Mushroom cultivation in Temperate Agroforestry

Potential Agroforestry practices, growing methods, and native edible saprophytes to Sweden

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Swedish University of Agricultural Sciences, SLU
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Mushroom cultivation in Temperate Agroforestry. Potential Agroforestry practices, growing methods, and native edible saprophytes to Sweden

Svampodling utomhus i tempererade klimat. Potentiella Agroforestry-system, odlingsmetoder och ätliga saprofyter i Sverige.

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Abstract

Traditions of outdoor cultivation of edible fungi in woodland conditions have been practiced in North-East Asia for centuries. This outdoor mushroom production method was exported to North America almost 40 years ago and provides an additional income for small-scale forest farmers, the agroforestry practice closest to woodland conditions. However, in any agroforestry system with suitable conditions mushroom production can be included. Besides production of edible fruiting bodies, mushroom production has the potential to create local waste management with by-products from Agriculture and Forestry. The by-product from mushroom production called Spent Mushroom Substrate (SMS) can be used as a biofertilizer to close the loop of a circular food producing agroforestry system. Additionally, mushrooms intercropped with vegetables and trees has shown to increase soil fertility, biological activity, and main crop quality. The interest in mushroom productions is increasing in Sweden with hobby-cultivators growing a wide range of native and foreign species but no upscaled outdoor mushroom production exists. In Sweden, a rough third of the most common 100 native edible mushrooms are saprophytic with 15 species used by hobby-cultivators. All these saprophytic mushrooms could theoretically be used for outdoor production within temperate agroforestry systems. Four of the potential mushrooms are Lions Mane (*Hericium erinaceus*), Oyster (*Pleurotus ostreatus*), Enoki (*Flammulina velutipes*) and King Stropharia (*Stropharia rugosoannulata*). All these native mushrooms could be used in forest farming practices. The mushrooms requirements for shading and wind protection can be provided in intercropping with crop plants of varying heights. This sheltering from plants could be provided in the agroforestry practice alley cropping. Potential mushrooms for alley cropping or intercropping within alley cropping are King Stropharia, Oyster and Morels (*Morchella* spp.). Further research and try-outs are needed to understand which native or non-native mushrooms could be used within agroforestry in the many varying conditions of Sweden.

Keywords: Circular systems, macrofungi, edible fruitbodies, outdoor mushroom production, waste management, by-product substrates, sustainable agriculture, sustainable forestry

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2. Introduction

Long before terrestrial lifeforms inhabited the lands, a fundamental coevolution occurred between the kingdom of fungi and the kingdom of plants (Lutzoni et al. 2018). This interaction between fungi and plants has been invoked as crucial to both kingdoms macroevolutionary success (ibid.). Thanks to this success there are over 50 ways fungi can be utilized industrially, including the production of food and beverages from fungi, the use of fungal agents in strategies against plant disease and for pest control, as well as various ways for enhancing plant development within forestry, agriculture, and horticulture (Hyde et al. 2019).

Many ecosystems are dependent on the ability of fungi to break down organic matter (Dai et al. 2021). This decomposing activity results in a consistent return of carbon, nitrogen, hydrogen, and other minerals to the ecosystems in usable forms (ibid.).

Modern agriculture and forestry face the task of avoiding harmful environmental and social effects while simultaneously providing an estimated 9 billion humans by 2050 with their basic needs (Wilson & Lovell 2016; Adams & Pfautsch 2018). The consequences on ecosystems from modern agriculture and forestry are successively appearing as research continues. An example is that some fungal communities in agricultural landscapes can be wiped out after a single application of commercial fertilizers (Petersen & Læssøe 2019). Another example is that modern forest management still introduces seedlings of alien tree species after the clearcuttings of native forests, creating an even-aged tree population with a huge loss of microhabitats (ibid.). These breaks in continuity significantly reduce fungal activity, not least in the mycorrhizal community which can take centuries to recover (ibid.).

Sustainable solutions to both modern agriculture and forestry may lie within the multifunctionality of agroforestry systems (Wilson & Lovell 2016), that provides a broad range of sociocultural, economic, and environmental benefits. Agroforestry, a resilient land-use system that mimics nature's design (ibid.), contribute to 9 out of 17 UN's sustainable development goals (SDG) (IISD 2018). These goals concern poverty reduction (SDG1), hunger alleviation (SDG2), health and well-being (SDG3), gender equality (SDG5), access to clean water (SDG6), sustainable energy solutions (SDG7), responsible agriculture (SDG12), climate action (SDG13), and biodiversity conservation and sustainable land management (SDG15).

The interaction between plants and fungi could be one of the most undervalued links in circular food production systems inspired by natures design (Stamets 2000). Since agroforestry is a system that derive solutions and inspiration from natural ecosystems, it is of interest to explore the integration potential for edible mushroom production within its practices.

2.1 Aim and research questions

The aim of this bachelor thesis is to investigate the integration potential of outdoor mushroom production into temperate agroforestry systems. This work will focus on edible saprophytic mushrooms since mycorrhizal fungi have proven to be extremely challenging to domesticate for mushroom production (Stamets 2000).

The specific research questions are:

- Which mushroom production systems are already used within temperate agroforestry systems?
- Which native species of edible saprophytic mushrooms are suitable for agroforestry systems in Sweden?
- Which production systems are most suitable for selected native fungal species considering production in agroforestry systems?

2.2 Limitations

Agroforestry is a widely used concept. Therefore, focus of this work will be on systems and practices within temperate areas and seasons resembling temperate conditions. In a similar way, native species of edible saprophytic mushroom include a wide array of species. Focus will be on edible mushrooms. Mushrooms with unexplained cases of poisoning will be excluded. Four species native to Sweden are selected for their wide-spread and accessible information regarding cultivation and present use by Swedish hobby-cultivators: Lions Mane (*Hericium erinaceus*), King Stropharia (*Stropharia rugosoannulata*), Enoki (*Flammulina velutipes*) and Oyster mushroom (*Pleurotus ostreatus*).

3. Background

3.1 Temperate Agroforestry Systems

The definition of agroforestry according to the Food and Agriculture Organization of the United Nations (2015) is the following:

> "Agroforestry is a collective name for land-use systems and technologies where woody perennials (trees, shrubs, palms, bamboos, etc.) are deliberately used on the same land-management units as agricultural crops and/or animals, in some form of spatial arrangement or temporal sequence". (FAO 2015)

Agroforestry originated from tropical food production systems (USDA National Agroforestry Center n.d.a). In areas with temperate climates, agroforestry is divided into five specific practices (ibid.). These practices are forest farming, windbreaks, alley cropping, riparian forest buffers and silvopasture.

Forest farming is defined by high-value crop cultivation beneath the shelter of a managed forest canopy (USDA National Agroforestry Center n.d.c). The trees providing the canopy are often high-quality trees grown for wood or other tree products. This managed woodland provides conditions for plants and fungi that otherwise are extinct or forbidden to forage (ibid.). An additional agroforestry practice included here is forest gardening. Within forest gardening practices, the trees are often cultivated from start with the purpose to mimic woodlands, whereas forest farming often takes place beneath an already existing forest canopy (Mudge & Gabriels 2014).

Windbreaks are often defined by their primary purpose, to slow the wind (USDA National Agroforestry Center n.d.f), which allows more favourable conditions for soils, crops, wildlife, livestock, and people (ibid.). These also provide valuable ecosystem services and can be used for timber and non-timber produce (ibid.).

