

Domestication, Evaluation of Yield and Substrates of Wild Enoki Mushroom (*Flammulina velutipes*)

Sabitra Pradhan¹, Tshering Choki¹, Chenchu Dukpa¹ and Tshering Wangmo¹

Abstract

Domestication and cultivation of a local Enoki mushroom (Flammulina velutipes) isolates were conducted to assess its viability for commercial production and its suitability on different substrates. The experiments were carried out in three stages. The first trial examined whether the wild strain could be successfully domesticated on sawdust substrates. The results demonstrated successful domestication, with the first flush yielding significantly more than subsequent flushes ($p < 0.001$), indicating nutrient depletion and reduced productivity in later harvests. In the second phase, the local strain was compared with four commercial enoki strains. Based on a single first harvest, the local strain yielded significantly less than the commercial hybrid strains ($p < 0.001$). However, the local strain produced taller fruiting bodies and exhibited less variability in stipe length than three of the commercial strains. In the third phase, three sawdust substrates namely oak, alder, and poplar were tested for their effects on the colonisation rate and yield of the local strain. There was a highly significant difference ($p < 0.001$) in the number of days to first harvest: 63 days on alder, 65 days on poplar, and 70 days on oak. However, there was no significant difference in yield at the first harvest across substrates. Overall, the productivity of the local strain was comparatively lower than that of the commercial strains. Nevertheless, the native strain demonstrated strong adaptability, a high level of stability in productivity, and desirable fruiting characteristics, indicating its potential as a resilient strain for cultivation.

Keywords: *Bhutanese wild enoki; Domestication; Enoki Mushroom; Yield comparison; Substrates*

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1 Introduction

Mushrooms have gradually been recognised as a nutritious and functional food, rivalling both plant and animal foodstuffs. They contain high levels of protein (up to 35%), crude fibre (19%), vitamins, and minerals, with minimal fat and calories and no starch, thereby qualifying them as a healthy food for diabetic, hypertensive, and cardiovascular patients (Hamza et al., 2024). In addition to their nutritional importance, mushrooms possess significant pharmacological properties, including antioxidant, immunomodulatory, and anticancer activities (Chang & Miles, 2004).

Global mushroom production has increased dramatically over the last three decades, rising by up to 13.8-fold from 1990 to 2020 (FAOSTAT, 2022). Similarly, Singh et al. (2020) estimated global mushroom production for 2018–2019 at approximately 43 million tonnes. The majority of production is concentrated in Asia (82.8%), with smaller contributions from Europe (12%), the Americas (4.5%), Oceania (0.4%), and Africa (0.3%) (FAOSTAT data, as reported by Market.US & Market.biz, 2026). Major cultivated species include shiitake (26%), wood ear mushroom (21%), oyster mushroom (16%), button mushroom (11%), enoki (7%), king oyster (5%), straw mushroom (1%), and other minor species (13%).

Among these, *Flammulina velutipes*, commonly known as enoki, enokitake, or needle mushroom, is valued for its delicate flavour, crisp texture, and medicinal properties. Belonging to the family Physalacriaceae, it is widely cultivated in East Asia, particularly in China, Japan, and Taiwan. Enoki cultivation is typically carried out on lignocellulosic substrates such as straw or sawdust, where both substrate type and fungal strain significantly influence yield and quality (Chang & Miles, 2004).

Nutritionally, *F. velutipes* comprises approximately 58% carbohydrates, 27.5% protein, 7% fat, and 7.4% ash (Ko et al., 2007, as cited in Cai et al., 2013). The mushroom is rich in polysaccharides and exhibits strong antioxidant activity (up to 99.7%), making it a suitable candidate for nutraceutical and functional food applications (Yeh et al., 2014). Enoki polysaccharides have also been reported to possess antioxidant and anticancer properties in *in vitro* studies (Ko et al., 2007). These attributes make it a promising functional food and nutraceutical ingredient.

