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Interactions between fungi and other microorganisms for better fungal products: a review

Matas Gavenauskas,

Reda Iršėnaitė,

Jurga Motiejūnaitė

Nature Research Centre,
Institute of Botany,
47 Žaliųjų ežerų St.,
Vilnius 08406, Lithuania

Under natural conditions, substrates are occupied by sets of different micro-organisms that interact with one another in synergistic or antagonistic relationships. These interactions can influence the growth, development, and biochemistry of economically important fungi, enhance their beneficial properties, stimulate the growth of fruiting bodies, or accelerate the growth of mycelium used for the production of various products and biotechnology processes where fungi are involved. The paper presents a literature review covering known interactions between fungi and bacteria, fungi and actinomycetes, and between different fungi that can be used to promote the production of fungal products or that need to be taken into account in order to avoid production losses. A brief overview of fungi and micro-organism co-culture strategies is provided as well.

Keywords: basidiomycota, ascomycota, bacteria, actinomycetes, synergy, antagonism

INTRODUCTION

Under natural conditions, the same niche is occupied by various microorganisms – fungi, bacteria, archaea, actinomycetes, myxomycetes which interact with each other. These interactions can influence fungal morphology, developmental patterns and biochemical processes (Bertrand et al., 2014).

Bacteria and fungi can form a variety of associations which often change the nutrition process of one or both partners. These interactions can also lead to distinctive contributions to biogeochemical cycles and biotechnological processes and therefore can be of great importance in agriculture, forestry, environmental protection, food production, and medicine (Frey-Klett et al., 2011). Although bacteria and fungi interact constantly in nature, mycologists usually study fungi in complete isolation, and fungal-bacterial interactions are less frequently studied (Hock, 2001). In most cases of known fungal-bacterial associations, bacteria provide the fungus with one form of metabolic benefit or another while the fungus often provides bacteria with a suitable living environment (Kobayashi, Crouch, 2009). One of the best-known examples of the beneficial effects of bacteria on fungi is the so-called mycorrhizal helper bacteria: they

* Corresponding author. Email: matas.gavenauskas@gamtc.lt

can be useful for mycorrhizal fungi by promoting the establishment and functioning of mycorrhizal associations (Deveau, Labbé, 2016). Some bacteria help to break down complex organic matter: for example, cellulose-degrading bacteria can break down plant material making the nutrients from it more readily available for fungal growth (Imran et al., 2016). Antagonistic relationships between bacteria and fungi may lead to revealing diverse chemical compounds, which may not be present in axenic cultures (Marmann et al., 2014).

Meanwhile, actinomycetes are known to act exclusively as antagonists for fungi (Silva et al., 2021). Interactions of archaea and myxomycetes with fungi are not well known, though both are abundantly present in the environments with fungi, including dead wood (Rinta-Kanto et al., 2016).

Interactions between fungi may be as variable as interactions between fungi and other microorganisms, though, following Hiscox et al. (2014), competition is the most common association and it may result in several outcomes. In the case of macrofungi, their interactions may take form of antagonism, mutualism or parasitism or the relationship can shift from one type of interaction to another.

The aims of this paper were (1) to summarise all known interactions between fungi and other microorganisms that are used in obtaining better fungal products or may be helpful in the production, (2) to summarise antagonistic interactions between fungi and other microorganisms that may hamper fungal produce, and (3) to elucidate mechanisms of these interactions for better understanding of beneficial co-cultures in production.

METHODS

For the review, we selected the relevant literature by conducting a reference search at two levels. At the first level, we performed a search of Clarivate Analytics Web of Knowledge and Google Scholar using keywords from the titles, keywords, and abstracts of papers, such as: lignicolous fungi + bacteria; soil fungi + bacteria; interactions + fungi + bacteria; fungi + actinomycetes; fungi + myxomycetes; mushroom growth promoting bacteria; lignicolous fungi + interspecific interactions; fungi + synergies; fungi + antagonistic; co-cultures + fungi + growth. Additional literature was found by a snowball search. After the screening of resulting hits at both search levels, they were finalised in 74 articles that were identified as relating to the subject of the present paper. The literature search was performed from February 2023 till March 2024.

RESULTS AND DISCUSSION

Micro-organisms that promote fungal fruit body growth

Fungal fruit body growth can benefit from the presence of certain bacteria that have a symbiotic relationship with the mycelium or provide functions or substances that have growth-promoting effects. The fruit bodies of some macrofungi are difficult to grow in standard cultivation media, in parts due to the lack of symbiotic microorganisms upon which fruit body formation depends (Rainey et al., 1990). The mechanism of this interaction is that the bacteria remove the fungal autoinhibitors (Noble et al., 2003) or that the bacteria cause stress to the mycelium, which promotes fruit body formation (de Boer et al., 2008). Hyphae of *Agaricus bisporus* and *Pleurotus ostreatus*, the most popular edible cultivated fungi, interact directly with bacterial communities on the substrate. Among the best known are the interaction where *Pseudomonads* remove the inhibitory volatile C8 compounds and ethylene, a process promoting the growth of the fruit bodies of the fungi. Based on this knowledge, co-culture strategies for fruit body production have been developed to mimic the natural environment. Cho et al. (2003), for example, showed that formation of primordia was promoted and the development of fungal fruit bodies was enhanced following inoculation of pure cultures of *Pleurotus ostreatus* mycelium with strains of fluorescent *Pseudomonas* spp. isolated from the mycelial plane of commercially produced mushrooms.