Alley cropping is defined by row-plantation of shrubs and/or trees to create alleys in between where horticultural or agricultural crops are cultivated (USDA National Agroforestry Center n.d.b). The trees or bushes used in various combinations or singlehandedly provide lumber, hardwood veneer, fiber, fodder, fruit, nuts and/or enhanced soil quality (ibid).

Riparian forest buffers are defined as an area adjacent to a lake, stream, or wetland with a mixture of shrubs, trees, or other perennial plants (USDA National Agroforestry Center n.d.d). The buffers are managed mainly to serve conservation benefits and are rarely used for production of harvestable crops. Conservation benefits include filtering agricultural land runoff of pesticides, nutrients, and animal waste. These buffers also stabilize eroding banks and provide shelter, shade, and food for aquatic life. Additionally, these also provide corridors and wildlife habitat for terrestrial animals.

Silvopasture is defined by the intentional integration of trees for forage and grazing livestock on the same pasture (USDA National Agroforestry Center n.d.e). These areas providing forage, fodder and forest products are intensively managed to provide short and long-term sources of income. The rotation of the grazing animals and time for plant-regeneration are key elements in silvopasture management (ibid.). Livestock potentially include cattle, goats, sheep, horses, chickens, turkeys, ostriches, or animals used for hunting (ibid.).

Mudge & Gabriels (2014) show that when agroforestry practices are combined, these achieve synergies in between which further strengthens the systems existing dynamics, resilience, and biodiversity. The following two images (Figure 1) display how these practices can interact and function adjacently. Infinitely more examples and advantageous combinations can be put together when applying the inclusive definition of agroforestry.

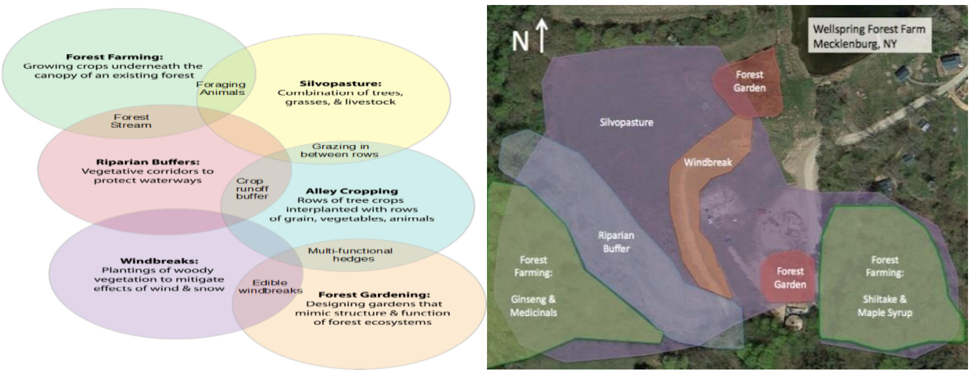

Figure 1. Examples of how agroforestry systems can be combined in North America. (Mudge & Gabriels 2014)

3.2 Mushroom ecology

Mushrooms are commonly known as the fleshy macroscopic body of a fungus, typically found above ground or on its food source. The purpose of producing these fruit bodies is sexual reproduction by dispersion of propagules in the form of spores (Petersen & Læssøe 2019).

Fungi used for mushroom cultivation can be categorized into three fundamental groups: saprophytic, parasitic, and mycorrhizal (Dai et al. 2021). The widely cultivated ones belong to the saprophytes (ibid). Saprophytes break down dead or decaying wood. Parasitic fungi feed off a living host, often benefiting from causing detriment and death its host (Stamets 2000). Parasitic fungi have so far been unwanted for mushroom cultivation. Mycorrhizal fungi on the other hand, often have a mutually beneficial arrangement of exchanging nutrients with its host (ibid.). Due to many and unstudied variables, the domestication of mycorrhizal fungi for mushroom production has proven to be challenging and unpredictable (ibid.).

Numerous saprophytic mushrooms are considered facultative parasites (Stamets 2000), meaning that if conditions are favourable these can behave parasitically. For example, classical saprophytes like the Oyster mushroom species (*Pleurotus* spp.) can colonize a dying tree and live long after its death (ibid.).

Saprophytic fungi are key recyclers on earth and are divided into three groups: primary, secondary, and tertiary decomposers (ibid). All three groups of decomposers can inhabit the same location (ibid.). Each saprophyte has its own unique set of enzymes to decompose lignin and cellulose, and when one species has broken down the wood to its maximal potential, another saprophyte with a complementary set of tools can take over and continue (ibid.). The primary decomposers break down wood and are found in woodlands (ibid.). Domesticated woodland species include the above mentioned *Pleurotus* species along with King Stropharia (*Stropharia rugosoannulata*), and Shiitake (*Lentinula edodes*) (ibid.).

The secondary decomposers depend on the previous group's activity to further colonize and break down the substrate to a state where it can prosper (Stamets 2000). These decomposers often grow on composted material after the prior decomposition by other fungi, bacteria, actinomycetes, and yeast (ibid.). The cultivated Button mushroom (*Agaricus* spp.) is a classic example of secondary decomposers (ibid.).

Once the secondary decomposers have done their part, the tertiary decomposers take over (ibid.). These are known as the soil dwellers, an amorphous group that can survive for years in habitats waiting for the products of the prior decomposers (ibid.). The edible Orange Peel Mushroom (*Aleuria aurantia*) is a typical example from this group (ibid.).

In the Northern latitudes, many mushrooms prefer shade and benefit from indirect sunlight (ibid.). Mushrooms do not photosynthesize but many are photosensitive and require a stable light source during fruit body development to avoid malformation (ibid.). Only a few mushrooms favour long-lasting exposure to direct sunlight (ibid.).

3.3 Mushroom production

The primary and secondary decomposers have shown to be the most feasible for cultivation (Stamets 2000). Several variables need to be met to select the best mushrooms for cultivation (ibid.). The availability of raw materials, climate and mushroom strains must all interact ideally for a successful cultivation (ibid.).

The majority of cultivated mushrooms in the world are from the genera *Lentinula* (22%), *Pleurotus* (19%), *Auricularia* (18%), *Agaricus* (15%), *Flammulina* (11%), *Volvariella* (5%) and others (10%) (Royse et al. 2017). New mushroom strains are continuously developed and made available for commercial uses (Baars & Hesen 2008).

When designing outdoor systems for mushroom production, native species are generally easier to cultivate than exotic ones due to fewer variables (Stamets 2000). Approximately 100 out of 10.000 wild Scandinavian mushroom species are considered to be edible and tasteful mushrooms (Svampguiden n.d.). A third of these mushrooms are saprophytic, facts about these are presented in *Appendix 1*.

3.3.1 Available mushroom substrates

Being heterotrophs (Sharma 1991), the fungi degrade organic material to produce the energy needed for growth. In mushroom production the material used to “feed” the fungal strain is called mushroom substrate (Stamets 2000). This substrate can consist of almost any plant material with the right moisture content, structural composition, and pH-level for the chosen strain (ibid.).

Often the substrate is first mixed and heat-treated and then the mushroom is introduced by inoculation (ibid). For most mushroom substrates, there is a need for heat-treatment to suppress other competing microorganisms (ibid.). This specific need for heat-treatment depends on the competitive nature of the chosen strain (ibid.). An example is that oyster mushroom (*P. ostreatus*) only needs pasteurization (60-82°C), while many other strains and genera demand sterilization (121°C) (ibid.).

