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Review

Beneficial interactions between bacteria and edible mushrooms

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ABSTRACT

Mushroom-forming fungi establish mutual beneficial interactions with plants and degrade organic waste. These fungi also play an important role in human societies to produce mycelium materials, as a source of medicinal compounds, and as food. Bacteria interact with mushroom-forming fungi not only as competitors for nutrients and as pathogens but also to establish beneficial interactions. This review discusses the positive interactions of bacteria during the different stages of the life cycle of the white button mushroom *Agaricus bisporus* and other highly consumed mushroom-forming fungi. Bacteria are key in forming a selective substrate, in providing nutrients, in stimulating growth and mushroom formation, and in protection against pathogens. Implications for the mushroom industry are being discussed.

1. Introduction

Mushroom-forming fungi play key roles in nature by establishing mutual beneficial interactions with plants (mycorrhizae) and by degrading organic waste. These fungi are also important for mankind. For instance, their fruiting bodies are used as a material. Amadou is the spongy material from the inner part of *Fomes fomentarius* mushrooms that has been used for thousands of years to dry objects, to make hats and purses, and as tinder (Pegler, 2001). Nowadays, mushroom forming fungi are used for a wide range of materials including thermal insulation and acoustic panels, and packaging and construction materials (Grimm and Wösten, 2018; Wösten, 2019). Use of mushrooms as food or as a source of medicinal compounds is even more important at this moment. A 63 billion US dollars sales of edible and medicinal mushrooms was reported in 2013 (Royse *et al.*, 2017), of which more than 60% represented by mushrooms for consumption. World production of cultivated, edible mushrooms increased more than 30-fold in the period from 1978 to 2017 (Royse *et al.*, 2017) and is expected to further increase. Total production of edible mushrooms was over 12 million tons in 2018 and is predicted to increase to over 20 million tons in 2026 (see https://www.fortunebusinessinsights.com/industry-reports/mushroom-market-100197). The increased consumption of edible mushrooms is stimulated, at least in part, by

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the need to reduce meat in the human diet. Mushrooms have a structure (i.e. mouthfeel) similar to that of meat, have a balanced composition of minerals and vitamins, are rich in fibre, and contain 2% protein (based on fresh weight) (Mattila *et al.*, 2002). *Lentinula* (shiitake and relatives), *Pleurotus* (oyster mushrooms), *Auricularia* (wood ear mushrooms) and *Agaricus* (white button mushrooms) represent the top four consumed edible mushrooms (Royse *et al.*, 2017). These mushrooms are cultivated on agricultural waste streams, waste streams from the wood industry or even on spent mushroom substrates. As such, cultivation of mushrooms is a well-known example of the circular economy where low-quality waste streams are converted into high-quality food (Grimm and Wösten, 2018).

Bacteria present in the substrate impact mushroom cultivation both in positive and negative ways. This review will discuss the positive interactions between bacteria and edible mushrooms during commercial cultivation with an emphasis on *Agaricus* and pseudomonads. Most of what we know about these positive interactions is restricted to *Agaricus*, which may be explained by the fact that other mushrooms, such as *Lentinula, Pleurotus* and *Auricularia,* are generally grown commercially on pasteurised or sterilised substrates, while *Agaricus* is grown on a non-axenic substrate. First, bacterial diversity at different stages of *Agaricus* cultivation will be discussed. Next, bacterial species and underlying mechanisms are addressed that support vegetative growth and mushroom production as well as protect against pathogens.

2. Bacterial diversity in compost, casing and on mushrooms of *A. bisporus*

Typically, the mushroom cultivation cycle of *A. bisporus* consists of four phases. Phase I (PI) and phase II (PII) involve substrate preparation, while during phase III (PIII) the substrate is colonized by *A. bisporus*. To induce fruiting body production, the substrate is topped by the so-called casing layer, which is done at the beginning of phase IV (PIV). This phase ends after harvesting 2–3 flushes of mushrooms. The microbiome in compost and casing and on mushrooms does not have a fixed composition but differs between the phases and depends on variables such as the recipe and preparation of the compost and casing (Neher *et al.*, 2013; Vieira and Pecchia, 2018; Fermor *et al.*, 2000). For readability, we will limit our discussion to some lead articles that systematically assessed the microbiome during the different stages of *A. bisporus* mushroom production.

2.1. *Bacterial diversity during production of* Agaricus bisporus *substrate*

In contrast to many other microbes, *A. bisporus* grows well in a humic-rich substrate. In nature, this substrate is formed from non-woody litter such as that of leaves. Microbes remove readily available carbon, nitrogen, and minerals from the litter. Degradation and decomposition of this biological material results in the formation of humic substances. These substances consist of supramolecular associations of self-assembling heterogeneous and relatively small molecules derived from lignin, other recalcitrant aromatic compounds and proteins (Piccolo, 2002). This illustrates the importance of microorganisms, including bacteria, in the life cycle of *A. bisporus*; they create a selective substrate in which this mushroom-forming fungus can thrive. Commercial white button mushroom production also makes use of a substrate that is processed by microbial activity. In the Netherlands, the substrate results from composting a mixture of wheat straw, horse manure and gypsum, while chicken manure can be used as an additional nitrogen source (Gerrits, 1988). A selective environment for *A. bisporus* growth is created during PI and PII by conversion of easily accessible compounds, such as free sugars, amino acids, cellulose and hemicellulose into microbial biomass (Ross and Harris, 1983). At the end of PII, 50–60% of xylan and cellulose in the substrate has been degraded, but lignin is still largely intact (Jurak *et al.*, 2015).

Little is known about the fungal community in PI and PII compost. Cao *et al.* (2019) showed that it is dominated by ascomycetes. The genera *Gibellulopsis, Alternaria, Microidium, Chaetomium, Gonapodya*, and *Trichoderma* dominate PI, while *Microidium, Chaetomium, Mycothermus*, and *Gonapodya* are most abundant in PII. Notably, *Scytalidium thermophilum* (also known as *Humicola insolens*) was previously reported to dominate the fungal biota of compost (Straatsma *et al.*, 1994; Kertesz and Thai, 2018) but was not found by Cao *et al.* (2019). This may well be due to the different substrates that were used to grow *A. bisporus*.

