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MINI-REVIEW

Compost bacteria and fungi that influence growth and development of *Agaricus bisporus* and other commercial mushrooms

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Abstract

Mushrooms are an important food crop for many millions of people worldwide. The most important edible mushroom is the button mushroom (*Agaricus bisporus*), an excellent example of sustainable food production which is cultivated on a selective compost produced from recycled agricultural waste products. A diverse population of bacteria and fungi are involved throughout the production of *Agaricus*. A range of successional taxa convert the wheat straw into compost in the thermophilic composting process. These initially break down readily accessible compounds and release ammonia, and then assimilate cellulose and hemicellulose into compost microbial biomass that forms the primary source of nutrition for the *Agaricus* mycelium. This key process in composting is performed by a microbial consortium consisting of the thermophilic fungus *Mycothermus thermophilus* (*Scytalidium thermophilum*) and a range of thermophilic proteobacteria and actinobacteria, many of which have only recently been identified. Certain bacterial taxa have been shown to promote elongation of the *Agaricus* hyphae, and bacterial activity is required to induce production of the mushroom fruiting bodies during cropping. Attempts to isolate mushroom growth-promoting bacteria for commercial mushroom production have not yet been successful. Compost bacteria and fungi also cause economically important losses in the cropping process, causing a range of destructive diseases of mushroom hyphae and fruiting bodies. Recent advances in our understanding of the key bacteria and fungi in mushroom compost provide the potential to improve productivity of mushroom compost and to reduce the impact of crop disease.

Keywords *Agaricus bisporus* · Button mushroom · *Pleurotus* · Compost · Thermophilic fungi · *Pseudoxanthomonas* · *Mycothermus*

Introduction

Cultivated mushrooms are an important food source for many people around the world, with global production estimated at over 10 million tons per year (Food and Agriculture Organization of the United Nations 2014). Over two thirds of the production of edible mushrooms are harvested in mainland China, where mushrooms form a more traditional role in food and medicine than they do in many Western countries, and where they provide a living for over 25 million mushroom farmers (Zhang et al. 2014b). The most important edible mushroom genus grown commercially is *Agaricus* (mainly *Agaricus bisporus*, the button mushroom), which makes up about 30% of the global market (Royse 2014). Other important edible genera include *Pleurotus* (5–6 species of oyster mushrooms that are cultivated commercially), *Lentinula* (shiitake), *Auricularia* (3–4 species of woodear mushrooms), *Flammulina* (enoki), and *Volvariella* (paddy straw). Edible mushroom production is dominated by a few species where the technology for large-scale industrial cultivation has been optimized (Chang and Miles 2004), but in many countries large numbers of small-scale farms also exist, and there are increasing attempts to domesticate local wild mushrooms for production purposes (Mwai and Muchane 2016).

Cultivated mushrooms are saprophytes which grow by degrading natural lignocellulosic substrates, which are commonly available in large volumes as agricultural or industrial byproducts. The methods for commercial cultivation of

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mushrooms on these substrates can be divided into three broad groups. The first group includes cultivation of many wood-degrading mushrooms that were traditionally grown on wood logs or harvested from trees. Some of these, such as *Lentinula*, are now grown on artificial logs of compacted, sterilized sawdust, while others, such as *Flammulina*, *Pholiota* (nameko), or *Auricularia* are cultivated on a partly composted mixture of sawdust and other components (bran, straw, corncobs), which is sterilized at high temperature (121 °C) before inoculation with mycelium (Chang and Miles 2004; Sanchez 2010). Because of the rigorous sterilization process, these mushrooms are essentially grown in axenic culture. The second group of cultivation methods either uses uncomposted substrates directly, or uses partially composted substrates that have not been subjected to a rigorous sterilization process. This includes methods commonly used for *Pleurotus* and *Volvariella* species, though *Pleurotus* is also sometimes grown on sterilized sawdust substrates. These are fast-growing and adaptable genera capable of rapid bioconversion of a broad range of substrates (e.g., rice straw, bagasse, cornstalks, waste cotton, stalks, and leaves of bananas (Chang and Miles 2004; Thongklang and Luangharn 2016). The substrates are usually not sterilized before inoculation, though a pasteurization step may be included in the process, and the mushrooms therefore grow in competition with other microorganisms on the substrate. The most industrially complex process is the cultivation of *Agaricus*, which is grown on a pasteurized straw-based compost which requires lengthy preparation, but allows selective growth of the *Agaricus* mycelium over competitor organisms.

For mushrooms grown in fully sterilized substrates, such as *Lentinula*, the rate of mycelium growth is dependent on enzymatic degradation of lignocellulose by the mushroom itself and is independent of other microbes. Addition of particular bacteria or other fungi could potentially stimulate either growth or fruiting, but this has not been investigated in any depth. For *Pleurotus* and *Agaricus*, by contrast, growth of the mycelium and production of the commercial fruiting body are dependent not only on the mushroom itself, but also on bacteria and other fungi in the substrate. These bacteria and fungi play critical roles at several different stages of production (Fig. 1), including (i) conversion of the lignocellulose feedstocks into a selective, nutrient-rich compost for mushroom growth; (ii) interactions with the fungal mycelium during hyphal elongation and proliferation through the substrate; and (iii) induction of fruiting body formation during cropping. In addition, several bacterial and fungal taxa act as pathogens of the mushroom crop, causing either a reduction in yield or severe loss of quality.