Domestication and cultivation of *F. velutipes* have been extensively studied in East Asia, where enoki is one of the most commercially important edible fungi. China alone produces an

estimated 2.1–2.4 million metric tonnes of enoki mushrooms annually, making it the world’s largest producer, followed by Japan and South Korea at comparatively lower production levels (Industry data, 2025). Yield and quality are significantly influenced by environmental factors such as substrate composition, temperature, humidity, photoperiod, and carbon dioxide concentration (Rezaeian & Pourianfar, 2017; Sakamoto, 2018).

In Bhutan, mushroom cultivation has predominantly focused on shiitake (*Lentinula edodes*) and oyster mushrooms (*Pleurotus* spp.), with recent diversification into nameko (*Pholiota nameko*) and *Ganoderma* species. Although Bhutan possesses rich mushroom diversity and favourable agro-climatic conditions, the potential for enoki cultivation remains largely unexplored due to its stringent environmental requirements (Sakamoto, 2018). Wild strains, however, may offer better adaptation to local conditions and provide opportunities for diversification. Therefore, investigating their domestication is both necessary and timely to meet the increasing demand for enoki mushrooms, particularly in high-end hotels driven by the growing popularity of hotpot and noodle-based cuisines.

Bhutan harbours a rich diversity of wild mushrooms, including the valuable edible species *F. velutipes*. There is considerable potential for the domestication, cultivation, and breeding of this species to develop indigenous Bhutanese strains. To date, limited work has been undertaken on the domestication and cultivation of wild edible mushrooms in the country, primarily due to a lack of facilities and technical expertise.

In response, the National Mushroom Centre (NMC) has initiated efforts to collect and domesticate selected wild edible mushroom species. This initiative aligns with the broader objective of promoting the sustainable use of wild mushrooms while reducing dependence on wild harvesting. To alleviate pressure on natural populations and ensure long-term sustainability, one of the most effective strategies is the domestication and cultivation of saprophytic mushrooms using locally available resources.

This study was therefore conducted to assess the yield potential of a local enoki strain, followed by an evaluation of its growth, yield, and morphological characteristics in comparison with commercial strains, and finally to determine its performance on three different common sawdust substrates (oak, alder, and poplar). The specific objectives were to:

1. Domesticate the local strain of wild enoki.
2. Assess the production of local and commercial strains.

3. Assess the yield and performance of the local enoki strain using three different types of sawdust substrates.

2 Materials and Methods

2.1 General

This study comprised three different independent trials designed to achieve the objectives outlined above. All three trials were carried out at the National Mushroom Centre (NMC), Wangchutaba, Thimphu, Bhutan. The local enoki strain utilized in the study was cultured from a specimen maintained in the NMC Fungarium identified with collection number as BNF01350. This specimen had originally been collected from the Royal Botanical Garden in Serbithang, Thimphu. For the second phase of the study, commercial enoki strains obtained from Thailand and India were used to compare with the local strain.

For all three phases of the trial, the container bottles made of polypropylene were used as it can withstand high temperature and pressure of autoclaving. Each bottle had a capacity of 800 ml and was filled with 430 g of substrate prior to sterilisation.

As enoki mushrooms require temperatures below 10°C during the pre-fruiting stage, the trials were conducted during the cooler months (November to March). All three phases of the study were conducted using a Completely Randomised Block Design (CRBD).

The first phase of the trial (domestication) was carried during the winter of 2023, using 20 bottles containing oak sawdust medium were supplemented with 40% rice bran. The second phase, conducted in December 2024, utilized a substrate composed of 60% oak sawdust enriched with 20% rice bran and 20% wheat bran. Each of the five treatments had 50 replicates (sample bottles), resulting in total of 250 sample bottles.

In the third phase of the trial, conducted from November 2024 to March 2025, the local enoki strain was cultivated on three different sawdust substrates: oak (*Quercus griffithii*), alder (*Alnus nepalensis*), and poplar (*Populus wuana*). Each substrate (62%) was mixed with nutrient supplements consisting of rice bran (20%), wheat bran (6%), and corn cob (12%), and each treatment was replicated 40 times.

2.2 Substrate sterilization, inoculation and incubation

The moisture content of the substrates prior to sterilisation was maintained at 67%. The substrates were sterilised at 121°C for one hour at 15 psi using a Coslab-manufactured

vertical high-pressure top-loading sterilisation unit, and were cooled overnight in a sterile room before inoculation.