As shown by Kumari, Naraian (2021), inoculation with *Glutamicibacter arilaitensis* MRC119 can be used as an organic substitute to improve the fruit body yield and biological efficiency of *Pleurotus* spp. fungi.

It has long been known that microorganisms present in the casing layer are of vital importance for the establishment of *Agaricus bisporus* fruit bodies (Eger, 1972). Park, Agnihotri (1969) reported that the addition of *Arthrobacter terregens*, *Rhizobium meliloti* and *Bacillus megaterium* to the axenic casing layer promoted the growth of *A. bisporus* fruit bodies. Primordia formation in axenic cultures is also induced by other *Pseudomonas* species, but not every *Pseudomonas* isolate has stimulatory properties, and the effect may also depend on the strain of *Agaricus* (Fermor et al., 2000; Noble et al., 2009). Zarenejad et al.(2012) found that *Pseudomonas putida* was the most effective for growth promoting and fruit body yield of *A. bisporus* increasing inoculum among the 23 bacterial strains tested. Colauto et al. (2016) named *P. putida* as a crucial microorganism responsible for the degradation of the 1-octen-3-ol linkage and *A. bisporus* fruit body formation. Cho et al., 2003 showed that *Pseudomonas fluorescens* strains can promote primordia formation, mycelial growth and fruit body productivity of *Pleurotus eryngii* and *Pleurotus ostreatus*. In general, the composition of the bacterial populations that inhabit fungal fruit bodies is strongly determined by fungal identity and may have species-specific symbiotic relationships (Pent et al., 2017). These relationships may include shaping of a fungus fruit body (Zhou et al., 2017), control of pathogen impact (Tsukamoto et al., 2002), etc. All these findings strongly suggest that inoculation of the fungal mycelium with particular bacteria may have beneficial applications for mushroom production.

There are no data about beneficial effects on fruit body productivity when co-cultivating different species of fungi; rather to the contrary, as shown by the co-cultivation of different *Pleurotus* species (Carabajal et al., 2012). However, co-cultivation of different fungal species or strains may increase the production of secondary metabolites, improve nutrient metabolism and potential applications in bioremediation and biotechnology (Xu et al., 2023). Liu et al. (2015) found that concentrations of active constituent cordycepin in the fruiting bodies of *Cordyceps militaris* increased when it was co-cultivated with filamentous ascomycete *Monascus ruber* (Yu et al., 2021). Macromycete *Inonotus obliquus,* produces a wide range of bioactive substances in the wild, but only few in submerged liquid cultures. Zheng et al. (2011) tested a submerged co-culture system of *I. obliquus* with *Phelinus punctatus*. These two basidiomycetes are not found growing together in nature, but their co-culture led to increased levels of a number of metabolites (Yu et al., 2021).

Mycelial growth-promoting microorganisms

Bacteria impact different development stages of fungi, not only fruit body production: they converse and adapt substrates, degrade toxic compounds and promote hyphal elongation during substrate colonization by mycelium (Suarez et al., 2020). In nature, beneficial bacteria may co-migrate with fungal hyphae, as was shown in the example of *Burkholderiaceae* strains (Yang et al., 2016) or may move along hyphae, supplying them with essential growth factor thiamine, as in the case of *Bacillus subtilis* and *Aspergillus nidulans* (Abeysinghe et al., 2020). Nutrient cycling bacteria can contribute to the availability of nutrients for fungal growth. For example, nitrogen fixing bacteria convert atmospheric nitrogen into the forms readily available for fungi, promoting their growth and providing a continuous source of nitrogen for mycelium and fruit bodies of wood-degrading basidiomycetes (Shamugam, Kertesz, 2023). Wood-degrading basidiomycetes have developed strategies to create optimal nitrogen concentrations in their substrates. They may recycle nitrogen from dying mycelium, uptake and transfer nitrogen from the soil to the wood, etc (Lindahl, Finlay, 2005). Tsuneda, Thorn (1994) suggested that bacterial lysis may be another strategy of fungi to obtain nitrogen. Brunner, Kimmins (2003) showed that the highest rates of nitrogen fixation were found in the more advanced stages of

decay, which would support the hypothesis that only some bacteria are lysed to maintain bacterial densities, as bacterial growth is driven by the oligomers released by fungal enzymes. *Pleurotus ostreatus* and *Lentinula edodes* are known to be capable of attacking bacteria on low nutrient agar, for example, certain strains of *Pseudomonas fluorescens* and *Pseudomonas tolaasii*. Fungal hyphae penetrate into and lyse bacterial colonies, thus obtaining nutrients from bacteria. *P. ostreatus* is also known to significantly reduce numbers of bacterial colony forming units in soil and straw (Gramms et al., 1999).