This review will focus primarily on the importance of bacteria and fungi in mushroom compost during the production of *Agaricus bisporus* and *Pleurotus ostreatus*. Several excellent reviews are available that discuss bacterial-fungal interactions in a range of other environmental, agricultural, and clinical areas (Frey-Klett et al. 2011; Kobayashi and Crouch 2009; Scherlach et al. 2013). A number of other studies provide overviews of the composting of general municipal and agricultural wastes (Chandna et al. 2013; De Gannes et al. 2013a, b; Hultman et al. 2010; Partanen et al. 2010), and highlight the influence of feedstocks and process parameters on fungal and bacterial diversity and succession in the resulting composts (Neher et al. 2013).

Diversity and succession of bacteria and fungi in mushroom compost

A. bisporus is commercially grown on a composted substrate prepared in a thermophilic, microbial process from wheat straw and/or horse stable bedding, nitrogen-containing additives, the most common which are poultry manure, seed meal, or synthetic nitrogen (urea or ammonium nitrate), and gypsum (Chang and Miles 2004; Royse and Beelman 2016; Straatsma et al. 2000) (Fig. 1). The wheat straw is usually soaked for 3–10 days before mixing with the other feedstocks (Noble and Gaze 1996), and then subjected to a period of aerobic, thermophilic composting (phase I) during which the compost temperature rapidly rises to 80 °C due to microbial activity (Straatsma et al. 2000; Zhang et al. 2014a). Phase I can take up to 14 days to complete (Noble et al. 2002) but can be completed as quickly as 6 days (Weil et al. 2013), and serves primarily for growth of the microbial population at the expense of soluble components of the feedstocks, since there is relatively little decrease in the total content of complex carbohydrates (cellulose, hemicellulose) or lignin (Jurak et al. 2015). In phase II, the compost is held at 58–60 °C for 2 days in tunnels that are designed to provide uniform temperature and airflow into the compost (Noble and Gaze 1996), followed by a "conditioning" or "curing" period, in which the compost is maintained at 48–51 °C for 2–3 days (Straatsma et al. 2000). This is a period of intense microbial activity, and by the end of phase II, 50–60% of the cellulose and hemicellulose in the original feedstocks has been degraded (Jurak et al. 2015). During the same period, the excess ammonia released during the thermophilic phase has been assimilated by the microbial biomass in the compost (Miller et al. 1991; Wiegant et al. 1992). The microbial community present at the end of phase II represents a climax community, into which *A. bisporus* is introduced, usually as grain spawn grown on millet or rye. The mycelium of *Agaricus* takes approximately 16 days to fully colonize the mature compost (Jurak 2015; Royse and Beelman 2016), initially utilizing bacterial and fungal biomass as a key source of nutrition and then progressively breaking down over 50% of the lignin (Jurak et al. 2015).

Although it is possible to grow *A. bisporus* mycelium on non-composted wheat straw, yields are low and the process is