Inoculation of the substrates was carried out using a UR Bio-coction-manufactured laminar airflow cabinet equipped with HEPA (High Efficiency Particulate Air) filters, a powder-coated body, and UV lighting to maintain a sterile environment.

The inoculated sample bottles were incubated in a dark room, where the temperature was maintained between 16°C and 22°C and relative humidity between 70% and 80%, until mycelial colonisation was complete. The fully colonised bottles were then transferred to sprouting (fruiting) chambers.

2.3 Initiating sprouting

The caps of the substrate bottles was removed, and approximately 3 - 5 cm of the hardened top layer of the colonized medium were manually scraped off in order to promote the initiation of pin heads. A room temperature of 13°C - 16°C and humidity of 90 - 95% were maintained to induce the sprouting of mushroom pinheads.

2.4 Fruiting

Pinheads emerged within 12–15 days, after which the room temperature was lowered to 5°C –6°C and the relative humidity was adjusted to 80–90% to regulate growth and maintain mushroom quality. When the fruiting bodies extended 2–3 cm above the bottle mouth, cylindrical plastic collars or sleeves were fitted to encourage the development of long, slender stipes.

This method creates a microenvironment with elevated CO₂ levels around the fruiting bodies, promoting elongation as the mushrooms grow towards fresh air (Ikeda et al., 2021), resulting in the development of long, slender stipes and compact caps, characteristic of high-quality enoki mushrooms. Harvesting was carried out after about one week, or when the stipe exceeded 12 cm in length and the caps had not fully expanded.

2.5 Data collection and statistical analysis

Data were recorded for parameters including days to first harvest, interval between flushes, fruit body length and fresh yield weight. The data were analysed using Stata version 15.1 (StataCorp LLC). One-way ANOVA was applied assess significant differences among treatment means, followed by post-hoc pair wise comparisons using Bonferroni-correction.

3 Results and Discussion

3.1 First phase – Domestication Trial

The first phase of the study evaluated the ability of the wild enoki strain to produce fruiting bodies on an artificial sawdust substrate under controlled conditions. Additional observations included morphological traits, yield performance, the number of subsequent flushes, and sensory qualities after cooking.

3.1.1 Morphological description

As reported in the NMC Annual Report 2020-2021, the wild enoki specimen collected from the Royal Botanical Garden in 2019 was characterized as follows: Cap: 1–6 cm in diameter, convex at the early stage and becoming broadly convex to flat at maturity. The surface is sticky when fresh. The cap colour ranges from dark orange-brown to orangish brown or yellowish brown; often paler toward the margin, fading with age, with the margin becoming striated. Stipe: 2–5 cm in length and 3–10 mm in thickness, uniform or slightly enlarged toward the base. The texture is firm, and the colour varies from whitish to pale to yellowish brown or orange-brown when young. The stipe is covered from the base upwards with a dark brown to blackish velvety layer.