The bacterial community in PI and PII compost has been studied in more detail. Both phases are dominated by Firmicutes, Proteobacteria and Actinobacteria (Fig. 1), while the phylum Deinococcus-Thermus may be very dominant in PI as well (Carrasco *et al.*, 2020; Kertesz and Thai, 2018; Székely *et al.*, 2009; Zhang *et al.*, 2019a). PII is often characterised by a decrease in the relative abundance of Firmicutes, whereas Actinobacteria increase in abundance (Cao *et al.*, 2019; Carrasco *et al.*, 2020; Kertesz and Thai, 2018; Song *et al.*, 2021; Zhang *et al.*, 2019a). *Bacillus* (Cao *et al.*, 2019; Carrasco *et al.*, 2020; Kertesz and Thai, 2018; Zhang *et al.*, 2019a), *Ruminiclostridium* (Cao *et al.*, 2019; Song *et al.*, 2021; Zhang *et al.*, 2019a) and *Thermobacillus* (Cao *et al.*, 2019; Song *et al.*, 2021; Zhang *et al.*, 2019a), which all belong to the Firmicutes, are most frequently found to be among the most abundant genera in PI. In contrast, *Pseudoxanthomonas* (Proteobacteria) (Székely *et al.*, 2009; Zhang *et al.*, 2019a), *Thermobacillus* (Firmicutes) (Cao *et al.*, 2019; Song *et al.*, 2021) and the Actinobacteria *Thermopolyspora* (Cao *et al.*, 2019; Song *et al.*, 2021; Zhang *et al.*, 2014, 2019a), *Thermobifida* (Song *et al.*, 2021; Székely *et al.*, 2009), and *Thermobispora* (Cao *et al.*, 2019; Song *et al.*, 2021) are often identified as most abundant genera in PII (Fig. 1). Together, substrate production involves a complex microbial community, during which the 'self-heating' stage in PI, resulting from high microbial metabolic activity, causes a shift from mesophilic to thermophilic bacteria. Interestingly, Ahlawat and Vijay (2010) used a single bacterial species for composting. To this end, sterilised substrate containing wheat straw and bran, gypsum and chicken manure was inoculated with a *Staphylococcus* species that had been isolated from *A. bisporus* compost. Physicochemical properties of the compost were similar to that of the control, while mushroom harvest was even up to two days earlier and also resulted in a higher yield.

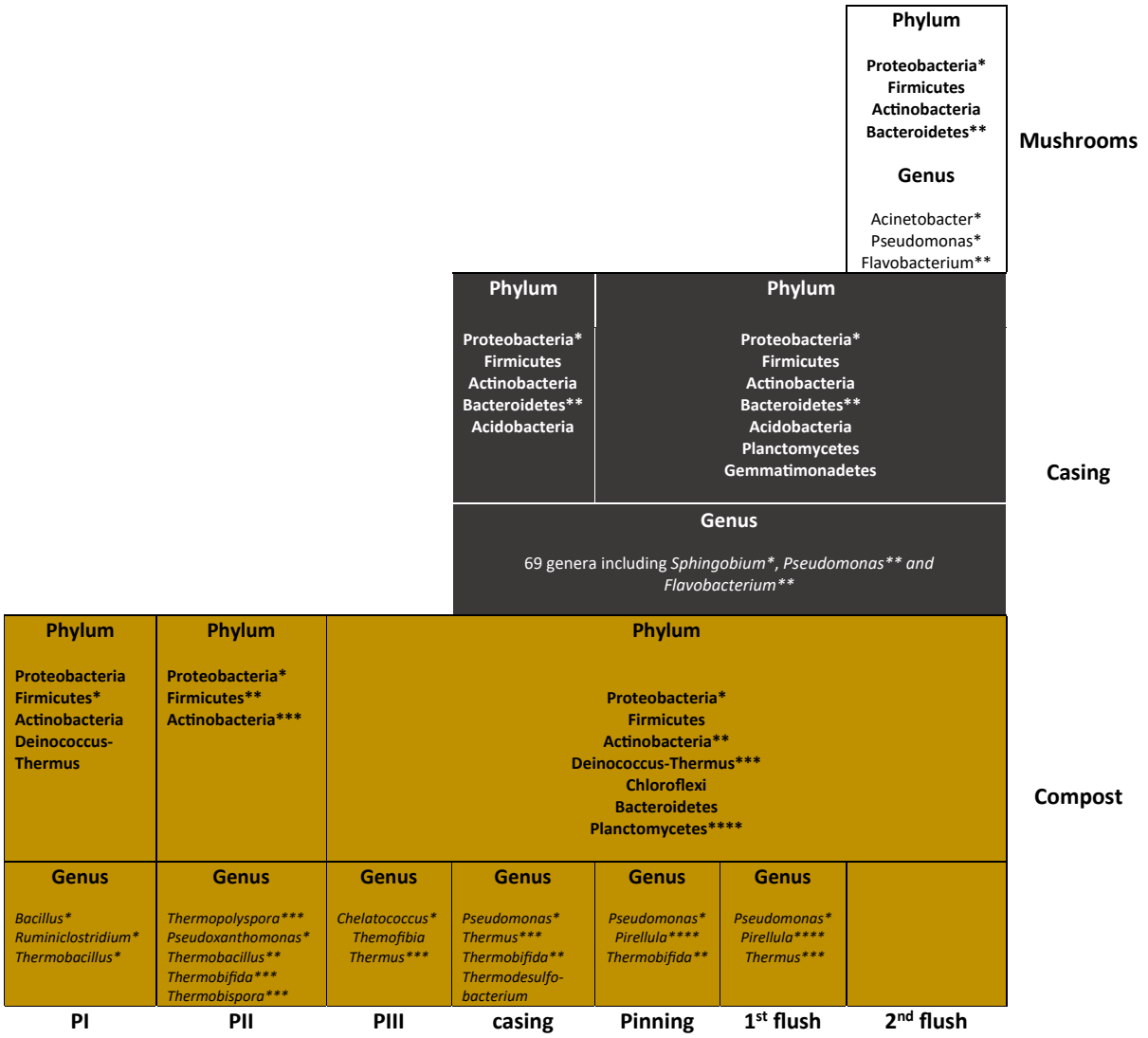

Fig. 1 – Dominant bacterial phyla and genera in compost and casing and on mushrooms of *A. bisporus* (for references see the main text). *Asterisks* indicate to which phylum a genus belongs.

Thus, a complex community seems not always necessary to convert agricultural waste into productive compost.

2.2. *Bacterial diversity during vegetative growth of* Agaricus bisporus

Introduction of *A. bisporus* spawn in PII-end compost initiates PIII of mushroom production. PIII takes 16–19 days during which the compost is fully colonised. This is accompanied by degradation of 50% of the lignin, with an additional decomposition of 15% of the xylan and 10% of the cellulose (Jurak *et al.*, 2015). The fungal community in PIII compost becomes dominated by *A. bisporus*, replacing the previously dominant ascomycetes (see section 2.1) (McGee *et al.*, 2017a). The bacterial population also decreases during PIII (Carrasco *et al.*, 2020; Vos *et al.*, 2017). Vos *et al.* (2017) proposed that *A. bisporus* feeds on bacteria with a preference for Gram-negative bacteria. They hypothesize that *A. bisporus* farms these microbes by feeding them simple sugars that result from lignocellulose degradation by extracellular enzymes released by the fungus. The bacteria would upgrade these breakdown products for instance by producing vitamins that *A. bisporus* itself cannot produce. Similarly, other mushroom-forming fungi including *Pleurotus* can feed on bacteria (Barron, 1988).