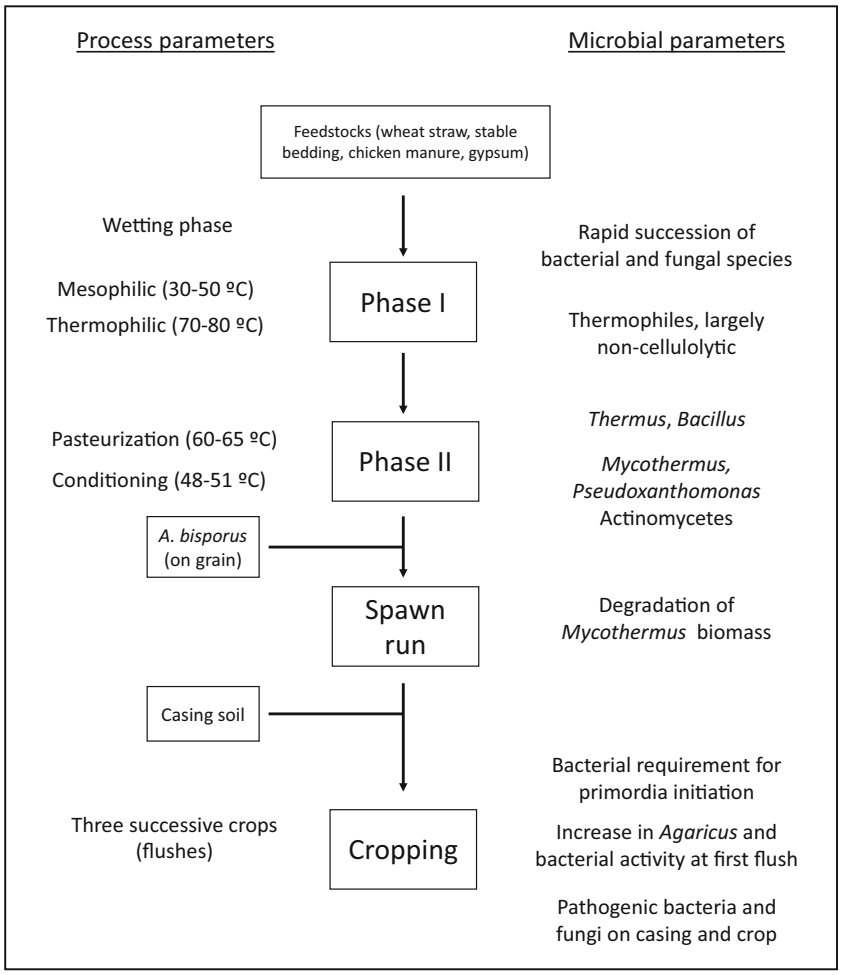

Fig. 1 Overview of composting and cropping for *Agaricus bisporus* highlighting the importance of bacteria and fungi in the process

not used commercially (Mamiro et al. 2007). The composting process provides specificity for *Agaricus* cultivation because it converts the wheat straw into a mixture of microbial biomass and humus-lignin complexes which are not available to competing fungi, but which *Agaricus* can access by degrading living and dead thermophilic fungal and bacterial biomass (Bilay and Lelley 1997; Fermor et al. 1991; Straatsma et al. 1994b; Vos et al. 2017). The selectivity for *Agaricus* can be removed by artificial lysis of phase II compost biomass (chemical treatment or prolonged high temperatures), which allows many other contaminant ascomycetes to grow. However, if the sterilized compost is reconditioned by adding microbes that bind the released nutrients into fresh microbial biomass, then the selectivity for *Agaricus* can be restored (Ross and Harris 1983a; Straatsma et al. 1989).

The microbes in mushroom compost are introduced with the feedstocks, though they can also be enriched by the use of recycled compost leachate (sometimes called "goody water") in the wetting process (Kertesz and Safianowicz 2015). A clear succession is seen in the mushroom compost community, which has been studied by cultivation-based analysis (Hayes 1968; Ryckeboer et al. 2003; Singh et al. 2012; Siyoum et al. 2016) and by a number of cultivation-independent techniques, including fingerprinting methods (Wang et al. 2016) coupled to DNA sequencing methods (Siyoum et al. 2016; Szekely et al. 2009; Vajna et al. 2010, 2012) and, most recently, by metagenomic or amplicon sequencing of bacterial and fungal communities (Kertesz et al. 2016; Langarica-Fuentes et al. 2014; McGee et al. 2017; Souza et al. 2014; Zhang et al. 2014a). Most of these studies have been done on *Agaricus* compost, though partially composted *Pleurotus* compost has also been examined (Vajna et al. 2010, 2012). Cultivation-based analysis of phase I compost has yielded largely actinobacterial and *Bacillus* isolates [reviewed in (Ryckeboer et al. 2003)], but this method provides a very limited window on the microbial diversity present, since many compost bacteria and fungi are not readily cultivable, Many studies have also focused on single time points within the composting process, providing a limited overview. More recent DNA sequencing studies have provided evidence for the presence of a wealth of other microbes in compost and their succession, with a broad range of phyla involved (Fig. 2). The most dramatic changes in microbial populations in compost occur during the initial wetting period

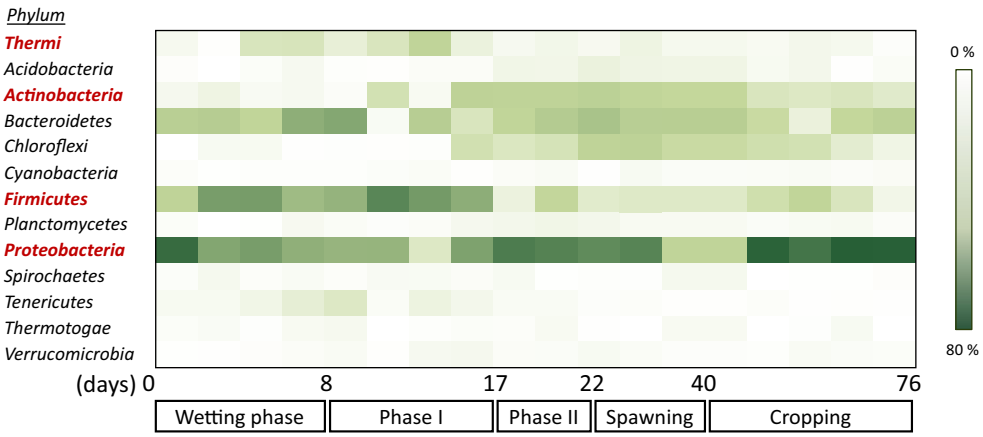

Fig. 2 Bacterial phylum succession in mushroom compost during composting, spawn run, and cropping of *Agaricus bisporus*. Bacterial communities were determined by Illumina Miseq sequencing of the 16S rRNA gene (Kertesz et al. 2016). The heat map shows relative sequence abundance of the indicated phyla at different stages of the process