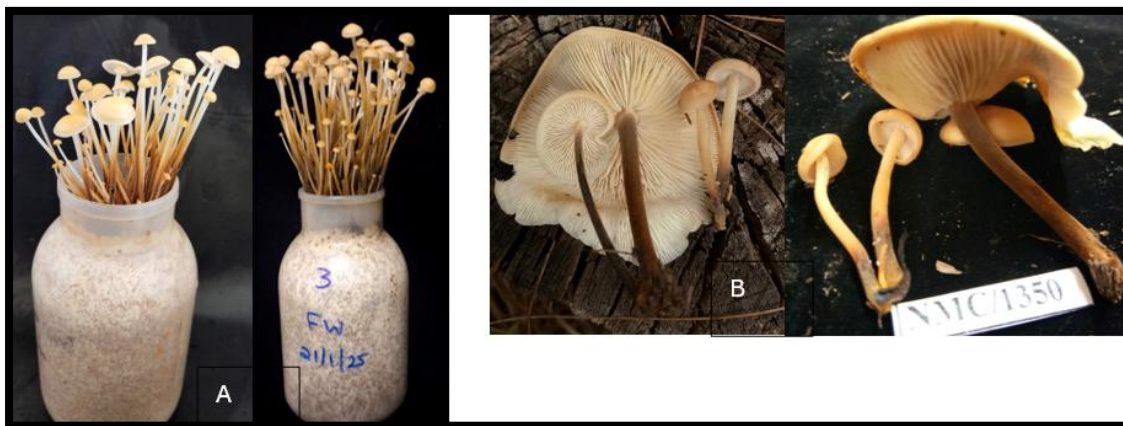


Figure 1. Enoki domesticated (A) from the wild specimen (B)

Figure 1 present images of the domesticated enoki (A) alongside the wild specimen (B) from which it was derived using the tissue culture techniques. In this trial, the domesticated enoki exhibited few minor differences from its parent source. The cap size reduced to 1.3–2.3 cm in diameter, while the stipe length increased significantly to 12–14 cm and the cap colour paler. This result indicates controlling factors such as light duration, CO₂ concentration (through the use of cylindrical plastic collar), and temperature below 10 °C effectively induced the desired traits of cultivated enoki, mainly smaller caps and elongated stipes.

3.1.2 Yield

The local enoki strain performed well, producing an average yield of 31 g per bottle during the first flush, followed by three additional flushes (Figure 2).

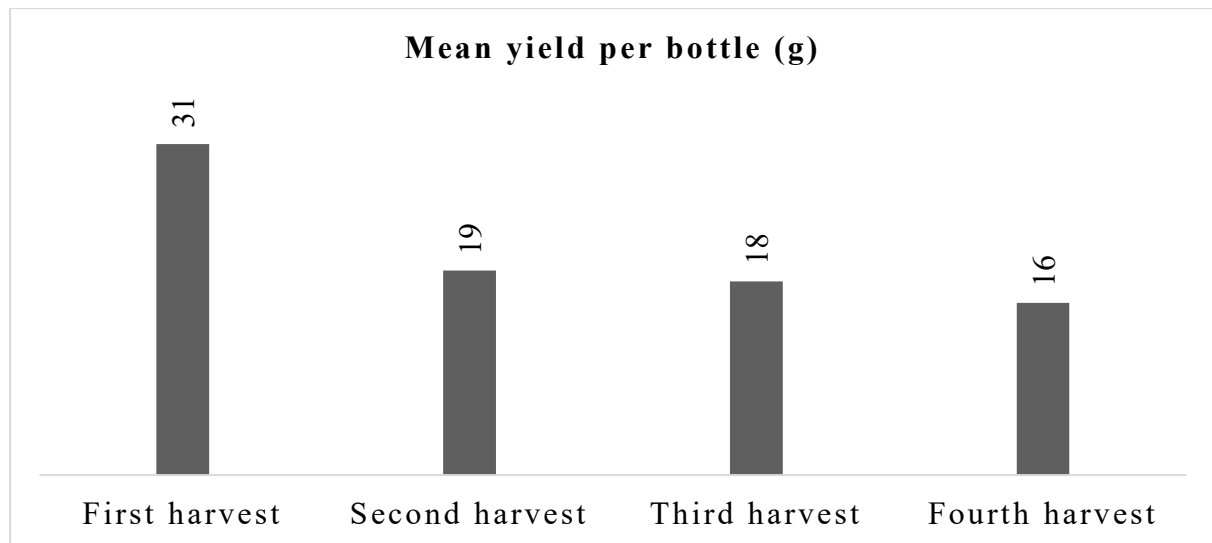


Figure 2. Mean yield of four flushes (g/bottle)

Although variations among the four flushed were visually apparent in Figure 2, a one-way ANOVA indicated highly significant differences (Table 1). Post-hoc pairwise t-tests with Bonferroni correction showed that the first flush produced significantly higher yields than the subsequent flushes ($p < 0.001$), while no significant differences were observed among the second, third and fourth flushes.

