane bagasse, corncob, cotton waste, sunflower seed hulls, cereal straws (Royse & Chen, 2005), alone or mixed with additives (wheat bran, millet, rye, and rice bran) (Atila, 2019; Kumla et al., 2020).

The current review is the first to integrate findings on using different types of hardwood sawdust and agro-industrial byproducts, offering practical guidance for optimizing substrate selection when cultivating shiitake mushrooms.

Shiitake cultivation methods

In the wild, shiitake grows on oak or similar hardwood trees of the *Fagaceae* family (Menolli et al., 2022). On an industrial scale, shiitake mushrooms were traditionally cultivated on wood logs of the “shi” tree (*Castanopsis cuspidata*), measuring 7–15 cm in diameter and 100–150 cm in length. In such type of cultivation, wood logs are drilled with holes (1–1.5 cm wide and 1.5–2 cm deep) spaced 20–30 cm apart and inoculated by a plug spawn of matching size that was inserted into the holes and sealed with beeswax (Mudge et al., 2013). However, this method requires an incubation period of 6–12 months and consumes considerable forest resources (Mata et al., 2013). Therefore, the cultivation of shiitake on “synthetic” or “artificial” sawdust logs has been adopted

(Ashrafuzzaman et al., 2009; Gaitán-Hernández et al., 2014). This technique consists of inoculating the grain spawn of shiitake into sawdust blocks composed of 80% hardwood sawdust and 20% starch-rich additives like wheat or rice bran (conventional formula). The type of hardwood sawdust used significantly affects the mycelia colonization and yield, as well as the size, flavor, and composition of the produced mushrooms (Ramkumar et al., 2010; Sassine et al., 2024); also, wheat or rice bran, when added, supplies essential proteins and nutrients for optimal mycelial growth (Royse, 1997). Therefore, the choice of substrate is an important factor during shiitake cultivation. Nevertheless, cultivation of shiitake on sawdust blocks resulted in higher yields, enhanced shiitake mushroom quality, and a reduced growth cycle timing (up to 2-3 months) compared to the traditional method (Eira & Montini, 1997; Royse, 1997; Chung et al., 2021).

Substrates investigated in the cultivation of shiitake

1) Cultivation of *Lentinula edodes* on natural wood logs

Originally cultivated on *Castanopsis cuspidata* and oak wood logs (Royse, 2009), *L. edodes* cultivation has evolved to include multiple wood log species as suitable growth media. Aji (2009) stated that in North America, shiitake cultivation thrived on beech families (*Fagaceae*), white oaks (*Quercus alba*, Linnaeus), and chestnut oaks (*Quercus montana* Willd.) rather than on the thinner-barked species of red oaks (*Quercus rubra*, Du Roi), scarlet oaks (*Quercus coccinea* Muenchh.), and pin oaks (*Quercus palustris* Muenchh.). Additionally, the following tree logs were reported as suitable for growing shiitake mushrooms: Nepal Alder (*Alnus nepalensis*), Indian Chestnut (*Castanopsis indica*), Himalayan Birch (*Betula alnoides*), Common Walnut (*Juglans regia*), Chinese guger tree (*Schima wallichii*) (Manandhar, 2005), Alder (*Alnus* spp.), Poplar (*Populus* spp.), Beech (*Fagus* spp.), and Maple (*Acer* spp.) (Przybylowicz & Donoghue, 1990). Moreover, Bruhn et al. (2003) reported that shiitake's biological efficiency (BE) (mushroom fresh weight/substrate dry weight *100) on sugar maple (*Acer saccharum*) logs was lower than on oak (*Quercus alba* or *Quercus rubrum*) logs, while Bruhn et al. (2009) showed the opposite in another experiment. Similarly, Frey et al. (2020) reported that *Lentinula edodes* exhibited lower productivity and reduced economic returns when cultivated on red maple (*Acer rubrum*) logs compared to white oak (*Quercus alba*). On the other hand, Shieh et al. (1991) found that shiitake cultivation on China fir (*Cunninghamia lanceolata* (Lamb.) Hook logs in Taiwan was commercially unfeasible.