Forestry and agricultural by-products can be used to serve as the base medium, generally referred to as the “fruiting substrate” (Stamets 2000). To accelerate the mushroom life cycle within the primary decomposers, fast rotting tree materials from deciduous trees are favoured (ibid.). Poplars, cottonwoods, and alders are preferred over the denser, resistant woods such as maples and oaks (ibid.). Remarkably, many mushrooms prosper on base materials unusual to their natural environment (ibid.). Even though Oyster mushrooms turn up in the wild on deciduous hardwoods, these grow well on numerous other materials, including seed hulls, cereal straw, corncobs, sugarcane bagasse, cotton textiles, coffee waste and paper by-products (Sánchez 2010). To enhance yields the substrate is usually enriched with a protein- and carbohydrate-rich supplement (Stamets 2000). Protein-rich (nitrogenous) materials of a wide variety can be used to enrich the substrate (ibid.). Many of these materials are grains or grain derivatives, like rice, ground corn, wheat- or oat bran, etcetera (ibid.).

Substrates for the secondary decomposers must be of a more decomposed material to allow them to thrive (Stamets 2000), which is the case for the widely cultivated *Agaricus* species. When growing for example the Portobello mushroom (*Agaricus brunnescens*), the material often consists of straw materials as a base substrate, supplemented with manure and gypsum that together is thoroughly composted (ibid.). The mushroom industry within the *Agaricus* genera has a vast variety of supplements that can be used for different reasons (Munshi et al. 2010). When in need of enhancing nitrogen contents, organic sources are better than inorganic, because they also supply carbon, phosphorus, potassium and exhibit greater heating capacity during composting (ibid.). Examples of available nitrogen sources are fruit concentrates, molasses, ground rye grains, wheat flour, wheat bran, and linseed meal (ibid.). During composting and before inoculation (Stamets 2000), the compost undergoes high-temperature fermentation to encourage thermotolerant synergists (*Actinomycetes* spp.) and suppress contaminants. This natural pasteurization through composting kills pathogens and pests, making the substrate suitable for mushroom growth (Munshi et al. 2010). After inoculation and incubation, the sporophore production is promoted by adding a relatively biological inert material as a surface layer (ibid.). This inert layer is known as the casing material and often consists of sterilized soil (ibid.).

3.3.2 Growing methods

There are various methods of producing mushrooms (Stamets 2000), but they all depend on fresh and vital spawning culture produced from a sterile environment.

This is to ensure there are no contaminants or other unwanted strains following the mushroom offspring, known as the spawn (ibid.). To produce the spawning culture, the chosen strain is initially collected from spore-prints or wild mycelium, later to be fed and reproduced on agar (ibid.). When this strain has successfully colonized the agar-dish, it is then inoculated into a sterile substrate, such as autoclaved grain for further colonization (ibid.). Once the mycelial network has fully colonized a chosen substrate, the product is finally called “spawn” (ibid.). This spawn has various shapes, intentionally adapted for further uses (ibid.). For example, when growing mushrooms on logs, the substrate forming the spawn could be in the shape of plugs (ibid.). These plugs are sturdy and easy to manage when inserting them into pre-drilled wooden holes.

When in possession of a chosen spawning culture there are numerous ways of producing mushrooms indoors and outdoors. To avoid exclusion of future solutions for outdoor mushroom farming, common methods for both will be included. What works inside in one system might work outside in another and vice versa. Information about new mushroom cultivation methods is continuously emerging (Wendiro et al. 2019).

Some of the most spread and common growing methods are presented below and further information can be found in Stamets (2000).

Tray Culture: A traditional indoor approach first developed with cultivation of the Button Mushroom, consisting of substrate-filled trays upon trays to increase space efficiency. Spacious intervals between trays provide room for fruit bodies, manual harvest, and airflow. In the Netherlands this system is still used for other mushrooms as well.

Vertical Wall Culture: Individually wrapped substrate-units, stacked upon each other, and inserted into holding frames, creating hanging walls with vertical openings. These sideway-openings are interspaced to provide room for fruit bodies, manual harvest, and airflow. Developed originally for growing Oyster mushrooms indoors.

A-Frame or Slanted Wall Culture: Substrate-filled bags stacked upon each other to build sloping fronts. The slightly tilted front provides easier manual harvest from the vertically emerging fruit bodies. This method is used in indoor cultivation of Black Reishi (*Ganoderma lucidum*).

Bag & Column Culture: Hanging or stationary substrate-filled bags with fruit bodies emerging all around. These see-through plastic solutions allow activity oversight within the substrate and vertical fruiting 360 degrees. Systems with bag culture started within the Button mushroom industry and are still in use to this day. Column cultures are bags in shape of columns and are today used indoors with some Oyster mushroom species (*Pleurotus* spp.).

Bottle culture: Substrate-filled reusable plastic bottles or jars, on trays or attached upon walls. These cultures are almost exclusively inoculated afterwards. Many medicinal and gourmet mushrooms are cultivated in these systems, most commonly indoors.

Log culture: This outdoor and indoor method was developed in China and Japan over a thousand years ago. Growing on logs is the least demanding method regarding the need for specialized skills but is considered the most labour-intensive. Logs are taken from deciduous trees, drilled, inoculated, stacked, and mushrooms harvested. This technique is especially suitable for cultivating Oyster, Nameko (*Pholiota nameko*), Reishi and Lions Mane (*Hericium* spp).

A new variety of the log culture method is Totem stacks. These logs are cut in desired lengths, then inoculated in the cut areas and re-put together to create one standing mushroom unit (Grace & Mudge 2015). To promote fungal establishment and conserve moisture, the logs are bagged during the incubation period (ibid.). This technique is suitable for Lions Mane (*Hericium* spp.) and Oyster mushrooms (Cornell University 2022).

3.4 Methodology

This thesis is based on a literature study and information in the form of books, articles, and web pages. The information was gathered from various search engines, primarily from Google Scholar and Web of Science.

Keywords: temperate agroforestry, agroforestry systems, forest farming, forest gardening, alley cropping, intercropping, riparian forest buffers, windbreaks, silvopasture, mushrooms, edible fungi, macrofungi, saprophytes.

Especially useful, when outlining the fundamentals for the background was the book “Growing Gourmet and Medicinal Mushrooms” by Paul Stamets. Stamets is a mycologist and well-experienced mushroom cultivator. The book aided in giving scientific up to date knowledge about why and how mushrooms could be cultivated, while at the same time providing an information base for organic mushroom cultivation in outdoor systems.

4. Results

4.1 Overview of mushroom production in Agroforestry

4.1.1 Production on logs, totem stacks, stumps and in raised beds

The most widely cultivated mushroom for temperate agroforestry is the Shiitake mushroom, often intercropped in Forest farms with other high value non-timber crops such as goldenseal (*Hydrastis canadensis*) and ginseng (*Panax* spp.) (Mudge & Gabriel 2014). Cultivation of Shiitake has a long practice on logs and is reliably used outdoors (Stamets 2000). Almost any deciduous tree that retains its bark for several years can be used to cultivate Shiitake on logs (Bruhn & Hall 2008). Shiitake also has the highest commercial demand among mushrooms (Mudge 2009). This mushroom is not native to Sweden (Artdatabanken 2020) but can act as a reference point to when a mushroom producing system becomes successful. Mudge (2009) states that cultivation strategies for other mushrooms within forest farming are not yet as perfected as for Shiitake.