Table 1. Summary of one-way ANOVA of fresh weight of local enoki among different flushes

Source	SS	df	MS	F	Prob > F
Between groups	2275.06	3	758.35	23.05	0.0000
Within groups	1842.66	56	32.90		

This analysis was crucial in determining the economic feasibility of continuing production up to the fourth harvest. Yield declined progressively, decreasing by 38% in the second flush, 41% in the third, and 48% in the fourth compared to the first flush. This trend aligns with the finding from previous studies on edible mushrooms such as *Pleurotus ostreatus*, where the first flush accounts for the majority of the total yield due to rapid utilization of available nutrients (Kim et al., 2020; Zhang et al., 2018).

The average interval between the first and second flushes was 22 days, and between the second and third flushes was 24 days. These results suggest that, for commercial production, it may not be economically efficient to retain the substrate in the fruiting chamber beyond the first flush, considering the additional energy and labour required to maintain optimal conditions. However, for household or hobby cultivation, the results demonstrate that the local enoki strain is capable of producing multiple flushes. Growers may continue production up to fourth harvest, provided that adequate moisture, temperature, and ventilation are maintained.

3.1.3 Evaluation of taste

A preliminary sensory evaluation was conducted using mushrooms harvested from the trial. The fruiting bodies were prepared as curry and hotpot soup. The local enoki strain cultivated on oak sawdust substrate exhibited a pleasant flavour and a firm, crisp texture. Compared to commercial strains, the relatively larger caps provided a desirable bite size. Additionally, the caps developed a slightly slimy texture when cooked, which was particularly suitable for soup-based dishes.

3.2 Second phase of the trial

3.2.1 Yield Comparison of Local Enoki with commercial strains

Yield comparison was conducted using only the first flush (Table 2) because although the Thai Golden strain also yielded additional flushes, whereas the other commercial strains did not produce any further flushes. However, it is important to note that the local strain produced satisfactory yield in subsequent flushes.

Table 2. Summary of one-way ANOVA on first flush yield of five enoki strains.

Source	SS	df	MS	F	Prob > F
Between groups	84243.61	4	21060.90	35.25	0.0000
Within groups	152375.20	255	597.54		

Table 3 shows that the local strain yielded the least, with highly significant differences compared to the commercial strains.

Table 3. Mean yield of the first flush of five enoki strains

Strain	Mean Weight (g) ± SD	SE
Local Enoki	30.39 ± (10.48)	---

Enoki Thai Golden	64.68 ± (14.08) ^a	4.22
Enoki Indian	72.38 ± (27.91) ^a	4.41
Enoki 1	83.58 ± (26.39) ^b	4.29
Enoki Thai	71.14 ± (31.42) ^{ac}	4.46

Note: Means with the same superscript letters are not significantly different.

Among the four commercial strains, Thai Golden recorded the lowest mean yield at 64.68 g per bottle. The yield of the local enoki strain's yield was more than half lower than that of Thai Golden. Nevertheless, in terms of multiple fruiting ability, the local strain produced up to four flushes (Figure 1), Thai Golden up to two flushes, while the other three strains fruited only once. Commercial strains are typically selected for high yields in the first flush, as growers are generally less interested in subsequent flushes due to declining profit margins.

3.2.2 Comparison of height among the strains

Height of the enoki biomass is key quality parameter. For most commercial applications, a minimum height of 10 cm is preferred, while premium grade products typically reach around 15 cm. Figure 3 illustrates the height of the fruiting bodies of the local and commercial strains after the removal of the plastic collars. In addition to height, other morphological traits, such as fruit body colour, are also presented in Figure 3. Commercially cultivated *F. velutipes* (enoki mushroom) is characterized by elongated stems and small caps, features that enhance visual appeal and are generally associated with a tender texture that are highly in the fresh mushroom market (Lee et al., 2025; Zhang et al., 2025).



Figure 3. From left to right - Thai Golden, Local and the other three commercial strains which are predominantly white

However, the experimental results differed markedly from expectations. With the exception of Thai Golden, the other three commercial strains exhibited shorter fruiting body heights than the local enoki strain. The local strain also showed greater uniformity in height, whereas the commercial strains displayed wider variation, including occasional outliers (Figure 4). Comparable findings have been reported in domestication studies of Shiitake (Chang & Miles, 2004) and oyster mushrooms (Rezaeian & Pourianfar, 2017), where wild strains in some cases outperformed commercial strains in specific morphological traits.