2) Cultivation of *Lentinula edodes* in sawdust blocks

Recent studies investigated the use of lignocellulosic materials of various agro-industrial and forest residues in shiitake cultivation by selecting materials based on their availability in specific production areas (Kumla et al., 2020). Based on the conventional substrate formula made from hardwood sawdust and additives, various combinations of hardwood were mixed in different proportions and investigated in shiitake cultivation (Chen et al., 2016).

2.1) Agro-industrial residues as shiitake substrates

The use of agro-industrial residues as a substitute for oak sawdust caused varying effects; while some residues have led to changes in shiitake yield, others have only influenced its nutritional or medicinal properties, without impacting yield. For instance, the use of vineyard sawdust alone in the growing substrate of shiitake improved its phenolic compound content compared to oak sawdust, but they did not enhance the biological efficiency (Gaitán-Hernández et al., 2020). Also, mixing vineyard sawdust with wheat bran delayed mycelial colonization (by a range of 22.2 to 22.7 days), reduced BE (by a range of 19.9 to 65.7%), and decreased shiitake mushroom protein content relative to the control (oak sawdust) (Baktemur et al., 2022; Sassine et al., 2024). In the other hand, mixing oak acorns with vineyard sawdust accelerated harvest by 6.7 days relative to the control and produced a yield of 556.2 g/kg, compared with 597.0 g/kg obtained from oak sawdust. Similarly, substrates composed solely of oak acorns yielded comparably to oak sawdust (552.0 g/kg), and hastened harvest by 9.3 days compared to the control (Sassine et al., 2024).

On the other hand, *Lentinula edodes* has been successfully cultivated on hazelnut residues. Puliga et al. (2022) reported that the shiitake's ability to degrade hazelnut enhanced overall mushroom quality. Similarly, a substrate mixture comprising 75% hazelnut husk, 10% wheat bran, and 15% beech wood chips or wheat straw produced yields comparable to the control substrate composed of beech wood chips (Özçelik & Peksen, 2006).

Furthermore, apple sawdust was recommended in the cultivation of *L. edodes*. Yu et al. (2022) mentioned that cultivating *Lentinula edodes* strain LD0040 on a substrate composed of 80% apple sawdust, 18% wheat bran, and 2% gypsum increased the BE to approximately 80%, comparably to that obtained on oak sawdust. However, they stated that a particular consideration should be given to shiitake cultivation on apple sawdust, as trace amounts of chlorpyrifos, Hg, As, Cd, and Cr were detected in the mushrooms, although all levels remained within safe limits. Moreover, according to Worrall & Yang (1992), *Lentinula edodes* isolate WC 545 exhibited a faster and denser mycelial colonization, and a high yield (84 g/log) when cultivated on a substrate mixture of apple pomace and ash compared to oak sawdust alone.

Further, the use of corncobs in the substrate supported high mushroom yield and ameliorated the nutritional composition and quality of mushrooms (Philippoussis et al., 2007). According to Xu et al. (2020), a substrate formula consisting of 40% corn cobs, 10% corn straw, 30% oak sawdust, 18% bran, 0.5% gypsum, and 0.5% lime improved the firmness and the nutritional composition (calcium, manganese, and iron) of shiitake mushrooms, and increased the BE by 8.82% compared to oak sawdust. Further, Yu et al. (2021) mentioned that substrate mixtures containing 18–58% corncobs increased the BE to a range of 64.55–70.71% (compared to 57.15% on oak sawdust). Additionally, a substrate formula composed of 50% corncob, 28% sawdust, 20% wheat bran, and 2% gypsum supported rapid mycelial growth of *Lentinula edodes* strain CCMJ2806 (2.96 mm/day), high yield (of 722.08 g/log), high BE (of 80.23%), large mushroom caps and stipes, and enhanced shiitake nutritional composition (ash (~6.5 g/100 g),

polysaccharides (4.51 g/100 g), phosphorus (3.0–3.3 mg/g), potassium (~20 mg/g), sodium (~0.4 mg/g), and calcium (~2.0 mg/g)). In the other hand, Baktemur et al. (2020) reported that introducing corn cobs into shiitake substrates increased the sulfur content of the mushrooms, therefore affecting their characteristic odor.