Apart from the bacterial cell counts, also the bacterial diversity decreases during PIII (Carrasco *et al.*, 2020). The Proteobacteria represents the dominant phylum during this phase, accounting for approximately 50% of the total bacterial community (Carrasco *et al.*, 2020; McGee *et al.*, 2017b). Other dominant phyla include Firmicutes, Deinococcus-Thermus and Gemmatimonadetes (Fig. 1). The relative abundance of Firmicutes and Gemmatimonadetes increases during PIII with *Chelatococcus* (Proteobacteria), *Themofibia* (unknown phylum) and *Thermus* (Deinococcus-Thermus) being the most abundant genera (Carrasco *et al.*, 2020) (Fig. 1). The increased abundance of Firmicutes is consistent with the observation of Vos *et al.* (2017) that Gram-positive bacteria become more dominant in PIII.

2.3. *Bacterial diversity during fruiting of* Agaricus bisporus

Formation of white button mushrooms is initiated in PIV by topping the compost with a casing layer that consists for instance of peat and lime. Colonization of the casing layer takes 7 days, during which CO_2 levels are high and relative humidity is 85%. Mushroom formation is induced by lowering CO_2 levels and compost temperature to as low as 18 °C and by increasing relative humidity up to 90% (Visscher, 1988). Mushroom formation often happens in two or three consecutive flushes, with each successive flush generally yielding less mushrooms. During PIV, 44, 29, and 8% of cellulose, xylan, and lignin is degraded, respectively, when compared to the end of PIII (Iiyama *et al.*, 1994; Chen *et al.*, 2000; Jurak, 2015). Thus, a significant amount of the organic compounds remains unused in the compost after cultivation of button mushrooms.

2.3.1. *Bacterial diversity in the compost after casing*

Bacterial diversity increases in compost when it is topped with casing soil. At the same time, diversity also increases in the casing (Carrasco *et al.*, 2019, 2020). Many of the dominant phyla in PIII compost remain dominant after application of casing (Fig. 1). Proteobacteria are still the dominant phylum with an increase in Bacteroidetes and a decrease in Actinobacteria (McGee *et al.*, 2017b). Some genera are consistently found to be dominant in the compost after casing including *Pseudomonas* (Proteobacteria), *Thermus* (Deinococcus-Thermus), *Thermobifida* (Actinobacteria) and *Thermodesulfobacterium* (Thermodesulfobacteria) (McGee *et al.*, 2017b) (Fig. 1).

No major changes in bacterial diversity occur within the compost after induction of mushroom formation (McGee *et al.*, 2017b). Proteobacteria remain the dominant phylum at the moment of pinning and during the first flush, while Actinobacteria are most dominant during the second flush (Fig. 1). The dominant genera during pinning include *Pseudomonas* (Proteobacteria), *Pirellula* (Planctomycetes), and *Thermobifida* (Actinobacteria) (Fig. 1) (McGee *et al.*, 2017b). On the other hand, *Thermus* (Deinococcus-Thermus), *Pseudomonas* (Proteobacteria), and *Pirellula* (Planctomycetes) are among the dominant genera during the first flush, while *Rhizobium* (Protobacteria) and *Sphaerobacter* (Chloroflexi) are among the dominant genera in the second flush.

2.3.2. *Bacterial diversity in casing and on mushrooms*

During PIV, the casing layer shows a distinct bacterial community when compared to the compost (Carrasco *et al.*, 2019). Proteobacteria, Actinobacteria, Firmicutes, Bacteroidetes, and Acidobacteria are the main phyla of bacteria in the casing (Pecchia *et al.*, 2014; Carrasco *et al.*, 2019) (Fig. 1). During *A. bisporus* colonization, the relative abundance of the Proteobacteria increases, while that of Actinobacteria and Firmicutes decreases. In addition, Gemmatimonadetes and Planctomycetes are among the abundant phyla again (Carrasco *et al.*, 2019; Taparia *et al.*, 2021). A total number of 69 bacterial genera were found in the casing layer and the composition was relatively constant up to the third flush of *A. bisporus* mushrooms (Taparia *et al.*, 2021) with *Sphingobium* and *Pseudomonas* (Proteobacteria) and *Flavobacterium* (Bacteroidetes) as abundant genera (Carrasco *et al.*, 2019; Taparia *et al.*, 2021) (Fig. 1).

Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes are the most abundant phyla on mushrooms (Carrasco *et al.*, 2019) (Fig. 1). The bacterial composition of the mushrooms is more similar to that of the casing than that of the compost. For instance, 6 of the 10 dominant genera in casing samples (including *Flavobacterium* and *Pseudomonas*) were also among the most abundant on the mushrooms. From this it was concluded that the bacterial diversity on the *A. bisporus* fruiting bodies is mostly shaped by the casing.

2.3.3. *Pseudomonads are abundant in compost and casing and on mushrooms*

Different studies have shown that pseudomonads are abundantly present in compost and casing during phase III and IV of the crop cycle, as well as on *A. bisporus* fruiting bodies. Some studies, using culture-dependent methods, reported a relative abundance of 14–41% up to 85% of pseudomonads in the casing layer (Zarenejad *et al.*, 2012; Colauto *et al.*, 2016). Also culture-independent techniques show that these bacteria are relatively abundant and increase in abundance during the crop cycle, especially during primordia formation (pinning) and at the onset of the first flush of mushrooms (Carrasco *et al.*, 2019, 2020; McGee *et al.*, 2017b; Pardo *et al.*, 2005). In fact, *Pseudomonas* becomes the second most abundant genus in the compost during the first flush and the most abundant genus in the second flush (Carrasco *et al.*, 2020). A similar increase in relative abundance of *Pseudomonas* is observed in the casing layer, where *Pseudomonas* occurrence increases from being residual on the first day of casing to the fourth and second most abundant genus during the first flush and at the end of the second flush, respectively (Carrasco *et al.*, 2020). During later flushes, the relative abundance of *Pseudomonas* generally decreases in the compost and casing layer (Carrasco *et al.*, 2019, 2020; McGee *et al.*, 2017b). It has been suggested that this decline in *Pseudomonas* causes the reduction in yield during later mushroom flushes (see section 3.2 for mechanisms that would be involved) (Carrasco *et al.*, 2019). *Pseudomonas putida* is one of the pseudomonads that is abundant in compost and casing. It represents up to 47% and 23.5% of the *Pseudomonas* cells and the total bacterial population in casing, respectively (Samson *et al.*, 1987; Noble *et al.*, 2003; Colauto *et al.*, 2016; Fermor *et al.*, 2000), and is also dominant in compost (Siyoum *et al.*, 2016).