Successful production of Lions Mane (*Hericium* spp.) on totem stacks from American beech (*Fagus grandifolia*), was demonstrated in a forest farming system in upstate New York during a 5-year period (Grace & Mudge 2015). Peak production of Lions Mane occurred during the third and fourth year (ibid.). The levels of peak production were comparable to the commercial yield of shiitake mushrooms cultivated in forests (ibid.). Locally isolated strains of *H. americanum* had better results than the commercial strain of *H. erinaceus*.

Among the saprophytic edible mushrooms King Stropharia is one of the most recently domesticated ones (Bruhn et al. 2010). In Missouri for two years, experiments were conducted to understand this mushroom's suitability for forest farming (ibid.). The results showed that production of mushrooms was greater when using mixed wheat straw (*Triticum* spp.) and wood chips than the sole use of wood chips. The wood chips used came from hybrid poplars (*Populus* spp.) and were mixed with soil and slightly composted before use. The wheat straw was leached, fermented, and covered with the same wood chips-soil mixture as a casing material. Experiments were conducted in raised beds similar to tray culture, except in the soil directly. The amount of used mycelia for each system during inoculation differed (ibid.), the denser and shallower system with chips required less spawn than the more loosely packed system with cased straw beds. Covering the ground with fabric before adding the substrates did not increase mushroom production and only needs to be provided if anticipating competitor insects or fungi (e.g., *Armillaria* spp.) (ibid.). In this area beds are advised to be built and inoculated during average temperatures of 20-29°C, to achieve a fast colonization (ibid.). Bruhn et al (2010) concludes that further research is needed to find the most productive bed dimensions, to evaluate alternative methods of casing, and to find possible ways for renewing existing beds with fresh substrate.

Whenever a tree is cut, it creates a stump susceptible to microorganisms (Stamets 2000). To avoid unwanted organisms to colonize the stump it can be inoculated with any primary decomposer fungi suitable for the tree and location (ibid.). Fruiting takes time from stumps (Bruhn 1998), even with Oyster mushroom species it can require three growing seasons to produce mushrooms from inoculation. This stump inoculation technique can be more effective in mixed tree stands, where neighbouring trees would be less likely to root graft (ibid.).

4.1.2 Production on lignocellulosic by-products

There are more than 200 waste materials from forestry and agriculture that can be used for mushroom production as mixtures or single substrates for edible mushroom production (Poppe 2000b).

Numerous Dutch experiments with King Stropharia have been conducted since spring 1997 on agricultural waste in a garden with shrubs and trees (Poppe 2000a). These wastes consisted of: Sunflower peels, chopped summer pruning wood, chopped winter pruning wood, chopped straw, corn cobs, sawdust, grass husk and combinations. After 6-8 weeks after inoculation, the first mushrooms appeared through the casing layer (ibid.). The first harvest came from the chopped pruning woods, followed by straw, sawdust, and grass husk. The highest yield on average was obtained from the chopped winter pruning wood. This easy outdoor cultivation of King Stropharia can be considered very promising during summers in temperate zones (ibid.). Poppe (2000a) states further that cultivating King Stropharia outdoors is more fitting outdoors than indoors, where contamination risk is prevalent from *Trichoderma* sp.

During a 5-year period, field experiments with Oyster mushroom production on waste dendromass were evaluated in Slovakia (Pavlik & Halaj 2019). The substrate used was from Aspen trees (*Populus tremula*) and focused on the most valuable part, the tree trunk. Results showed significant economical returns over this period (ibid). Pavlik and Halaj (2019) implies that this could be a viable option within small-scale forest management when deciding how to use low value and low quality dendromass from Aspen and other tree species. The location used was under the natural conditions of a forest stand and can therefore be categorized as a forest farming system.

4.1.3 Intercropping – co-cultivation of plants and mushrooms

Studies in Longquanyi (Song et al. 2021), China, displayed that both yields of Peach (*Prunus persica*) and the Morel mushroom (*Morchella* spp.) increased when intercropped together. A possible reason for this lies within the soil improving qualities from the fungi. Soil tests before and after showed improved soil physicochemical properties. These properties included maximum field capacity, soil bulk density, total porosity, non-capillary porosity, organic matter, and availability of zinc and potassium. Additionally, continuous intercropping decreased soil fungal diversity and improved soil enzyme activities (ibid.). This decrease in soil fungal diversity can be interpreted as something desired when suppressing unwanted fungal pathogens (Parada et al. 2012).

In China, Chen et al (2012) launched an orchard-intercropping try-out consisting of Oyster and Pear (*Pyrus* spp.) during a 3-year period. The focus of the try-out was to elucidate the effect of Oyster on soil biological activity and quality of pear fruit. Results showed an increase in the microbial community, along with a significant improvement in soil fertility and fruit quality. The mycelium was tilled into the soil.

In China, King Stropharia has become popular in forest farming operations since the Chinese government encouraged cultivation of economically valuable mushrooms in forestlands (Gong et al. 2018). This easy grown mushroom can reach a high yield through extensive management (ibid.). Experiments with cultivation regimes of *S. rugosoannulata* under the shade of nursery stocks in Northern China showed results in increased soil organic matter and available phosphorus content (ibid.). The one-year interval regime had the greatest soil nutrient content (ibid.). Soil bacterial groups, including Acidobacteria, increased abundantly post-cultivation of King Stropharia (ibid.). Gong et al. (2018) suggest that King Stropharia is beneficial for the soil nutrient conditions in the forest and recommends the one-year interval regime for farming practices.

In central China, Zhang et al (2015) studied the cultivation of King Stropharia in a citrus orchard. In the study, significant increases in nitrogen content and soil carbon were observed. Zhang et al. (2015) states that this further proves that King

Stropharia could promote the mineralization and formation of various nitrogen sources and active carbon.

There is no information on intercropping of mushrooms and vegetables, specifically together with trees, other than within forest farming practices. Without trees, the following two examples with mushrooms intercropped with vegetables cannot be defined as agroforestry practices but mentioning them opens for future possibilities to use them as such.

Field experiments in the southeastern U.S. by Wells (2020) have shown that King Stropharia and the Elm Oyster mushroom (*Hypsizygus ulmarius*), when intercropped in mulches for vegetables, need new field try-outs in conditions that would further favour the mushrooms. The experiments did not produce any mushrooms and did not improve the soil. Straw mulch and sawdust were used as substrates. The complexity of variables and other unknown factors may have contributed to this experiment's absent productivity goals (ibid). Wells (2020) states that the lack of details when replicating something shown in books is a source of error, what is applicable in one condition may not be applicable in another due to inadequate substrate, poor mushroom genetics or unfavourable environmental conditions. Additionally, the overall heat was not adequate for King Stropharia in this hoop house system and the Elm oyster were not suitable for the experiment's outdoor conditions (ibid.). Replacing Stropharia with more heat tolerant compost mushrooms such as Almond Portobello (*Agaricus subrufescens*) and the Elm oyster with other more vigorous Oyster mushroom species (*Pleurotus* spp.) were suggested (ibid).

Research trials during two winters in Egypt (Hamed et al. 2021), with Oyster mushroom (*Pleurotus columbinus*) intercropped with cauliflower (*Brassica oleracea* var. *botrytis*) and cabbage (*Brassica oleracea* var. *capitata*) significantly improved the yields and quality of both vegetables. The mushroom was introduced as bag cultures at the beginning of curd or even head formation of the vegetables. The mushrooms developed an even quality with both vegetables, but total mushroom yield was higher with cauliflower than with cabbage. Rice straw was used as a substrate. The winters of Egypt could reflect summer conditions in temperate areas. The outside collected straw used as a substrate, needed to be pasteurized because the mushroom strain demands it. The small size of bags probably made it logistically convenient to heat-treat them indoors prior to outside placement.