Moreover, mixing sugarcane bagasse with animal manure has been reported as suitable substrate mixtures for shiitake cultivation. Desisa et al. (2023) and Desisa et al. (2024), mentioned that a substrate mixture of 80% sugarcane bagasse and 20% chicken manure increased BE by approximately 40% and enhanced mushroom protein and fiber contents (by 5.93%, and 1.37% respectively) compared to sugarcane bagasse. Also, a substrate mixture of 80% sugarcane bagasse and 20% cow dung improved BE (by approximately 20%), increased mushroom ash content (by 0.74%), and accelerated fruiting (by 1.7 days) compared to sugarcane bagasse. Conversely, rice straw alone in the growing media was found to be less suitable for shiitake cultivation. Gao et al. (2020) reported that adding 20 and 40% rice straw into a mixture containing oak sawdust and wheat bran increased free amino acid and monosodium glutamate (MSG) mushroom contents but did not significantly affect yield. However, supplementing the same substrate mixture with 60% rice straw produced yields comparable to oak sawdust, achieving a BE of approximately 49%.

Other types of residues have also been investigated for *Lentinula edodes* cultivation. For instance, Annepu et al. (2023) reported that sawdust from the tooni tree (*Toona sinensis*) is more suitable for shiitake cultivation than wheat straw, with the DMRO-388s strain exhibiting the highest BE (around 80%) among all tested strains (DMRO-35, 51, 297, 388s, 410, and 412). Moreover, Abdullah et al. (2022) investigated the effect of mixing *Phragmites australis* sawdust with either *Trifolium* or *Sesbania sesban* on the growth media composition and found that these mixtures reduced the substrate C/N ratio, and increased the nitrogen, phosphorus, and potassium contents in the shiitake substrate by the end of the cultivation cycle. Furthermore, Cobos et al. (2021) investigated the performance of the shiitake strains LEN97, LEN954, and XLEC241 on two substrate mixtures: Mixture 1 (30% peat moss, 20% banana leaves, 24% oak sawdust, 16% millet seed, 5% cottonseed hull, 5% CaCO₃) and Mixture 2 (40% wheat straw, 50% oak sawdust, 5% cottonseed hull, 5% CaCO₃). They found that LEN954 and XLEC241 grown on both mixtures achieved high BE (~82.8%), and all three strains exhibited high protein content on both mixtures (16.71–17.10%). In addition, residues such as peach-palm (*Bactris gasipaes*) (De Lima et al., 2020), barley malt bagasse (Oliveira & Cuquel, 2023), and sunflower seed husks (Curvetto et al., 2002) have shown potential as total or partial alternative substrates to oak sawdust in shiitake cultivation. Increasing the proportion of barley malt bagasse improved agronomic parameters (Oliveira & Cuquel, 2023), while the mixture of sunflower seed husks and wheat bran (8:2) increased the total BE to 112% (Curvetto et al., 2002). Moreover, Sassine et al. (2024) reported that mixing olive pruning residues with oak acorns (BE = 532.3%) in the substrate of *Lentinula edodes* strain 3782 produced yields comparable to those obtained with oak sawdust (BE = 597.0%), although fruiting and harvest were delayed.

2.2) Forest residues as shiitake substrates

Studies investigating the use of forest residues in shiitake cultivation are limited. However, when investigated, some forest hardwood sawdust improved yield and mushroom composition, while others did not.