and during phase I (Kertesz et al. 2016). This period sees rapid assimilation of easily accessible nutrients such as free sugars and amino acids from the compost, and the changes in the most abundant bacteria probably reflect the rapid succession of bacteria and fungi that can use these compounds. Initially, these are mesophilic pioneer organisms such as *Solibacillus*, *Comamonas*, *Acinetobacter*, *Pseudomonas*, and *Sphingomonas* (Kertesz et al. 2016; Vajna et al. 2012).

As temperatures begin to increase in phase I, peaks are seen in populations of thermophilic *Bacillus*, *Paenibacillus*, and uncharacterized Clostridia and Proteobacteria. The most abundant actinobacteria present are *Corynebacterium* and *Streptomyces* (Zhang et al. 2014a) and, although they make up only a small fraction of the total bacterial population, analysis of the cellulase gene diversity reveals that these actinobacteria are cellulolytic (Zhang et al. 2014a). The taxon evenness in the compost increases to reach a maximum at the end of phase I, with an increase in thermophilic taxa. *Thermus thermophilus* is a key member of the bacterial population at this point (Kertesz et al. 2016; Szekely et al. 2009), and Thermi are relatively important, though they disappear again later during composting (Fig. 2).

The dynamics of fungal diversity are similar to the bacteria changes during phase I. Initial pioneers such as *Lewia*, *Rhizomucor*, and *Aspergillus* are overgrown by *Talaromyces*, *Thermomyces*, *Thermus*, and unclassified taxa as temperature and pH rise (Kertesz et al. 2016; Straatsma et al. 1994b). Most of these organisms are not cellulolytic although some of them will break down hemicellulose, and cellulose and hemicellulose are indeed only marginally depleted during phase I (Jurak et al. 2014). Pioneer fungi grow by utilizing other carbon sources in the compost, and once these alternative carbon sources are exhausted, the fungal population is replaced by cellulose degraders such as *Mycothermus thermophilus* and *Chaetomium thermophilum*, with *M. thermophilus* being the climax species in phase II compost (Kertesz et al. 2016; Souza et al. 2014).

Mycothermus (Scytalidium) and other thermophilic microbes—nutrition for *Agaricus*

During phase II, the microbial community dynamics change completely with rapid succession of different genera appearing in phase I being replaced by a comparatively stable microbial community during conditioning. The dominant fungal species during the conditioning process is *M. thermophilus* [previously *Scytalidium thermophilum* or *Torula thermophila* (Natvig et al. 2015)]. This species is a thermophilic, cellulolytic ascomycete which is a dominant component of many composting systems and plays an important role in degradation of polymeric carbohydrates. Isolates of this species from compost secrete a suite of over 60 different cellulases, hemicellulases, and other glycosyl hydrolases (Basotra et al. 2016).

The importance of thermophilic bacteria and fungi in mushroom compost production was recognized very early (Chanter and Spencer 1974; Eicker 1977; Stanek 1972). Thermophilic fungi, in particular, grow rapidly during the conditioning period, removing free nutrients from the compost and assimilating the ammonia released by ammonification (Ross and Harris 1983b). This physiological activity provides a selective environment for growth of *Agaricus* by immobilizing nutrients in a form unavailable to competitor molds (Ross and Harris 1983a). Unlike competing ascomycetes, the *Agaricus* mycelium aggressively decomposes both living and dead bacterial and fungal biomass to obtain the nutrients it requires (Fermor and Wood 1991). This has been shown by growth of *Agaricus* on [^{14}C]-labeled *Bacillus subtilis* cells leading to direct uptake of the isotope into the fungal mycelium (Fermor et al. 1991). *Agaricus* also disintegrated *Mycothermus* cultures on agar medium even through a layer of cellophane, causing complete loss of viability in the latter fungus (Op den Camp et al. 1990). In a cropping setting, the amount of living bacterial biomass in phase II compost (measured as phospholipid fatty acids) decreases by about 75% after addition of *Agaricus* and the

abundance of thermophilic fungal biomass also decreases dramatically (Vos et al. 2017). The mycelium of *Agaricus* seems to be partly selective for *Mycothermus* and does not degrade other thermophilic fungi so effectively (Straatsma et al. 1994b), but the reasons for this are not known.