4.1.4 Outdoor pre-treatments of mushroom substrates

As mentioned above mushroom substrates are usually pre-treated to reduce the competitive microflora. As in the cultivation methods above regarding forest farming, none of them used pasteurized or sterilized substrates. The main reason for this with logs is the natural casing called bark, which protects from excessive moisture loss and competitor microorganism such as other fungi (Mudge & Gabriels 2014). When it comes to King Stropharia it simply doesn't need this pre-treatment (Svamphuset n.d.b). It is therefore when growing on logs, stumps, totem stacks or in raised beds, imperative to use fresh material of the highest quality (ibid.).

Not having a need for these pre-treatments saves time and therefore money. There are numerous waste materials that don't have the freshness many mushrooms require to thrive. Species such as *Hericium* spp. are sensitive to contaminants and demand complete substrate sterilization (121°C) (Stamets 2000). This must be done in a sterile environment to ensure success (ibid.). On the other hand, some species such as the vigorous Oyster mushroom only need pasteurization (ibid.). Outside pasteurization methods include:

- Heat pasteurization
- Lime bath treatment
- Peroxide treatment
- Cold Fermentation

Straw can be pasteurized with heat, soaked in hot water (71-76°C) for an hour (NAMA 2022). Straw can also be pasteurized when soaked in unheated water mixed with hydrated lime (Calcium hydroxide) or quicklime (Calcium oxide) for 2-4 hours, known as the lime bath treatment (ibid.). Another pasteurization method is with water and 3% peroxide for 24 hours, the straw needs to be repeatedly soaked with water before treatment (ibid.). Cold fermentation is done by soaking the straw for 7-14 days depending on the amount (ibid.). The straw is fermented by anaerobic bacteria which are then killed by aeration before inoculation (ibid.). These examples of substrate pasteurization are limited to straw, other materials may have other requirements and pasteurization methods could need to be adapted accordingly.

4.2 Native species for Agroforestry systems

The fungal biogeography of Sweden is divided into 4 zones (Petersen & Læssøe 2019), from north to south: the alpine, boreal, hemiboreal and the nemoral continental zone. These zones are governed by two gradients, the increasing precipitation from east to west and the decreasing temperature from south to north.

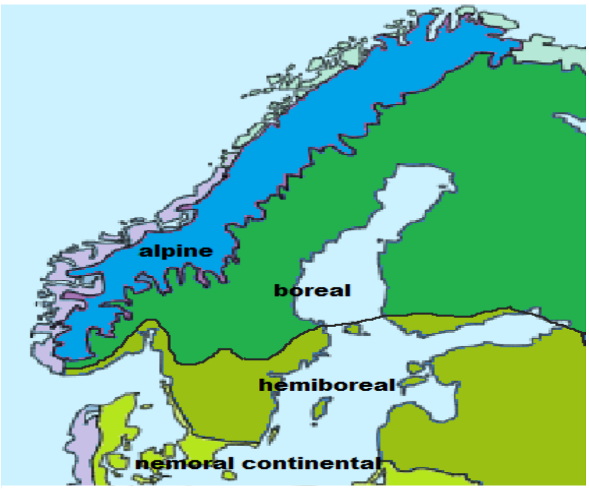

Figure 2. The fungal biogeography of Northern Europe. Redesigned from Wikipedia (2006) with inspiration from Petersen & Læssøe (2019).

Among the 33 species of edible native saprophytes producing fruiting bodies presented in *Appendix 1*, 15 species have mycelium which can be commercially obtained from supplying companies such as Mycelia (2022) and Svamphuset (n.d.a). Out of these 15 species, four are chosen (Table 1), due to their current use in outdoor cultivation by hobby-scale growers. These four are presented in detail below.

Table 1. Selected native edible saprophytic fungi and with their trivial and Swedish names.

Latin name	Trivial name	Swedish name
Hericium erinaceus	Lions Mane	Igelkottstaggsvamp
Flammulina velutipes	Enoki or Enokitake	Vinterskivling
Pleurotus ostreatus	Oyster	Ostronmussling
Stropharia rugosoannulata	King Stropharia or Wine Cap	Jättekragskivling

Lion's Mane: In Sweden and other countries this mushroom is critically endangered with specimens observed in the hemiboreal and the nemoral continental zone (Artdatabanken 2020). It grows naturally in deciduous forests on the stem of dying or dead trees, most often beech and oak (Hallingbäck & Aronsson 1998). Hobby cultivators grow this mushroom outdoors in log cultures (Svamphuset n.d.a). As mentioned previously, totem stacks have shown promise to be an option for upscaled production for forest farming practices. The mushroom also prefers beech and oak when cultivated on logs (Svamphuset n.d.a).

Enoki: In Sweden this mushroom has been observed in all biogeographical zones with higher concentrations in the hemiboreal and nemoral continental zones (Artdatabanken 2020). It is found in mixed and deciduous forests on stumps, dead stems, and roots from Willow trees (Hallingbäck & Aronsson 1998). Rare observations have been made on aspen, birch, and other deciduous trees (ibid.). It has also been well observed in agricultural landscapes (Artdatabanken 2020). Hobby cultivators grow this mushroom outdoors in log cultures (Svamphuset n.d.d). As mentioned before this mushroom is one of the most cultivated mushrooms in the world within indoor production (Royse et al. 2017). It has no upscaled tradition outdoors. By being log-grown outside, proper moisture and shade conditions can be provided within forest farming practices. Preferred log substrates are beech, poplar, willow, ash, oak, maple, and other broadleaf trees (Svamphuset n.d.d).

Oyster: In Sweden this mushroom has been observed in all biogeographical zones with higher concentrations in the hemiboreal and nemoral continental zones (Artdatabanken 2020). It is found in mixed and deciduous forests on dead or alive wood from willow, beech, birch, poplar and rarely on coniferous trees (Hallingbäck & Aronsson 1998.). Hobby cultivators grow this mushroom outdoors on common log cultures and on totem stacks (Svamphuset n.d.c; Cornell University 2022). As mentioned before this mushroom is one of the most cultivated mushrooms in the world within indoor production (Royse et al. 2017). There is no tradition to be found about upscaled production outdoors, but it's believed by Grace & Mudge (2014) to be a distant second to Shiitake concerning outdoor cultivation. By being log-grown outside, proper moisture and shade conditions can be provided within forest farming practices. Preferred log substrates are birch, oak, ash, poplar, maple, willow, and other broadleaf trees (Svamphuset n.d.c).

King Stropharia: In Sweden this mushroom with four observations the last 25 years, has been found in the nemoral continental and southern hemiboreal zone (Artdatabanken 2020). It is a foreign mushroom that spread passively to Sweden after the 19th century and is found to reside and reproduce (ibid.). It is found in deciduous forest or cultivated lands in urban landscapes on wood chips, litter, and nutritious soil such as compost heaps and fertilized soil (ibid.). As mentioned before, Bruhn et al (2010) concluded that substrates combined of straw and wood chips have shown to give higher yields in forest farming practices. As also mentioned in another subsection, solely using substrates such as winter pruning wood could be an option (Poppe 2000a). Shavings and sawdust from any deciduous trees or any straw may be used (Svamphuset n.d.b). This species can be cultivated in any bedlike structure such as raised beds in vegetable frames. Stropharia is a wanderer and spreads easily to its niches in nearby areas (Stamets 2000). It is perceived to be unique by naturalizing itself to the site to an extent where no further spawn is needed but could need extra help withstanding frost with an extra layer casing consisting of wood chips (Mudge & Gabriels 2014).