3. Bacterial species promoting vegetative growth and mushroom formation

3.1. *Bacterial species promoting vegetative growth of mushroom-forming fungi*

Different *Pseudomonas species* have been reported to increase mycelium growth of *A. bisporus* (Rainey, 1991a), *Pleurotus ostreatus* (Cho *et al.*, 2003) and *Pleurotus eryngii* (Kang and Cho, 2014). In the latter case, indole-3-acetic acid (IAA) was identified as the growth promoting factor produced by *Pseudomonas*. This hormone stimulates mycelial growth at nM levels but inhibits growth at mM levels.

P. putida has been reported to stimulate growth of *Agaricus* (Rainey, 1991a Colauto *et al.*, 2016), but not every strain is

effective. For instance, strain PRS2000, normally used in bioremediation, even has an inhibitory effect on *Agaricus bitorquis* (Colauto *et al.*, 2016). The increased growth rate of *A. bisporus* caused by *P. putida* is accompanied by a decrease in branching and an increase in the subapical internode length of the hyphae (Rainey, 1991a). Moreover, the branching angle of the hyphae decreases in the presence of *P. putida*, and hyphae grow parallel to each other, a phenotype that often precedes mycelial strand formation (Baars *et al.*, 2020). Indeed, mycelial strands are formed when *A. bisporus* colonises *P. putida* colonies being most pronounced and numerous in the vicinity of these bacterial colonies (Rainey, 1991a). Mycelial strands predominantly form when C/N ratios are high (Watkinson, 1975). Strands of mushroom-forming fungi like *A. bisporus* and *Serpula lacrymans* transport phosphorous (Wells and Boddy, 1995), nitrogen (Arnebrant *et al.*, 1993; Herman *et al.*, 2020), carbon (Brownlee and Jennings, 1982) and water (Jennings, 1984). Thus, *P. putida* may increase transport capacity of nutrients and water through the mycelium and, possibly, to the mushrooms as well by changing the architecture of the mycelium. How *P. putida* triggers strand formation is unknown, but the stimulation of hyphal growth only occurs when *P. putida* is in contact with the mycelium.

P. putida exhibits positive chemotaxis towards *A. bisporus* mycelial exudates, followed by hyphal attachment (Grewal and Rainey, 1991; Rainey, 1991b). This hyphal attachment is mediated by electrostatic interactions and polysaccharides from both partners (Rainey, 1991b). Sugars in the exudate do not cause the chemotactic response, while the response to individual amino acids is also weak (Grewal and Rainey, 1991). In contrast, 50% of the total chemotactic response of *P. putida* towards *A. bisporus* mycelial exudates is obtained by a combination of 14 amino acids. Yet, 1-aminocyclopropane-1-carboxylate (ACC) (see section 3.2.2) elicits the strongest chemoattractant response and has therefore been proposed to be the 'key' component stimulating *P. putida* mycelial colonisation (Li *et al.*, 2019a; Gao *et al.*, 2020).

Next to pseudomonads also other bacterial species stimulate mycelial growth of edible mushrooms by mechanisms yet to be identified. A thermophilic *Bacillus* sp. increases mycelial growth upon addition during phase III of *A. bisporus* (Tautorus and Townsley, 1983), while bacterial strains belonging to the α- and γ-Proteobacteria, the Actinobacteria and the Firmicutes stimulate vegetative growth of *Agaricus blazei* in a co-culture plate assay (Young *et al.*, 2013). *Glutamicibacter arilaitensis* MRC119 improves vegetative growth and yield of the oyster mushroom *P. ostreatus* (Kumari and Naraian, 2021), while *Micromonospora lupini* stimulates mycelial growth of *Pleurotus florid* and reduces spawn running time of sterilised rye seeds (Suarez *et al.*, 2020).

3.2. *Bacterial species promoting fruiting of mushroom-forming fungi*

It has long been established that microorganisms in the casing layer are essential for fruiting of *A. bisporus* (Eger, 1961; Park and Agnihotri, 1969; Wood, 1976). Park and Agnihotri (1969) reported that *Arthrobacter terregens*, *Rhizobium meliloti* and *Bacillus megaterium* promote mushroom production after addition to axenic casing. Culture filtrates of these bacteria gave similar results, indicating that metabolites of these microbes induce mushroom formation. Addition of biotin, gibberellic acid or IAA also had an inducing effect on mushroom formation (Park and Agnihotri, 1969). Notably, follow-up research on these bacteria in stimulation of mushroom formation of *A. bisporus* has not been reported. In contrast, the role of *P. putida* and closely related species in stimulation of white button mushroom formation has been studied in some detail.

P. putida stimulates primordium formation of *A. bitorquis* on agar medium (Colauto *et al.*, 2016) and *A. bisporus* in axenic casing (Hayes *et al.*, 1969; Fermor *et al.*, 2000; Noble *et al.*, 2009). Supplementation of sterile casing with *P. putida* n12, which was isolated from casing and which was later renamed as *P. poae* n12, results in an equivalent number of primordia when compared to non-sterile casing (Fermor *et al.*, 2000; Noble *et al.*, 2009). Adding *P. putida* to non-sterile casing increases mushroom production up to 14%. Also other *Pseudomonas* species induce primordia formation in axenic cultures (Noble *et al.*, 2009). Yet, not every *Pseudomonas* isolate exhibits stimulatory activity and the effect may depend on the *A. bisporus* strain that is used. For instance, *P. poae* n12 stimulates primordia formation of *A. bisporus* A12 to a similar extent as non-sterile casing (Fermor *et al.*, 2000), but the effect is less strong in the case of *A. bisporus* A15 (Noble *et al.*, 2009).

Alternative casing materials with sorbing properties, such as charcoal, lignite and zeolite induce mushroom formation in axenic cultures, whereas bark, coir, peat, rockwool, silica and vermiculite cannot (Eger, 1961; Fermor *et al.*, 2000; Noble *et al.*, 2003). It was therefore proposed that microorganisms such as *Pseudomonas* stimulate mushroom production by removing self-inhibitory compounds produced by the *Agaricus* mycelium (Eger, 1961; Wood, 1976; Noble *et al.*, 2003, 2009). The most important inhibitory substances appear to be 1-octen-3-ol and ethylene (Noble *et al.*, 2009; Zhang *et al.*, 2016).