Bacterial diversity in phase II compost has traditionally been thought to be dominated by cellulolytic actinomycetes and bacilli (Ryckeboer et al. 2003). Recent cultivation-independent studies have shown a peak in *Actinobacteria* at this stage (Fig. 2) and have identified *Thermomonospora*, *Thermobispora*, *Thermopolyspora*, *Thermobifida*, and *Microbispora* as key genera (Silva et al. 2009; Szekely et al. 2009; Vajna et al. 2012; Zhang et al. 2014a). However, the most abundant bacterial taxon in both *Agaricus* and *Pleurotus* compost is *Pseudoxanthomonas taiwanensis*, together with *Thermus* and several bacilli (*Bacillus*, *Geobacillus*, *Ureibacillus*) (Kertesz et al. 2016; Vajna et al. 2012).

P. taiwanensis is only present in low numbers in phase I, because although it is thermophilic, its optimum growth is at 50 °C, and it does not grow above 65 °C (Chen et al. 2002). The population of *P. taiwanensis* increases as the temperature falls during compost conditioning and it is the most abundant bacterial species in mature compost (Kertesz et al. 2016; Szekely et al. 2009; Vajna et al. 2012). As a heterotrophic nitrifier, it is able to convert ammonia into N_2O (Chen et al. 2002), but how important this activity is in removing the abundant ammonia in phase II compost is not yet known. Unexpectedly, *P. taiwanensis* does not appear to break down cellulose, though it produces β-glucosidase and can utilize cellobiose (Chen et al. 2002; Kato et al. 2005). Nevertheless, it has been detected repeatedly as an essential component of stable cellulose-degrading consortia isolated from a variety of sources (Du et al. 2015; Kato et al. 2004, 2005; Wang et al. 2011), and efficient degradation of lignocellulose in bioethanol production, for example, relied on optimization of the *P. taiwanensis* abundance (Du et al. 2015). In one of these consortia, it seems to play its essential role by interacting with a cellulolytic species of *Clostridium* (Kato et al. 2004, 2005), and in mushroom compost, it may well be interacting in a similar way with *Mycothermus*. This is underlined by the fact that its abundance in phase II compost appears to increase in parallel to that of *Mycothermus* (Kertesz et al. 2016), but further studies are required to confirm the relevance of this finding.

Because the presence of thermophilic fungi can promote the growth rate of *Agaricus* mycelium up to two fold (Straatsma et al. 1994a), this fungal group, and in particular *M. thermophilus*, has been studied extensively as an inoculum to promote compost preparation and accelerate *Agaricus* growth (Bilay 2000; Sanchez et al. 2008; Sanchez and Royse 2009; Straatsma et al. 1994a; Wiegant et al. 1992). Although *M. thermophilus* has shown the greatest stimulation of *Agaricus* growth of a range of fungi tested, in its absence several other fungal species had similar effects (Straatsma et al. 1994b). Anecdotal evidence from mushroom farmers suggests that inoculation with *Mycothermus* may stimulate compost productivity on a farm scale, but in general, it is not necessary to add *Mycothermus* unless the compost has been pasteurized at too high a temperature, since naturally occurring strains of the fungus are always present (Ross and Harris 1983b; Straatsma et al. 1994a).

A number of studies have examined the addition of bacterial inocula to increase compost productivity and mushroom yield (Table 1). Inoculation with *Bacillus megaterium* or a thermophilic strain of *Staphylococcus* has been shown to promote mushroom production and advance cropping by several days (Ahlawat and Vijay 2010) and *Pseudomonas putida* also promoted hyphal extension of *Agaricus* in vitro (Rainey 1991). However, in another study, addition of *B. subtilis* or *B. megaterium* to compost along with the *Agaricus* spawn did not affect yield (Ekinci and Dursun 2014). A more thorough search for bacteria that promote compost productivity was also unsuccessful (Straatsma et al. 1994b). It should be noted, however, that these were all small-scale screening experiments using compost that was first sterilized at high temperature to selectively inactivate thermophilic fungi. It seems likely that promotion of *Agaricus* may require an interacting consortium of both bacteria and fungi for effective lignocellulose breakdown.

Bacterial involvement in formation of mushroom primordia and fruiting bodies

Formation of mushroom fruiting bodies is controlled by a range of environmental factors. Fruiting body primordia are initiated in response to a reduction in temperature compared with mycelial growth conditions and greater aeration to reduce levels of CO_2 (Chang and Miles 2004). The optimum ranges of these two factors vary for different species of mushrooms (Stamets and Chilton 1983). Transcriptomic studies of *Agaricus* have shown that a reduction in temperature is essential for further differentiation of primordia, and the level of CO_2 exerts quantitative control on the number of fruiting bodies formed (Eastwood et al. 2013). Many mushroom species also show a requirement for a change in nutrient availability, with high levels of nutrition favoring mycelial growth over primordia formation (Chang and Miles 2004). Nutrient supply governs outgrowth of the primordia, with the appearance of mushroom fruiting bodies in separate flushes governed by depletion of specific nutrients required by the primordia (Straatsma et al. 2013). Some species also require a change in pH or light conditions (Chang and Miles 2004).