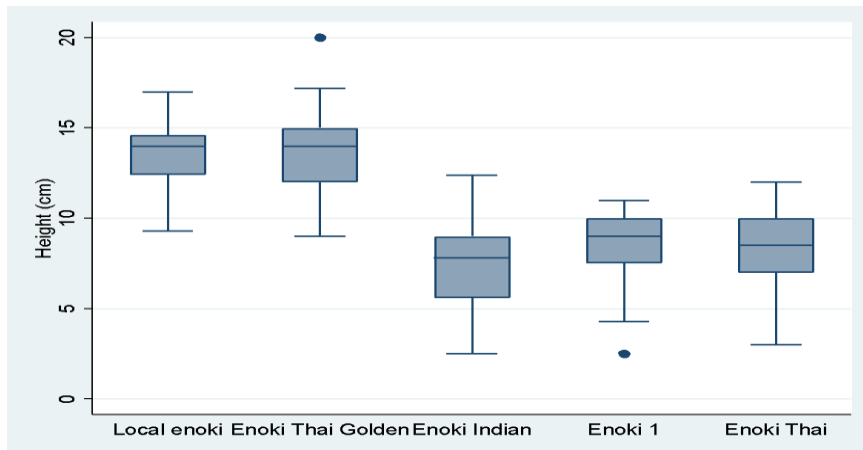


Figure 4. Boxplot showing data spread on height of the 5 strains

3.3 Third phase of the trial: Comparison of different sawdust on local strain

3.3.1 Rate of mycelial colonization and days to first harvest

The third phase of the trial evaluated the performance of the local enoki strain across three different types of sawdust substrates. Initial assessment focused on the rate of mycelial colonization. The time required for the local enoki mycelium to colonize the substrates varied notably among treatments, being fastest on alder (2) (mean \approx 48 days), moderate on poplar (3) (mean \approx 50 days) and the slowest on oak (1) (mean \approx 53 days). Figure 5 illustrates the progression of colonization across three different substrates overtime.

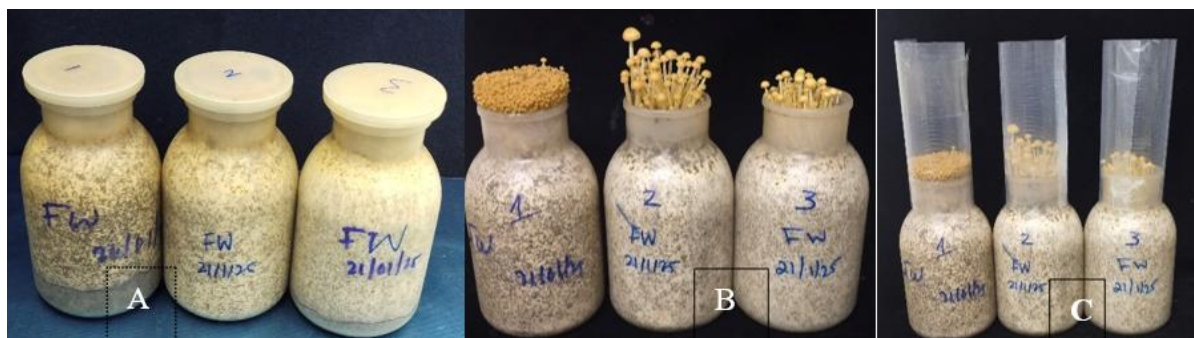


Figure 5. Difference of mycelium colonization and fruiting on different substrate; A=41 days, B and C=59 days with sleeves and without sleeves

Secondly, the time required to reach the first harvest was evaluated, a parameter closely associated with the rate of mycelial colonization. Days to first harvest is a critical factor in commercial production, as shorter production cycles are generally linked to enhanced profitability. One-way ANOVA indicated a highly significant difference among the three substrates ($F(2,110) = 21.04$, $p = 0.000$). The shortest time to harvest was observed on alder (62.84), followed by poplar (65 days), while oak required the longest duration (69.88 days). The significant difference was found between oak and the other two substrates, whereas no significant difference was observed between alder and poplar.