3.2.1. *The role of 1-octen-3-ol as an inhibitory compound*

Some of the VOCs that are produced by *Agaricus* inhibit primordia formation, of which 1-octen-3-ol has the strongest effect (Noble *et al.*, 2009). Biosynthesis of this volatile, also known as mushroom alcohol, by mushroom forming fungi is still unclear (Karrer *et al.*, 2021). It is produced from linoleic acid via the intermediate hydroperoxy-fatty acid. Lipoxygenases and/or dioxygenases are involved as well as a predicted hydroperoxide lyase (Fig. 2). Inhibition of primordium formation is also observed when 1-octen-3-ol is added to the air stream to which *A. bisporus*-colonised compost and casing is exposed. Once 1-octen-3-ol is excluded from the air stream, mushroom production is initiated again (Noble *et al.*, 2009; Eastwood *et al.*, 2013). This VOC would control early differentiation from vegetative hyphae to multicellular hyphal knots (Eastwood *et al.*, 2013). Yet, Berendsen *et al.* (2013) showed that vegetative growth is negatively affected by high 1-octen-3-ol levels and suggested that this inhibition causes the reduction in fruiting body formation.

Pseudomonads in the casing are able to metabolise 1-octen-3-ol and can even use it as a nutrient source (Noble *et al.*, 2009; Zarenejad *et al.*, 2012; Berendsen *et al.*, 2013). Degradation of this VOC, via an unknown mechanism, would alleviate the inhibition of primordium formation. Zarenejad *et al.* (2012) isolated 274 bacterial strains from casing of

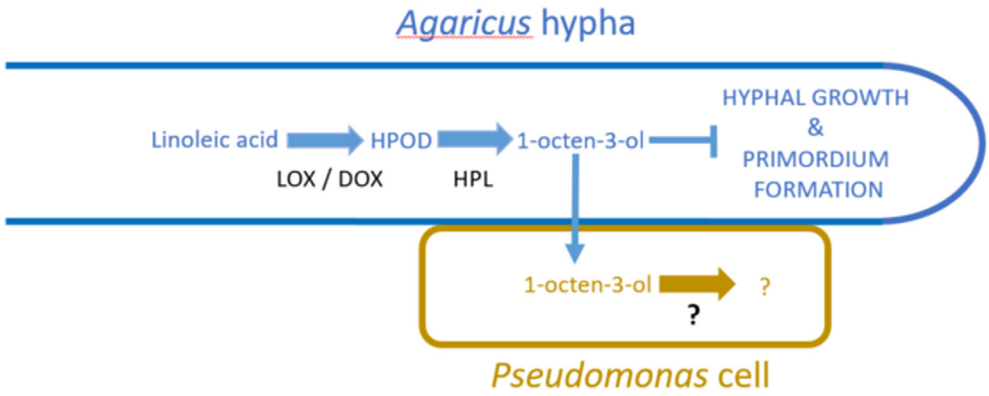

Fig. 2 – *P. putida* stimulates hyphal growth and mushroom formation by reducing *A. bisporus* 1-octen-3-ol levels. This compound is produced by *Agaricus* from linoleic acid by conversion of this fatty acid into hydroperoxy-fatty acids (HPOD) by lipoxygenases and/or dioxygenases (LOX, DOX). HPOD is cleaved by putative hydroperoxide lyases (HPL) into 1-octen-3-ol.

mushroom farms that included 23 *Pseudomonas* species. Out of these 274 bacterial isolates, 97% grew in the presence of 500 ppm 1-octen-3-ol, while 350 ppm inhibits *A. bisporus* (Eastwood *et al.*, 2013). This indicates that also other bacteria can play a role in removing this self-inhibitor of *A. bisporus*.

3.2.2. *The role of ethylene as an inhibitory compound*

The concentration of ethylene increases markedly (i.e. 10-fold) at the stage of rapid fruiting body expansion and veil-break (Turner *et al.*, 1975; Ward *et al.*, 1978; Wood and Hammond, 1977) and reduces again at later stages such as during sporulation. Ethylene is neither produced by the mushrooms (Turner *et al.*, 1975) nor by the mycelium in the casing (Ward *et al.*, 1978) but rather by the mycelium within the compost (Ward *et al.*, 1978). Addition of ethylene to compost extract agar does not affect mycelium growth or mushroom development (Ward *et al.*, 1978). However, reducing production of this VOC does impact these processes. An *A. bisporus* strain with antisense downregulation of the ethylene biosynthesis enzyme 1-aminocyclopropane-1-carboxylate oxidase (ACO) (Fig. 3) shows faster mycelial growth in sterilised compost than the wild-type and forms, in contrast to the wild-type strain, primordia in sterilised compost topped with sterilised vermiculite (see below) (Zhang *et al.*, 2016). Ethylene has been proposed to mediate its effect by reducing production of reactive oxygen species (ROS) (Chen *et al.*, 2013). Indeed, downregulation of NADPH oxidase genes that encode ROS producing enzymes in *Ganoderma lucidum* results in increased hyphal branching, a decreased fungal growth rate and the inability to form primordia (Mu *et al.*, 2014).

Inspired by the observation that methionine stimulates ethylene production in *Agaricus* mycelium (Ward *et al.*, 1978), Chen *et al.* (2013) proposed that this fungus has a similar ethylene biosynthesis pathway as higher plants (Fig. 3). In higher plants, methionine is converted in S-adenosyl-L-methionine (SAM) by SAM synthetase. SAM is subsequently transformed into ACC by ACC synthase (ACS), which is oxidised by ACC oxidase (ACO) to ethylene (Polko and Kieber, 2019). Indeed, two ACS genes and one ACO gene have been identified in *A. bisporus* (Zhang *et al.*, 2016). Moreover, Chen *et al.* (2013) were able to manipulate ethylene and ACC levels in *A. bisporus* by adding 5 mM amino-oxyacetic acid (inhibitor of ACS), cobalt (inhibitor of ACO), methionine or ACC to the substrate.