Out of the more than 200 by-products created from forestry and agriculture, over 50 derive or are created in temperate regions and can be used by the four selected native mushrooms (Poppe 2000b). Among these substrates a majority were known to be used primarily by Oyster mushrooms, followed by King Stropharia, Lions Mane and lastly Enoki (ibid.).

5. Discussion

Logs, totems, and raised beds are all methods used within temperate agroforestry systems but there is limited information about how to match these together in Sweden. The suitability for these mushrooms for production in Swedish agroforestry systems could be perceived as low but probable. “Low”, because of no or limited research about production in Sweden with native species, and “probable” because efforts have shown promise when using similar mushrooms and systems elsewhere in the world's temperate areas. What potentially works in one temperate place of the world could work in the temperate regions of Sweden when using similar or comparable species. Temperate areas with their similarities in temperature spans often differ in other climatic factors such as latitude, elevation, topography, vegetation, wind, etcetera. To increase the chance of success when replicating try-outs in other continents than its origin, it could be essential to understand which climatic factors are relevant for the mushroom strains requirements.

In Sweden, agroforestry systems are not yet widely established and little to no information about mushroom cultivation exists, except from hobby cultivators. Gathering data from current outdoor-mushroom hobby cultivators could be a first step to start this orientation through “which mushrooms on which sites, and how?”.

There are many strains from many genera available to order, furthermore there are a wide range of agricultural and forestry by-products available in every country. The availability of by-products from agriculture and forestry differs from location to location. Bruhn (1998) states that the array of mushrooms cultivated in each agroforestry location should be knowledge-based on strain productivity on available substrates. It is therefore the conditions of the agroforestry location and available by-products that determines the possible mushrooms to choose from.

5.1 Native Swedish species

As mentioned, approximately a third of Sweden's common wild edible mushrooms are saprophytic. Any of these mushrooms could be suitable for agroforestry systems. A rough division between the 33 mushrooms in *Appendix 1* can be made, the ones inhabiting wood directly belong to the primary decomposers and the ones directly inhabiting soil belong to the secondary decomposers.

The ones decomposing wood as a primary decomposer could be used in log cultivation, totem stacks or in raised beds outdoors. Most of these could be used in any agroforestry practice with conditions similar to woodlands or their natural biotope. The agroforestry practice resembling woodlands the most is forest farming.

The cultivars from the secondary decomposer-group are mostly grown indoors. In Sweden the mushroom production is dominated by the Button Mushroom (SSF 2017). *A. bisporus* is native and exclusively grown indoors (ibid.). Further research and try-outs are needed to understand the secondary decomposers feasibility for outdoor cultivation in temperate areas.

5.2 Forest farming

Forest farming is overall the dominating solution for growing high value crops such as edible and medicinal mushrooms outdoors. As mentioned previously, the most suitable agroforestry production systems for the selected native fungal species are log culture, totem stack culture and raised beds within forest farming practices. These mushroom production systems are the most spread within forest farming. Traditionally, forest farming practices have been favoured for mushrooms grown on logs. Log cultivation have been refined through centuries, almost exclusively with Shiitake (Stamets 2000). Following mushrooms probably prefers forest farming practices above others but conditional requirements can vary between strains.

5.2.1 Oyster mushroom

There are some indications that outside log-grown Oyster mushrooms are sold commercially and therefore viewed as a distant second to the established Shiitake within forest farming systems (Mudge & Gabriels 2014). However, there is no information about upscaled production of Oyster mushrooms. But being one of the most cultivated mushrooms indoors could give growers enough data to achieve success in outdoor try-outs. Oyster mushrooms are spread in all areas of Sweden and thus indicate that the variety of genes could be vast and serve as an “arsenal” gene pool in breeding of future strains.

Pavlik & Halaj (2019) implies that the forest experiment with Oyster on logs could be economically viable in small-scale forest management when using low value dendromass. When such by-products are available, research is needed to motivate such a try-out in Sweden since cost and trade-offs could vary from country to country as well as outcomes dependent on biogeography and other conditions.

5.2.2 King Stropharia

The broadened and somewhat upscaled production outdoors of King Stropharia seems to be limited to China. Stropharia is a strong candidate for further try-outs in other temperate areas. This conclusion is motivated by two main trait characteristics. The first is that it is perceived as a sun loving mushroom due to its resistance and willingness to grow in sun exposed sites, meaning that it could be used in areas where many other mushrooms would not prosper and therefore potentially broaden the role of mushrooms (The Mushroom Forager 2022). Although seen in sunny locations, it fruits better in part shade (Mudge & Gabriels 2014). The second characteristic is that the substrates don't need to be pasteurized or sterilized, making it easier to keep mushroom production altogether outdoors (Svamphuset n.d.b).

King Stropharia could be an option for crop rotation with the purpose to increase soil fertility (Wells 2020). Examples for this are for now just theoretical and calculating trade-offs from such an experiment are needed.

Further site-bound try-outs are needed to examine Stropharia´s integration together with vegetables for intercropping purposes, since text-book examples can be misleading (Wells 2020). This is however a mushroom that is grown outside in Sweden but information about this is limited (Artdatabanken 2020).

5.2.3 Lions Mane

Productive success in Sweden could be reached by replicating the previously mentioned experiments with Lions Mane (*Hericium* spp.). *H. erinaceus* is native to Sweden but critically endangered (Artdatabanken 2020). If commercial strains are shown to be inadequate, spore samples from local isolates could be collected with minimal impact on the mushrooms and reproduced for commercial try-outs.

5.2.4 Enoki

There is no tradition for upscaled production outdoors of Enoki mushrooms. But being one of the most cultivated mushrooms indoors could in theory give growers enough data to achieve success in outdoor try-outs. No information about commercial try-outs for outdoor production are to be found about Enoki mushrooms. Enoki is alike the Oyster mushroom spread in Sweden and could similarly provide a broad gene pool for future breeding of new strains.

5.2.5 Shiitake

If broadening the perspective to include non-native species, there is one saprophytic mushroom above others that could be a viable candidate for outdoor production in Sweden. The name is Shiitake and it originated from the northeast forests of Asia (Mudge & Gabriel 2014). The practice has been active for centuries on logs (ibid.). Shiitake has proven to be productive in other continents than its origin, where replicating traditional methods has shown success in the U.S for over three decades (ibid.). One major advantage with Shiitake is that the fruiting of mushrooms can be forced by cold water treatment which gives the grower predictable yields and possibilities to match sales with harvests (ibid.). As mentioned before, it can be cultivated on any deciduous tree log that retains its bark for several years (Bruhn & Hall 2008). However, try-outs are essential since all locations are different with corresponding variables, that all need to be considered for a positive production outcome. Unlike Oyster mushrooms that prefer low density woods in forest farming systems, Mudge & Gabriels (2014) recommends U.S. growers to use logs from native hardwoods. These hardwoods include oak, maple, and beech amongst many others (ibid.).