For commercial cultivation of *Agaricus*, formation of fruiting bodies is induced by overlaying the colonized compost with a layer of "casing," usually a mixture of peat and

Table 1 Promotion of mushroom growth by bacterial and fungal inocula

Mushroom species	Bacteria/fungi used	Source of inoculum	Applied to casing/ compost	Reported effect	Reference
Agaricus bisporus	*Bacillus megaterium*, *Staphylococcus* sp.	Compost	Compost	Increased yield, inhibition of pathogens	(Ahlawat and Vijay 2010)
A. bisporus	*Scytalidium thermophilum*	Compost	Compost	Faster mycelial growth, increased yield	(Coello-Castillo et al. 2009; Straatsma et al. 1994a; Wiegant et al. 1992)
A. bisporus	*B. subtilis*, *B. megaterium*	Compost	Compost	No effect	(Ekinci and Dursun 2014)
A. bisporus	*Pseudomonas putida*	Casing	Casing	Increased primordia formation	(Fermor et al. 2000)
A. bisporus	*P. putida*	Casing	Casing	Primordium induction due to ACC deaminase production	(Chen et al. 2013)
A. bisporus	*P. putida*	Soil	Casing	Yield increase	(Zarenejad et al. 2012)
A. bisporus	*Arthrobacter terregens*, *Rhizobium meliloti*, *Agrobacterium rhizogenes*, *B. megaterium*	Casing	Casing	Increased pinning	(Park and Agnihotri 1969)
A. blazei	Various Actinomycetales	Casing	Casing	Increased mycelial growth and yield	(Young et al. 2013)
A. blazei	*Exiguobacterium* sp., *Microbacterium esteraromaticum*, *P. resinovorans*	Casing	Casing	Increased yield	(Young et al. 2012)
A. bitorquis	*B. megaterium*, *Alcaligenes faecalis*, *B. circulans B. thuringiensis*	Casing	Casing	Increased yield	(Ahlawat and Rai 2000)
A. bisporus	*Mycothermus thermophilus*	n/a	Spawn	Increased mycelial growth	(Bilay 2000)
Pleurotus ostreatus	*Bradyrhizobium japonicum*	n/a	Spawn	Increased mycelial growth	(Zhu et al. 2013)
Pleurotus eryngii	*Pseudomonas* sp. P7014	n/a	Bottle culture	Increased mycelial growth	(Kim et al. 2008)
P. ostreatus	*P. putida*	Spent mushroom compost	In vitro	Accelerated primordial development	(Cho et al. 2003)
A. bisporus	*P. putida*	Casing	In vitro	Increased mycelial growth	(Rainey 1991)

lime. This casing layer contains a diverse bacterial population, and the presence of these bacteria is essential for primordia formation as fruiting does not occur with sterilized casing (Eger 1972; Hayes et al. 1969). Initiation of primordia in autoclaved or fumigated casing can be partially restored by addition of a bacterial inoculum (Eger 1972) with the best studied examples being *P. putida* or a related pseudomonad (Colauto et al. 2016; Hayes et al. 1969; Rainey et al. 1990). Alternatively, addition of adsorptive carbon-based materials such as activated charcoal will also restore fruit body formation (Noble et al. 2003). These results suggested that the stimulatory role of the bacteria is to remove an inhibitor of primordia formation. This compound has been identified as 1-octen-3-ol (Noble et al. 2009), which is a volatile compound produced by the *Agaricus* mycelium, that controls the early differentiation of vegetative hyphae to multicellular knots (Eastwood et al. 2013). A considerable proportion of bacterial isolates from the casing layer are were found to be tolerant to high levels of this compound and many of these isolates were also able to promote mushroom yields by up to 10% (Zarenejad et al. 2012). 1-Octen-3-ol is also important for other mushroom species; it is the dominant flavor component in *Pleurotus* (Misharina et al. 2009; Venkateshwarlu et al. 1999), and bacteria isolated from *Pleurotus* growing on Pangola grass (including *Bacillus cereus*, *B. megaterium*, *Enterobacter asburiae*, *Enterobacter cloacae*, *Kurthia gibsonii*, *Pseudomonas pseudoalcaligenes*, and *Meyerozyma guilliermondii*), were found to grow on 1-octen-3-ol and both

promote mycelial growth and induce fruiting of *P. ostreatus* in vitro (Torres-Ruiz et al. 2016).

Other bacterial metabolic pathways may also be important for stimulation of mushroom growth. For example, an ACC deaminase-producing strain of *P. putida* stimulated primordia formation in *Agaricus* but this property was lost in knockout mutants in the ACC deaminase gene (Chen et al. 2013). This suggests that ethylene, which is produced by *Agaricus* hyphae (Turner et al. 1975), acts as an inhibitor of mycelial growth and primordia formation (Zhang et al. 2016), and that *P. putida* can encourage *Agaricus* fruiting by lowering the levels of ethylene produced by *Agaricus*.