Fluorescent pseudomonads produce ACC deaminase (AcdS) that catalyses the cleavage of ACC to ammonia and α-ketobutyrate (Wang *et al.*, 2001) (Fig. 3). AcdS-producing bacteria are able to use ACC as a sole nitrogen source, thereby reducing plant ethylene levels (Li *et al.*, 2019a). As a consequence, plant growth is promoted and plant resistance to a variety of environmental stresses is increased (Polko and Kieber, 2019). Similarly, AcdS-producing pseudomonads may be involved in primordium initiation by reducing ethylene levels of the *A. bisporus* mycelium (Chen *et al.*, 2013). Indeed, co-culturing of an $AcdS^+$ wildtype *P. putida* strain reduces ethylene levels produced by *A. bisporus* and increases its hyphal growth rate, subapical internode length and dry weight. Furthermore, this strain induces abundant primordia when added to sterilised casing soil (Chen *et al.*, 2013). An $AcdS^-$ strain of *P. putida* shows opposite effects. The presence of the mutant results in a 59-fold higher ethylene level produced by *Agaricus*, which is accompanied by reduced hyphal growth rate, subapical internode length and dry weight. Moreover, the primordia count in sterilised casing in the presence of this bacterial strain is even lower when compared to its absence (Chen *et al.*, 2013). The introduction of the *P. putida acdS* gene into *A. bisporus* resulted in transformants with AcdS enzyme activity and a reduced ACC and ethylene content (Zhang *et al.*, 2019b). Concomitantly, mycelium growth rate on spawn and compost was up to 25% faster than wild-type *A. bisporus*. In addition, primordia of the *acdS* transformants were formed 3–5 days sooner and grew in higher abundance (up to 84% more primordia than wild-type) (Zhang *et al.*, 2019b). Together, production of AcdS by *P. putida* can exert a strong promoting effect on *Agaricus* hyphal growth and mushroom initiation (Fig. 3). This effect is not restricted to *Agaricus*; Dong *et al.* (2010) reported that a *Pseudomonas* strain that is closely related to *P. putida* promotes mycelial growth, mushroom initiation and fruiting body yield of *P. ostreatus*, *P. eryngii* and *Coprinus comatus*. AcdS was proposed to be responsible for these effects by decreasing ethylene synthesis. Other bacteria also produce this enzyme, including species from *Proteobacteria*,

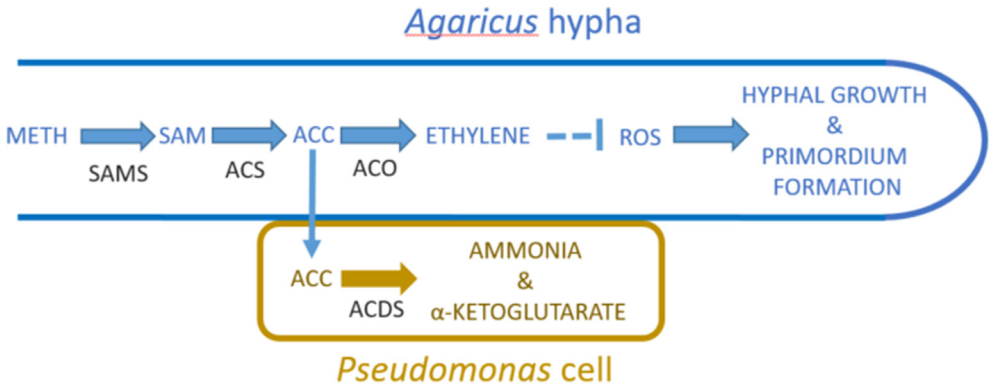

Fig. 3 – *P. putida* stimulates hyphal growth and mushroom formation by reducing *A. bisporus* ethylene levels. ACC produced by the fungus is taken up by the bacterium and converted into ammonia and α-ketoglutarate catalyzed by ACC deaminase (redrawn from Zhang *et al.*, 2019b). It has been proposed that ethylene reduces ROS levels, thereby inhibiting primordium formation. Meth: methionine, SAM: S-adenosyl-L-methionine, ACC: 1-aminocyclopropane-1-carboxylate, SAMS: SAM synthetase, ACS: ACC synthase, ACO: ACC oxidase, AcdS: ACC deaminase.

Flavobacteria, *Actinobacteria*, *Firmicutes* and *Bacteroidetes* (Gontia-Mishra *et al.*, 2017; Polko and Kieber, 2019). For instance, *Serratia rubidaea*, *Klebsiella pneumoniae* and *Bacillus cereus* were identified as the dominant AcdS-producing bacteria in the clay loam sub casing soil (Chen *et al.*, 2013). Thus, depending on the substrate other microbes can replace *P. putida* to reduce ethylene levels.

Accumulating evidence indicates that ACC is not only a precursor of ethylene in plants but also functions independently as a signalling molecule (Polko and Kieber, 2019). This seems not to be the case for growth and mushroom development in *A. bisporus*. Reducing ACO enzyme activity in *A. bisporus* by antisense constructs results in reduced ethylene production and increased ACC content. This is accompanied by faster hyphal growth in sterilised compost and induction of primordia in a sterile vermiculite casing layer (Zhang *et al.*, 2016). Moreover, a particular antisense *ACO* strain even produces close to 80% more primordia than the wild-type strain in non-sterile soil casing.

Stored mushrooms produce substantial levels of ethylene, which accelerates mushroom ripening and senescence and induces softening, browning and weight loss in post-harvest mushrooms (Li *et al.*, 2019b; Ni *et al.*, 2021). Notably, fresh fruiting bodies do not emit detectable levels of ethylene and are colonised by *P. putida* (Turner *et al.*, 1975), whereas post-harvest mushrooms that produce high levels of ethylene are not colonised by this bacterium (Siyoum *et al.*, 2016). This finding suggests that *P. putida* preserves mushroom caps by degrading ethylene.

4. Bacteria that protect against pathogens

Some bacterial species increase the yield of *A. bisporus* directly by promoting vegetative growth and mushroom formation (see section 3), while other species do so indirectly by inhibiting bacterial and fungal pathogens of *A. bisporus*. As examples, we will discuss bacteria that control the causative agents of bacterial blotch, green mould and dry bubble disease.

4.1. *Bacterial blotch disease*

Bacterial blotch disease is the most important disease of commercial mushrooms in terms of economic loss and global prevalence (Osdaghi *et al.*, 2019). It not only affects *Agaricus* but also, for instance, *P. ostreatus*, *P. eryngii* and *Flammulina velutipes* (Gonzáles *et al.*, 2009; Han *et al.*, 2012; Zhang *et al.*, 2013). In the case of *A. bisporus*, this disease causes discoloration of mature mushroom caps and, in severe cases, pitting and the formation of deep brown sunken lesions on the mushroom surfaces. Blotch disease is actually a group of diseases caused by different *Pseudomonas* species, of which *Pseudomonas tolaasii* is most known for causing brown blotch disease in *A. bisporus* (Tolaas, 1915). This pathogen is difficult to control as it is ubiquitous in compost and casing and can rapidly switch from a saprotrophic to a pathogenic form (Kertesz and Thai, 2018; Osdaghi *et al.*, 2019; Soler-Rivas *et al.*, 1999a). Other pseudomonads causing brown blotch disease are *Pseudomonas costantinii* (Munsch, 2002) and *Pseudomonas reactans* (Navarro *et al.*, 2018). *Pseudomonas agarici* can also cause brown discolorations (Geels *et al.*, 1994) but is also the causal agent of yellow blotch or drippy gill (Young, 1970). On the other hand, *Pseudomonas gingerii* causes ginger blotch (Wells *et al.*, 1996). Genome sequencing of bacteria isolated from affected cap tissue found in Western Europe has revealed a growing number of additional pseudomonads that can cause bacterial blotch disease. For instance, *Pseudomonas yamanorum*, *Pseudomonas edaphica* and *Pseudomonas salomonii* have been identified as novel bacterial blotch pathogens of *A. bisporus* (Taparia *et al.*, 2020).