5.3 Alley cropping

The intercropping of mushrooms and fruit trees could in theory be used in alley cropping practices with suitable conditions. However, the conditions of alley cropping systems differ greatly in comparison to forest farming. Sparse tree proximity within alley cropping generally creates more wind and sun exposure than the denser forest farms, something that needs to be accounted for when choosing a strain. Further research is needed to understand these conditions and the mushrooms suitability for different alley cropping solutions. Following mushrooms could be promising candidates for further evaluation within alley cropping practices.

5.3.1 Oyster mushroom

The previously mentioned try-out conducted in a pear orchard by Chen et al. (2012), showed that besides the increased soil fertility, a higher quality in pear fruit were obtained in orchards intercropped with Oyster mushrooms. Further research and try-outs are needed to evaluate this intercropping in other temperate areas such as Sweden.

As mentioned previously, *P. columbianus*, a relative to *P. ostreatus* exhibits success when intercropped together with cruciferous vegetables. Further research is needed to understand the use of *Pleurotus*-species for intercropping purposes within temperate regions such as Sweden. The intercropping of *P. columbinus* and cruciferous vegetables shows that the use of bag cultures may extend the production possibilities of mushrooms to new areas outside the well-established forest farming systems. Digging down the bags and having the opening at ground level, supposedly decreases the need of shading. With less need for shading, these intercropping systems could in theory be used in alley cropping systems where sun exposure is more prevalent.

5.3.2 Morels

As mentioned previously, the growing of Morel mushrooms in orchards have resulted in increased soil fertility and higher yields from both the Peach tree and mushroom fruitbodies (Song et al. 2021). Further research is needed to understand the outdoor cultivation of Morels (*Morchella* spp.), especially in temperate areas such as Sweden. *M. conica* & *M. esculenta* are native to Sweden (Artdatabanken 2020) and could be candidates for evaluation in Swedish orchards.

5.3.3 King Stropharia

The previously mentioned study of King Stropharia intercropped in a citrus orchard exhibited increases in soil fertility. King Stropharia with its sun-tolerant qualities could be a suitable mushroom for alley cropping. Further research and try-outs are needed to optimize the use of this vigorous mushroom within temperate areas such as Sweden.

5.4 Windbreaks

Shading environments can also be created within for example multiple row windbreaks (Wetzel et al 2006), making it possible to introduce species and methods suitable for forest farming to further diversify income streams. This means that any suitable area within agroforestry systems may function or be adapted to function as a site for mushroom production.

5.5 Silvopasture

No information is to be found about mushroom production exclusively within silvopastures. Although, if a mushroom producing Agroforestry system incorporates a silvopasture with ducks (Gabriel 2018), these can reduce the slug population, which would otherwise consume the mushrooms. To reduce the pressure from slugs, Gabriel (2018) advises to use the ducks on a rotational basis, 3-4 times during a season.

5.6 Sustainable forest management

Mudge & Gabriel (2014) stresses the fact that sustainable mushroom production should not jeopardize sustainable forestry. Meaning that trees should not be cut solely for mushroom production purposes, but as a side effect from sustainable forestry where trees need pruning and thinning (ibid.).

Besides benefitting agricultural practices, modern forestry could also incorporate forest farming solutions to become overall more sustainable. Rough estimations between the comparative market value of the Matsutake mushroom (*Tricholoma matsutake*) and the market value of timber, were determined within a 5,988-ha parcel in British Columbia (Wetzel et al 2006). The area estimated was a watershed consisting mostly of Douglas Fir (*Pseudotsuga menziesii*), balsam (*Abies balsamea*), hemlock (*Tsuga canadensis*) and some other minor species. Based on market values and a clearcutting system every 120-years, the timber from the clearcuttings would generate $426M and mushrooms $73M over the same period to a combined total of $499M (ibid.). Should this watershed area be converted into a forest farming system such as those practiced at the Kyoto Forest Experimental Station, Matsutake mushrooms and high-quality timber harvest would generate $1.28 billion during the same period (ibid.). Being a native species to Sweden and a mycorrhizal mushroom (Artdatabanken 2020), this serves only as a viable example for production when a forest already inhabits these mushrooms.

In Swedish forests, wild mushrooms can be viewed as an untapped resource. An investigation shows that out of the 480 million kilograms of mushrooms naturally produced annually in Sweden, approximately 3% are picked (Boman et al. 2002). This indicates that there are unused resources that could be utilized to diversify income streams and potentially assist in the transition of modern forestry towards increased sustainability.

The shading of the forest in a forest farming system is managed by thinning and pruning to achieve the right shading and moisture conditions for the mushroom

(Mudge & Gabriel 2014). In the case of Shiitake, the more shade the better (Mudge 2009). On the other hand, a denser canopy cover may reduce the saprotrophic yield of other mushrooms while enhancing the mycorrhizal richness (Santos-Silva et al. 2011), this was observed when studying wild fungal communities in Montado forest ecosystems, Portugal. Being in Portugal, this might not apply to temperate regions but shows that this can be an important variable to consider when choosing a mushroom strain to an agroforestry system, or vice versa, when adapting conditions to a chosen strain. Santos-Silva (2011) also observed that closer tree proximity favoured the mycorrhizal mushrooms over the saprophytic ones. This could mean that if a landowner already has desired mushrooms inhabiting the lands, together with knowledge of the area's ecology, favourable conditions could be replicated, quantified, and spread over similar areas within the land.

5.7 Risks & opportunities

There is not much information on the invasiveness of mushrooms, but domesticated strains can release spores and jeopardize the broader genetic diversity of wild strains (Liu et al. 2016). This was the case in China where the wild strains of Enoki had a broader genome than the cultivars (ibid.). Liu et al. (2016) concluded that if species with different spans of genetic diversity would mix it could result in genetic erosion of the wild germplasm. Practically this could mean that commercial strains of *H. erinaceus* could threaten the wild *H. erinaceus* when grown too close. Three tested species of *Hericium*, including *H. erinaceus* has shown similar spore dispersal ranges to most wood-decaying basidiomycetes (Boddy et al. 2011). The spores from basidiomycetes tend to fall 1 m from the mushroom, very few travel further than 100 m and some occasionally reach 1000 km (Hallenberg & Kúffer 2001). Protecting the wild germplasm is important to ensure a gene pool for future breeding of new strains (Liu et al. 2016).

Farming equipment and grazing may cause tree root damage to trees in alley cropping and silvopastoral systems (Bruhn 1998). This root damage and other damage made to trees could be susceptible for mushroom species such as Lions Mane, Shiitake and Oyster mushrooms (ibid.). As facultative parasites, these decay dead wood in branches and stems of living trees (Stamets 2000). Care is needed to prevent root and stem wounding of trees together with methods for efficient mushroom production (Bruhn 1998).

Opinions about the need for “aging” the logs after the cuts differ (Svamphuset n.d.a; Mudge & Gabriel). Bruhn (1998) implies that if the “aging” of substrate logs before inoculation results in a faster spawn run, then these maturing logs must become susceptible to the colonization of antagonistic fungi. Competitor fungi include *Diatrype* spp., *Trichoderma* spp., *Hypoxylon* spp., *Armillaria* spp., *Lenzites* spp., *Stereum* spp. and *Trametes* spp, among others (ibid.). Further research is needed to understand these interactions as well as the need for aging of different substrates for an increased production.

People in Sweden have a strong scepticism towards mushrooms and are considered to belong to one of the mycophobic countries (Sveriges Radio 2022). A thorough market analysis is therefore needed to understand to which extent the produced mushrooms can be sold. The challenging part is still to create a consistent outdoor production, preferably with known species to the consumer.