The bacterial population in casing increases dramatically after initiation of the first primordia but decreases during later flushes (Cai et al. 2009; Pardo et al. 2002). The species present are mostly proteobacteria related to *Pseudomonas*, *Pedobacter*, and *Caulobacter* (Fermor et al. 2000; Kertesz et al. 2016; Siyoum et al. 2010). As bacteria are required for initiation and growth of mushroom fruiting bodies, a number of investigators have screened compost or casing for "mushroom growth-promoting bacteria" that promote either mycelial growth or fruiting body formation. Most of the organisms identified have been applied to casing in an attempt to stimulate fruiting, and most of the growth-promoting strains found were *Pseudomonas* or *Bacillus* species (Table 1). The prevalence of these two genera probably reflects the culturing strategies used, since cultivation-independent methods reveal a very high diversity of bacteria present, many of which are uncharacterized (Kertesz et al. 2016; Siyoum et al. 2010). There has been little systematic study of the mechanisms by which inocula stimulate mycelial extension or initiation of primordia, or indeed whether they actively colonize *Agaricus* hyphae or are active on the casing itself.

Not unexpectedly, the fungal community found in button mushroom casing is greater than 90% *A. bisporus* (McGee et al. 2017), but over 200 other fungal species have also been detected, with highest diversity during first flush. *Mycothermus* is not detected at all, though other thermophilic fungi such as *Thermomyces* and *Myceliophthora* are still present, confirming the role of *Mycothermus* as nutrient source for growth of *Agaricus*. The dominant known taxa in casing are *Lecanicillium fungicola*, *Thermomyces lanuginosus*, *Aspergillus* spp., *Myceliophthora* spp., *Sordaria* spp., *Candida subhashii*, *Paecilomyces niveus*, and *Cercophora* spp. (McGee et al. 2017). The overall abundance of unknown fungal taxa is more than 20-fold higher than known taxa (excluding *Agaricus*) (McGee et al. 2017) suggesting that much remains to be learnt about the role of these fungi in this part of mushroom production. Interestingly, *Agaricus* activity (measured as ITS region cDNA abundance) reaches a maximum at first flush and then decreases substantially, and a range of unclassified taxa dominate the cDNA community for the remainder of the cropping period. During this period, the active taxa include *L. fungicola*, the causal agent of dry bubble disease (see below), suggesting that it can co-exist with *Agaricus* without causing disease, and that disease induction may require specific environmental factors (McGee et al. 2017).

Fungal and bacterial pathogens of *Agaricus*

While many of the bacteria and fungi described in the previous section have been shown to promote hyphal elongation or fruiting body formation of *Agaricus*, there has been little work to distinguish whether these organisms are actively colonizing the surface of the hyphae or living in the casing itself. Mushroom fruiting bodies, by contrast, have their own distinctive microflora. The cultivable population of microorganisms on button mushroom fruiting bodies includes pseudomonads, bacilli, and coagulase-negative staphylococci, together with the yeast *Rhodotorula* and several species of actinomycetes (Rossouw and Korsten 2017; Xiang et al. 2017). While the levels of human pathogens found on fruiting bodies are low (Venturini et al. 2011), bacterial contamination can cause postharvest deterioration (Beelman et al. 1989). A specific study of enterobacteria on button mushrooms at the point of harvest has revealed a considerable load of *Ewingella americana* (Reyes et al. 2004), which was confirmed in a recent report on microbial succession on healthy mushrooms at point of harvest (Siyoum et al. 2016). This organism is a potential human pathogen (Hassan et al. 2012), but it is better known as the cause of mushroom stipe necrosis in both *Agaricus* and *Pleurotus* (Gonzalez et al. 2012). The presence of *E. americana* on healthy postharvest mushrooms highlights the susceptibility of edible mushrooms to a variety of microbial diseases that can devastate crop production (Largeteau and Savoie 2010).

The most important of these are three fungal diseases, two of which have been reviewed recently (Berendsen et al. 2010; Carrasco et al. 2017). Cobweb disease (*Cladobotryum dendroides*) grows as a web-like mycelium over the surface of the fruiting bodies and produces large numbers of conidia that are readily dispersed by aerial means (Carrasco et al. 2017). Dry bubble disease (*L. fungicola*) produces severe outbreaks leading to formation of misshapen sporophores (Berendsen et al. 2010), and a similar effect is seen for wet bubble disease (*Mycogone perniciosa*), although this disease is less widespread and has not been studied as extensively (Khanna et al. 2003). Green mold disease (*Trichoderma aggressivum*) caused extensive crop losses in both America and Europe in the 1990s and continues to be a problematic disease worldwide. This disease is caused by two slightly different strains in America and Europe (*T. aggressivum f. aggressivum* and *T. aggressivum f. europaeum*) (Samuels et al. 2002), although the American pathovar has recently also been reported in Europe (Hatvani et al. 2017). *Pleurotus* is

also affected by green mold disease, but the disease is caused by a related but phylogenetically different species of *Trichoderma* (Kredics et al. 2009). Spores of both *L. fungicola* and *T. aggressivum* are sticky in nature, and are therefore mainly transmitted by insect or human vectors or in water (Fletcher and Gaze 2008). Interestingly, spore germination and growth of *L. fungicola*, *M. perniciosa*, and *T. aggressivum* are inhibited by 1-octen-3-ol, the *Agaricus* metabolite described previously that acts as a potent inhibitor of fruiting body formation, possibly allowing the pathogens to time their growth to coincide with appearance of the mushroom fruiting bodies (Berendsen et al. 2013).