According to El Sebaaly et al. (2024), maple sawdust was reported unsuitable for growing *L. edodes* because it delayed mycelia colonization (>70 days), fruiting (>80 days), and harvest dates (> 90 days), while reducing BE (<50%) compared with oak sawdust. Likewise, Ranjabar and Olfati (2016) reported that fir sawdust (*Abies lasiocarpa*) performed poorly in *L. edodes* cultivation, yielding a BE of 74.2% compared to 92.3% on oak sawdust. Also, the use of birch stem wood (*Betula pubescens*) to grow *L. edodes* required supplementation with different nitrogen sources to enhance the BE of the strain M3790 to 65.1%, with whey identified as the most effective nitrogen source due to its ability to promote lignin and hemicellulose degradation (Chen et al., 2020). Andrade et al. (2008) showed that *Eucalyptus citriodora* significantly enhanced shiitake production in Brazil by improving BE of two shiitake strains, LE-95/01 and LE-96/18, to 53.23% and 61.40%, respectively, therefore highlighting its superiority over other eucalyptus species used as cultivation substrate for shiitake. Likewise, El Sebaaly et al. (2024) recommended a substrate mixture composed of eucalyptus sawdust, oak sawdust, and wheat bran (2:2:1), which increased BE to 74.1%, maximized mushroom protein to 15.1%, and increased crude fiber and vitamin C contents to 5.4%, and 5.8mg/100g, respectively, while reducing carbohydrate levels compared to oak sawdust (BE=59.7%, crude fiber= 1.5%, and vitamin C= 4.5mg/100g).

2.3) Supplementation of the growing substrate of shiitake

Mushroom supplementation consists of adding nitrogen- or carbohydrate-rich additives to the growing media in order to enhance fungal growth and productivity (Carrasco et al., 2018). The dose and timing of supplementation are critical for achieving optimal results: when added before spawning, supplementation stimulates the vegetative growth (Cho, 2004; Naraian et al., 2008), whereas supplementation at the end of the mycelia run promotes fruiting (Pardo-Giménez et al., 2016). However, despite the importance of substrate supplementation, relatively few studies have investigated the effects of supplementation on the growth and yield of *L. edodes*. According to Kapoor et al. (2009), supplementing wheat straw with 10% rice bran or 20% wheat bran accelerated mycelial growth; also, when supplemented with 10% cottonseed meal or 10% soybean meal, wheat straw improved shiitake yield. Similarly, Ranjabar & Olfati (2016) reported that supplemented oak, maple, and fir sawdust with wheat bran achieved BE up to 94%; however, when supplemented with rice bran, they produced larger fruiting bodies (up to 33.5 g/mushroom). Further, Eira et al. (2010) found that supplementing corncob-based substrates with 10% rice bran significantly increased BE compared to non-supplemented mixtures. Moonmoon et al. (2010) reported that supplementing shiitake substrates with 25% wheat bran enhanced fruit body production, and with 40% wheat bran, it further improved mushroom quality. It maximized stalk and pileus diameters to 1.3 cm and 3.4 cm, respectively, and pileus thickness to 1.3 cm. Besides, mineral supplementation of

eucalyptus sawdust with nitrogen and phosphate increased mushroom yield to 92.89 g/kg when added at a rate of 0.05% and improved protein content when added at a rate of 0.50% (Queiroz et al., 2004). On the other hand, nano-supplementation of maple and apple sawdust by using a supplement rich in amino acids (Lithovit –Amino 25) increased biological yield as well as shiitake's crude protein and fiber contents in comparison with non-supplemented maple and apple sawdust, as found in the most recent study of Nabhan et al. (2025).

Conclusions

Overall, substrate selection is a key factor in *L. edodes* cultivation. This review emphasizes the diversity of substrates used and the role of supplementation in shiitake production. For wood log cultivation, shiitake thrives on oak wood logs, besides alder, chestnut, birch, walnut, poplar, and beech wood logs. In synthetic log cultivation, various agro-industrial residues showed positive effects on shiitake productivity and quality, especially when mixed with oak sawdust or oak acorns. With the exception of maple and fir sawdust, which performed poorly in shiitake cultivation, forest wastes enhanced shiitake biological efficiency when combined with nitrogen sources or oak residues. Most of the lignocellulosic materials investigated in early reports exhibited high biological efficiencies and better mushroom quality when supplemented with wheat bran, rice bran, cottonseed meal, or soybean meal in specific proportions. Nevertheless, research on alternative substrates to be used in shiitake cultivation is still limited. Also, the effect of substrate on the umami taste and shelf-life of *L. edodes* mushrooms has rarely been studied and requires further investigation.

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