While various pseudomonads cause bacterial blotch, other *Pseudomonas* species can control these pathogens. The capability of *Pseudomonas* species to effectively control bacterial blotch has mainly focused on suppression of *P. tolaasii*. Several pseudomonads including *P. putida*, *P. fluorescens* and *P. reactans* can reduce bacterial blotch up to 100% (Fermor *et al.*, 1991; Tajalipour *et al.*, 2014; Aslani *et al.*, 2018; Ghasemi *et al.*, 2020). The biocontrol effect likely involves competition for space and nutrients, as effective control mainly takes place when antagonists are applied before *P. tolaasii* is present at levels high

enough to cause disease (Fermor *et al.*, 1991). Inactivation of the main virulence factor of the pathogen, the lipodepsipeptide toxin tolaasin that induces brown blotch, is another mechanism (Fig. 4). The lipodepsipeptide WLIP (White-Line-Inducing-Principle) produced by *P. reactans* forms a precipitate with tolaasin. This leads to the formation of a white line between the two bacteria and has been used a test for the identification of *P. tolaasii*. Pre-treatment of mushroom caps with purified WLIP can prevent the symptoms of brown blotch caused by *P. tolaasii*, and has been proposed to act via sequestering of tolaasin (Soler-Rivas *et al.*, 1999b) (Fig. 4). However, WLIP is also toxic to various mushrooms, including *Agaricus* and *Pleurotus*, although less active compared to tolaasin (Lo Cantore *et al.*, 2006), making the compound and *P. reactans* less suitable for disease control. Bacteria of the genus *Mycetocola* also detoxify tolaasin and are able to suppress brown botch disease in *A. bisporus* and *P. ostreatus* (Tsukamoto *et al.*, 1998) They produce enzymes that cleave tolaasin resulting in an inactive linear form of the molecule (Hermenau *et al.*, 2020) (Fig. 4). In addition, *Mycetocola* spp. cleave a second cyclic lipopeptide required for swarming, named pseudodesmin, thereby blocking motility of the pathogen (Hermenau *et al.*, 2020) (Fig. 4). Other bacterial genera associated with wild mushrooms (i.e. *Bacillus*, *Pedobacter* and *Sphingobacterium*) have also been identified as tolaasin detoxifying bacteria and are able to suppress brown blotch disease on cultivated *P. ostreatus* and *A. bisporus in vitro* (Tsukamoto *et al.*, 2002).

Different bacteria isolated from wild fungi, including two *Pseudomonas* strains, produce VOCs that are able to reduce brown blotch symptoms on mushroom caps, although at various levels (Ghasemi *et al.*, 2021). The VOCs inhibit growth, affect morphology, and reduce swarming motility, hemotaxis and biofilm formation of *P. tolaasii* (Fig. 4). The main VOC produced by these *Pseudomonas* strains is octamethylcyclotetrasiloxane, which is a well-known antimicrobial compound. N-tetradecane and n-hexadecane are other VOCs produced by the bacteria that are known to have antimicrobial activity (Ghasemi *et al.*, 2021).

4.2. *Green mould disease*

Trichoderma aggressivum is the causative agent of green mould in *A. bisporus*. It is not a pathogen but rather a competitor of *Agaricus* (Seaby, 1996). Mushroom compost infected with the mould often appears normal even two weeks after inoculation with *A. bisporus*. After this, however, the compost turns dark green due to sporulation of *Trichoderma* (Rinker, 1996), which may be associated with brown spots on the mushroom caps and huge crop losses (Kosanovic *et al.*, 2020). One study assessed the interaction of *P. putida* and *P. tolaasii* with *T. aggressivum* (Kosanovic *et al.*, 2020). *P. tolaasii* culture supernatant inhibits *Trichoderma* growth by 57%, which may be due to the tolaasin toxin. In contrast, *P. putida* culture supernatant stimulates *T. aggressivum* growth by 44%. The ability of *P.*

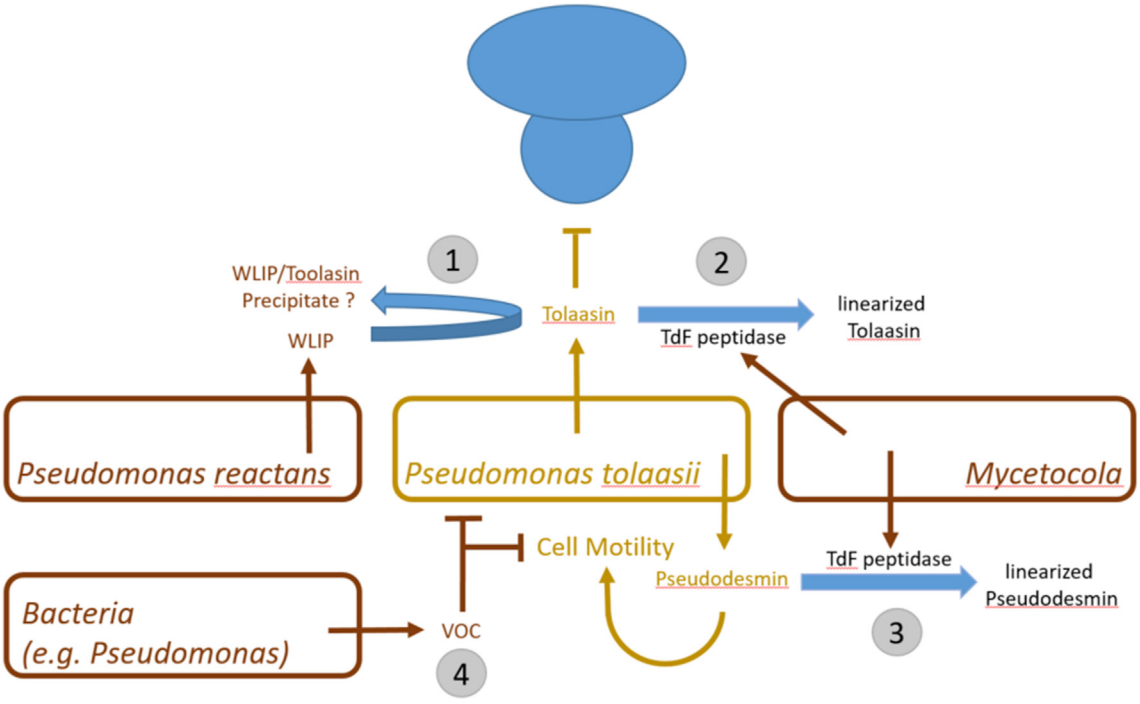

Fig. 4 – Pathogenicity of *P. tolaasii* can be inhibited by other bacteria via different mechanisms. Tolaasin may be inhibited by other cyclic lipodepsipeptides, such as the white line inducing principle molecule WLIP that is secreted by pseudomonads like *P. reactans* (1). Tolaasin can also be cleaved by peptidases that are secreted by *Mycetocola*, which results in an inactive linear form of the toxin (2). Similarly, such peptidases can linearize the swarming lipopeptide pseudodesmin. As a result, motility of the pathogen in inhibited (3). Motility can also be inhibited by VOC's that are released by different bacterial species, including Pseudomonads (4). These VOC's can also impact other processes of *P. tolaasii* such as growth and biofilm formation.