Alder, being a fast-growing deciduous species, typically has a less compact lignocellulosic structure and lower phenolic content compared to oak. This facilitates more efficient enzymatic activity and substrate degradation by the mycelium, resulting in faster growth on such substrates (Park et al., 2014). The results of this study therefore suggest that alder and poplar are suitable alternatives for enoki cultivation, as they are more readily available and considerably less expensive than oak.

3.3.2 Yield of enoki mushroom

The yield performance of the enoki mushrooms was subsequently evaluated across the three types of substrates. Unlike the commercial strains, the local enoki produced fruit bodies over multiple flushes, although the yields dropped sharply from the first to the second and more so by the third harvest. For the first harvest, mean yields were 31.60 g/bottle on oak, 30.77 g/bottle on alder, and 30.60 g/bottle on poplar, with one-way ANOVA indicating no significant difference ($F(2,110) = 0.30$, $p = 0.74$). In the second harvest, yields were 20.26 g/bottle for oak, 22.94 g/bottle for alder, and 21.35 g/bottle for poplar, again showing no significant difference ($F(2,98) = 1.10$, $p = 0.33$). When the first and second harvests were combined, total yields reached 47.93 g/bottle for oak, 51.36 g/bottle for alder, and 51.39 g/bottle for poplar, with no significant differences observed ($F(2,110) = 1.56$, $p = 0.21$). Data from the third harvest were excluded due to contamination in many samples, which rendered them unreliable for analysis. From a commercial perspective, growers are also unlikely to wait for a third harvest due to diminishing returns. Nevertheless, it was noteworthy that some samples, particularly from alder and poplar substrates remained uncontaminated and sufficiently vigorous to produce a third flush.

Substrate composition plays a critical role in determining mushroom productivity, as the physical and chemical properties of the medium directly influence mycelial growth, fruiting and overall yield. Hardwood substrates are widely regarded as suitable for enoki cultivation due to their balanced lignocellulosic composition and structural stability. This suitability is often attributed to the gradual and consistent nutrient release and superior water-holding capacity of hardwoods such as oak, which provide a stable condition for mycelial colonisation and fruit body development (Chang & Miles, 2004; Rezaeian & Pourianfar, 2017). Previous studies have similarly reported that substrates with moderate density and lignin content tend to produce consistent yields in enoki cultivation (Kang et al., 2016).

However, the findings of this study indicate that alder and poplar substrates perform comparably to oak in terms of yield. Moreover, when considering the shorter time required to reach the first harvest, alder and poplar demonstrated a clear advantage over oak. Similar trends have been reported in studies conducted in China and Korea (Han et al., 2025).

4 Conclusion

This study demonstrates that the wild Enoki strain from Bhutanese forest can be successfully cultured and domesticated under controlled environment. Manipulation of the micro-environment can be proved effective in inducing desired morphological characteristics, including reduced cap size and elongated stipes. The cultivated fruit bodies exhibited acceptable height, morphology and texture. Yields were also satisfactory especially when multiple flushes were taken in account. However, in comparison to the commercial strains, typically selected for a single, high yielding flush, the first flush yield of the local strain was approximately half or less.

With regard to substrate selection, the result indicate that Alder and Poplar sawdust perform comparably to Oak in terms of yield, while offering additional advantages such as faster mycelial colonisation and quicker time to harvest. These characteristics suggest that Alder and Poplar sawdust may be more practical substrate options. Further research should focus on optimizing environmental conditions and substrate supplplantation to enhance yield consistency, biological efficiency, and fruit body morphology across different cultivation systems.

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6 Authors' contribution statement

Sabitra Pradhan designed the study concept, conducted the trials and wrote the result and over all finalization of the paper, Tshering Chuki, helped during the trial and data collection as while as wrote the materials and method. Chencho Dukpa, constantly guided during the experiments and did the data analysis and review of the technical part of the paper and Tshering Wangmo was involved during the experiments as while as during the data collection and wrote the introduction part of the paper.

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