Pseudomonas species play a variety of different roles in mushroom casing. As described above, *P. putida* has been identified as the key casing organism that breaks down 1-octen-3-ol and induces fruiting body formation (Noble et al. 2009). *Pseudomonas* isolates have also been shown to antagonize *Lecanicillium* in casing, competing for iron and releasing antifungal compounds, though this is not sufficient to protect *Agaricus* effectively against dry bubble disease (Berendsen et al. 2012). *Pseudomonas* also cause a range of blotch diseases of *Agaricus* which cause severe crop losses. Brown blotch disease is caused by *Pseudomonas tolaasii*, a species which is endemic in compost and induces symptoms through production of an extracellular lipodepsipeptide toxin, tolaasin [see reviews by (Largeteau and Savoie 2010) and (Soler-Rivas et al. 1999)]. *Pseudomonas reactans* causes similar symptoms, releasing a related but distinct toxin to that produced by *P. tolaasii* (Wells et al. 1996). Because *P. tolaasii* is ubiquitous in the compost environment, it is very difficult to control, since it can switch rapidly between nonvirulent and virulent forms in response to environmental changes and possibly also in response to metabolites produced by *Agaricus* (Largeteau and Savoie 2010). *P. tolaasii* also attacks *Pleurotus*, causing yellow discolorations (Lo Cantore and Iacobellis 2014) and *Flammulina* (Han et al. 2012), causing black rot. Several other *Pseudomonas* species also cause commercially important diseases. *Pseudomonas gingeri* is the main causal agent of ginger blotch (Wong et al. 1982), and many different pseudomonads have similar effects, causing a range of discolorations (Godfrey et al. 2001). *Pseudomonas agarici* is responsible for drippy gill disease, degrading the extracellular matrix of the fruiting body and producing droplets of bacterial ooze on the lamellae of *Agaricus* (Gill and Cole 2000). A range of soft rot diseases of mushrooms are also caused by bacterial pathogens. These include *Burkholderia gladioli pv agaricicola*, which attacks a range of different edible mushroom species (Chowdhury and Heinemann 2006; Gill and Tsuneda 1997; Lee et al. 2010), *Janthinobacterium agaricidamnosum*, which causes soft rot in *Agaricus* (Chowdhury and Heinemann 2006; Lincoln et al. 1999), and *Pantoea* species that affect *Pleurotus* (Kim et al. 2015).

Control of these bacterial and fungal mushroom diseases is essential for the mushroom industry, as outbreaks can destroy a large proportion of the crop. Effective prevention has traditionally relied on maintaining good production hygiene, together with the strategic use of biocides and antifungals (Fletcher and Gaze 2008). A major restriction is that only a limited range of products have been approved for application onto mushroom crops. Alternative methods that are being developed include the use of essential oils and antagonistic bacterial species as biocontrol agents (Berendsen et al. 2012; Sokovic and van Griensven 2006), but improved molecular methods for early detection of infection and the selection of resistant mushroom varieties (Savoie et al. 2016) are also important in reducing the impact of these widespread pathogens.

Conclusions and outlook

Research into mushroom compost goes back at least to the work of Waksman in the early 1930s (Waksman and Nissen 1932), with the aim of optimizing microbiological and process parameters to maximize mushroom yields. Most of our present understanding of mushroom compost microbiology has come from cultivating isolates of thermophilic and cellulolytic bacteria and fungi from compost, and it is only recently that sequencing efforts have revealed that some of the most abundant and important organisms in compost have been overlooked by this method. High-yielding sustainable production of edible mushrooms is currently primarily hampered by inconsistency of the compost, caused by variability in the quality and composition of the feedstocks, and by changes in the microbial communities present. Our improved understanding of the microbiology of compost provides renewed potential to design consortia of bacteria and fungi that can be used in bioaugmentation to optimize composting of lower quality feedstocks, and to identify and validate biomarkers that can be used to assess the quality of a compost before cropping commences. More detailed studies are also required to explore the relationship between microbial activity and diversity in compost and casing during cropping. Most of the nutrients in mushroom compost are left untouched by the mushroom crop, illustrated by the fact that spent mushroom compost is a valued soil conditioner. Manipulation of microbial activity and nutrient availability during cropping may allow higher yields of mushrooms in later crop flushes. Finally, a more thorough understanding of the biocontrol of mushroom pathogens has the potential to increase the quality of the mushrooms produced. Mushroom compost is a completely recycled product produced from agricultural wastes, and the fungi and bacteria that define it allow us to enjoy mushrooms as truly sustainable foods.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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