putida to reduce the amount of 1-octen-3-ol (see section 3.2.1) may stimulate the growth of *T. aggressivum* (Berendsen *et al.*, 2013). Thus, both *P. tolaasii* and *P. putida* do not seem to be the biocontrol agent of choice for green mould disease by being pathogenic for *Agaricus* or by increasing growth of *T. aggressivum*, respectively. In contrast, *Bacillus velezensis* QST713 can be used to control *T. aggressivum*. A commercial product based on this bacterial strain is on the market in France and reduces yield loss due to *T. aggressivum*, while not affecting growth of *Agaricus* (Pandin *et al.*, 2018). The bacterium produces two lipopeptides, surfactin and fengycin, that are upregulated in response to *T. aggressivum* (Pandin *et al.*, 2019). Also other *Bacillus* species have antagonistic *in vitro* and *in vivo* activity against *T. aggressivum* (Tautorus and Townsley, 1983; Nagy *et al.*, 2012; Milijašević-Marčić *et al.*, 2017; Stanojević *et al.*, 2019). In some instances this activity has been shown to correlate with fengycin production (Nagy *et al.*, 2012).

4.3. *Dry bubble disease*

Lecanicillium fungicola is a pathogen of *A. bisporus*, *A. bitorquis* and *P. ostreatus*. It causes dry bubble disease in the case of *A. bisporus*, resulting in different symptoms depending on the time of infection (Berendsen *et al.*, 2010). Necrotic lesions on the mushroom cap surface may form when infection occurs late in mushroom development, while early infection may result in partially deformed fruiting bodies with often peeled or split mushroom stipes (called stipe-blow-out). Mushrooms may even deform completely forming masses of undifferentiated mushroom tissue, called dry bubbles.

Berendsen *et al.* (2012) investigated the potential of fluorescent pseudomonads isolated from *A. bisporus* casing to control dry bubble disease. *In vitro*, the fluorescent pseudomonads exhibited antagonistic activity towards *L. fungicola* both by siderophore-mediated competition and by antibiotic production. However, none of the isolated *Pseudomonas* strains effectively suppressed the disease *in vivo*. Similar to the situation with green mould disease, the suppression may be counteracted by the ability of the *Pseudomonas* strains to reduce the amount of 1-octen-3-ol (see section 3.2.1) that normally inhibits germination of *L. fungicola* spores (Berendsen *et al.*, 2013). Thus, like in green mould disease pseudomonads are inadequate to control dry bubble disease in *A. bisporus*. Interestingly, different *Bacillus* strains show antagonistic activity against *L. fungicola in vitro* while not affecting growth of *Agaricus* (Stanojević *et al.*, 2019), but their suitability as control agent for dry bubble disease *in vivo* remains to be determined.

5. Conclusion

Insight in the composition and dynamics of the microbial community of casing, compost and mushrooms can help to control quality of these products. Moreover, it may optimise and speed up mushroom production, reduce the impact of mushroom diseases, and offer leads for replacing non-renewable peat as a casing material.

Our understanding of the complexity and dynamics of the microbial community during mushroom cultivation has increased due to advances in culture-independent sequencing techniques. However, the interpretation of data is hampered by the variability of the culture conditions and a lack of standardization in data analysis. Moreover, most studies are based on amplicon sequencing that only gives information about the composition of the community but not about its activity. Other approaches, such as shotgun metagenomics, transcriptomics, and metabolomics do give such functional information and may in the future result in a better understanding of the factors that shape the microbial community and the function of the bacteria in mushroom cultivation.

Adding bacteria at different phases during cultivation is a promising strategy to increase productivity. They may act directly by stimulating vegetative growth and mushroom formation or indirectly by inhibiting pathogens. Pseudomonads are historically recognised as essential mushroom growth-promoting microbes during *A. bisporus* cultivation (Osdaghi *et al.*, 2019). The first mechanisms underlying these positive interactions have been unravelled. Removal of the self-inhibitory substances 1-octen-3-ol and ethylene that are produced by *A. bisporus* mycelium seems to be important mechanisms through which beneficial pseudomonads promote vegetative growth and primordia formation (Noble *et al.*, 2009; Berendsen *et al.*, 2013; Zhang *et al.*, 2019b). This mechanisms appears not to be restricted to *Pseudomonas* and *Agaricus*, but relevant for other bacteria and edible mushrooms.

Different bacterial genera, such as *Mycetocola* spp, have potential to control brown blotch disease caused by *P. tolaasii* during cultivation of *Agaricus* and *Pleurotus* (Fermor *et al.*, 1991; Tsukamoto *et al.*, 1998; Ghasemi *et al.*, 2020; Tajalipour *et al.*, 2014; Aslani *et al.*, 2018). They act by detoxifying tolaasin (Hermenau *et al.*, 2020) and by inhibiting growth and motility of *P. tolaassi* (Hermenau *et al.*, 2020; Ghasemi *et al.*, 2021). *Pseudomonas* species are less suitable for suppression of Green mould and Dry bubble disease caused by fungal pathogens. In fact, some beneficial pseudomonads may even stimulate these diseases by lowering 1-octen-3-ol levels that normally inhibit the pathogens to grow (Carrasco *et al.*, 2019; Kosanovic *et al.*, 2020). *Bacillis* species have been used to control these fungal pathogens, and a commercial product based on *Bacillus velezensis* QST713 is on the market (Pandin *et al.*, 2018). Disease suppression may involve the production of antifungal lipopetides that are active against the pathogenic fungi without harming *Agaricus* (Pandin *et al.*, 2019). Understanding the mode of action of these compounds and their specificity will contribute to the future use of bacterial biocontrol against fungal pathogens.

Most of our understanding on the positive interactions between bacteria and edible mushrooms comes from studies on a limited number of bacterial species and mushrooms. Studying other bacteria from microbial communities during cultivation of diverse edible mushrooms is expected to lead to various microbes that can be used to promote vegetative growth and mushroom formation. Moreover, understanding the mechanisms behind positive interactions may help to identify new strains as well as leads to develop supplements that can be added during cultivation.

Declaration of competing interest

The authors declare not to have competing interests.

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