Initial start-up cost for commercial outside mushroom farming is far less than investing in an expensive indoor climate chamber (CornellCALS 2021; Mudge 2009), especially when already having access to a piece of land or an area with suitable growing conditions. When established, outdoor growers can expand productions to use indoor practices as well (Bruhn 1998). Both outdoor and indoor production may be fuelled largely by using low-value substrate components derived from agroforestry (ibid.).

The future intercropping of mushrooms with plants could be motivated solely by their soil improving qualities. Further research and try-outs are needed to measure the benefits mushroom producing fungi have on soil in comparison to other organic and inorganic fertilizers. The occurrence of mushroom fruit bodies could be a good visual indicator that a suitable soil environment is created in for example orchards (Song et al. 2021).

The nutrient cycling *in situ* could be provided by many mushroom producing fungi in various agricultural sites and at the same time provide a protein-rich product for human consumption (Hyde et al. 2019). This nutrient cycling could result in a less need for adding fertilizers and promote a self-sustaining agriculture and forestry.

Mushroom production has the potential to integrate the use of numerous waste by-products from agriculture and forestry into circular production systems such as agroforestry (Poppe 2000b). From the primary decomposers (Stamets 2000), the by-product from mushroom production is called Spent Mushroom Substrate (SMS). A review with Leong et al. (2022) highlights the potential of SMS in a wide range of applications. These highlights include the reuse of SMS as substrate for further production of other mushrooms, animal feed, biofertilizer and soil amendment, pollution bioremediation and renewable energy production.

It can be concluded that mushroom production is a viable option to integrate into temperate agroforestry systems. For the Nordic conditions there are a wide range of different species available, and more are successively emerging for cultivation purposes (Mycelia 2022). Further research and try-outs are needed to enable commercial production in outdoor areas unfamiliar to mushroom cultivation.

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Appendix 1

Status*: Critically Endangered (CR), Least Concern (LC), and for foreign species Not applicable (NA). **Zone*:** Alpine (1), boreal (2), hemiboreal (3), and the nemoral continental zone (4), based on found specimens, not general occurrence (Artdatabanken 2020). See map at 4.2 *Native species for Agroforestry systems*.

Latin name	Swedish name	Status*	Zone*	Biotop	Substrate/Habitat requirements	Source
Agaricus arvensis	Snöbollschampinjon	(LC)	2-4	Park, garden & grassland.	Soil, especially lawns.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus augustus	Kungschampinjon	(LC)	2-4	Park, meadow spruce- and deciduous forest.	Litter, especially on needle-covers beneath old spruces. Calcinous soil.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus bisporus	Trädgårdschampinjon	(NA)	2-4	Road edges & gardens.	Litter, such as manure & compost heaps.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus bitorquis	Vägchampinjon	(NA)	2-4	Street- and road edges, gardens & park.	Bare soil, among grass & cracks between stone materials.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus campestris	Ängschampinjon	(LC)	2-4	Pasture, garden, park & mountain heath.	Soil, especially lawns.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus langei	Blodchampinjon	(LC)	2-4	Park & meadow-spruce forest.	Nutritous soil beneath spruce.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus sylvaticus	Skogschampinjon	(LC)	2-4	Coniferous forest, mainly spruce.	Litter, especially on needle-covers beneath old spruces.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus sylvicola	Knölchampinjon	(LC)	2-4	Beech- and coniferous forest.	Litter, especially on needle-covers beneath old spruces & in beech leaf-covers.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Agaricus urinascens	Vit Kungschampinjon	(LC)	2-4	Pasture, park & calcinous heath.	Soil.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Bovista nigrescens	Svartnande Äggsvamp	(LC)	1-4	Pasture, garden & park.	Soil, such as lawns.	Holmberg&Marklund(2014), Artdatabanken (1998; 2020)
Calocybe gambosa	Vårmusseron	(LC)	2-4	Pasture, garden, road edges & deciduous forest.	Nutritous & calcinous soil, among grass.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Cantharellula umbonata	Fläckkantarell	(LC)	1-4	Coniferous forest: pine-lichen forest- and forest marshes.	Acid & meagre soil among lichens & moss.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Clavulina cristata	Kamfingersvamp	(LC)	1-4	Grassland & mixed forest.	Soil.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Clitopilus prunulus	Mjölskivling	(LC)	1-4	Pasture, open mixed forest & park.	Soil, among grass.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Coprinus comatus	Fjällig Bläcksvamp	(LC)	1-4	Garden, grassland & road edges.	Nutritous soil, such as lawns.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Flammulina velutipes	Vinterskivling	(LC)	1-4	Mixed- and deciduous forest.	Logs, stumps & dead roots from Willow.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Hericium erinaceus	Igelkottstaggsvamp	(CR)	3-4	Tree-bearing grassland & deciduous forest	Prefers dead wood from oak & beech.	Artdatabanken (1998; 2020)
Hypholoma capnoides	Rökslöjskivling	(LC)	1-4	Coniferous forest, rarely deciduos forest.	Stumps & dead roots of pine & spruce, rarely birch.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Hypsizygus ulmarius	Almskivling	(LC)	1-4	Deciduous forest	Prefers wood from oak, alder, birch and elm. Parasite.	Artdatabanken (1998; 2020)
Kuehneromyces mutabilis	Föränderlig Tofsskivling	(LC)	1-4	Mixed- and deciduous forest, Rarely coniferous forest.	Stumps, often beech & birch. Rarely spruce stumps.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Langermannia gigantea	Jätteröksvamp	(LC)	2-3	Park, gardens, pasture & deciduous forest.	Nutritious soil in lawns and deciduous forest.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Lepista nuda	Blåmusseron	(LC)	1-4	Mixed forest, garden and shores.	Nitrogenous soil, favors coniferous needle litter & compost heaps.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Lepista saeva	Höstmusseron	(LC)	2-3	Park, garden, pasture & deciduous forest.	Calcinous bare soil, among grass in deciduous forest.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Lycoperdon perlatum	Vårtig röksvamp	(LC)	1-4	Pasture & mixed forest.	Soil, rarely on rotten wood.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Macrolepiota procera	Stolt Fjällskivling	(LC)	2-4	Pasture & open mixed forest.	Litter, favours loamy soil.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Marasmius oreades	Nejlikbrosking	(LC)	2-4	Park, garden & pasture.	Soil, such as lawns.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Morchella conica	Toppmurkla	(LC)	1-4	Forest, garden, ditch edges & burnt areas.	Loamy soil, prolifically grows on burnt spots.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Morchella esculenta	Rund Toppmurkla	(LC)	2-4	Garden, park & road edges.	Nutritous soil.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Pleurotus ostreatus	Ostronmussling	(LC)	1-4	Mixed & deciduous forest.	Prefers dead wood from willow, beech, birch & poplar. Parasite.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Pleurotus pulmonarius	Blek Ostronmussling	(LC)	1-4	Mixed & deciduous forest.	Prefers dead wood from birch & aspen. Parasite.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Sparassis crispa	Blomkålssvamp	(LC)	2-4	Coniferous forest, prefers pine forest with lingonberry & lichen.	On roots from dead or live pines & pine stumps. Parasite.	Svampguiden (n.d.), Artdatabanken (1998; 2020)
Stropharia rugosoannulata	Jättekragskivling	(NA)	2-4	Deciduous forest	Wood chips, litter and nutritous soil such as compost heaps and fertilized soil.	Artdatabanken (1998; 2020)

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