In bioremediation, mycelial and bacterial co-cultures are used to degrade complex organic contaminants. By combining bacteria and different fungi with complementary metabolic capacities, co-cultures can enhance the degradation and detoxification of pollutants in soil or aquatic environments (Espinosa-Ortiz et al., 2022). Co-cultivation of fungi can produce novel or improved secondary metabolites that are not produced by individual strains. Interactions between different strains can lead to the synthesis of unique compounds that may have pharmaceutical, agricultural or industrial applications (Marmann et al., 2014). On the other hand, co-cultivation of bacteria and fungi may depend upon the end-product to be achieved. The in vitro results of co-cultivation of *Bacillus aryabhattai*, *Lysinibacillus boronitolerans*, and *Pseudomonas putida* with *P. ostreatus* showed a significant positive impact on mycelial growth ($p > 0.05$) at 4–6 days of incubation, but there was no significant difference in the productivity of fungal fruit bodies (Hannah et al., 2020).

The specific outcomes and applications of co-cultures depend on the strains or species involved, the intended objectives, and the environmental conditions under which they are implemented. Bacterial stimulation of fungal physiology impacts mycelial growth as well. For example, Rainey (1991) found that *P. putida* strains promoted hyphal extension of *Agaricus* mycelia in vitro, Kamei et al. (2012) found that *Curtobacterium* sp. from dead wood stimulated the growth of *Stereum* sp., and Bontemps et al. (2013) found that *Streptomyces* spp. from forest soil promoted consistently and significantly the growth of the white rot fungus *Phanerochaete chrysosporium*, though none of these strains showed ligninolytic activity on their own.

Already in the 1970s, Blanchette, Shaw (1978) reported that co-culture with fungi and bacteria (*Enterobacter* spp.) and yeasts (*Saccharomyces bailii* and *Pichia pinus*) increased weight loss during decay of softwoods. Haidar et al. (2021) found that the combination of *Paenibacillus* sp. and *Fomitiporia mediterranea* on the sawdust of grapevine significantly increased wood degradation compared to that caused by the fungus alone. A similar enhancement of the degradation ability of white-rot fungus *Phlebia brevispora* was found when co-culturing the fungus with a mixture of *Enterobacter* sp. and *Pseudomonas* sp. strains. The low level of the degradation ability toward benzo(a) pyrene in axenic fungal culture was improved significantly in co-culture with bacteria (Harry-Asobara, Kamei, 2019). Suarez et al. (2020) demonstrated that bacterial isolates from fruit bodies of *P. ostreatus* showed lower enzymatic activities but promoted hyphae growth, while bacterial isolates from vegetative mycelium showed higher hydrolytic enzyme activities and inhibited hyphae growth. The bacteria that promoted mycelial growth also produced chitinase, while the inhibiting bacteria did not, strongly suggesting that the growth-promoting bacteria may act in part by disrupting the hyphae cell walls to obtain sugars and amino acids from the fungal mycelium and provide other nutrients in return (Suarez et al., 2020).

Wood decaying fungal species can form synergistic interactions, too. Chen et al. (2019) reported a higher degradation ratio of lignin and cellulose in a *Phanerochaete chrysosporium* and *Trichoderma viride* co-culture. Similar results were achieved for co-culture of *Trametes hirsuta* and *P. ostreatus* (Yang et al., 2020). Kaur et al. (2019) reported a significant increase in laccase, lignin peroxidase, and manganese peroxidase activities using *P. ostreatus* and *P. chrysosporium* co-culture on rice straw. Mutualism

between fungal species can occur when their physiological activity is complementary, when, for instance, one fungus synthesises or releases a compound that the other fungus requires but cannot otherwise obtain or produce. For example, *Nematospora gossypii* and *Bjerkandera adusta* can grow in co-culture in the laboratory, but not individually, in axenic cultures, on a medium lacking biotin, inositol, and thiamine. The former species can synthesise thiamine, but not biotin or inositol; meanwhile the latter can synthesise biotin and inositol but not thiamine (Boddy, 2016). Kumar et al. (2019) showed that co-culture of *Trametes ljubarskyi* and *Rhodotorula mucilaginosa*, which was capable of efficient laccase production, may be capable of differential synthesis of multiple oxidoreductases, antioxidants, and membrane-associated proteins that would be beneficial for the survival of these two fungi.

Co-cultures involving several organisms may have even more complex promoting impact. For example, cultivation of *Polyporus umbellatus* relies on *Armillaria gallica* (Xing et al., 2021; Xing et al., 2013). Adding strain CACMS001 (*Rhizobium* sp.) to the co-culture of these two fungi increased their mycelial growth by 21% and 78%, respectively, and significantly increased the extracellular xylanase activity of *A. gallica*.

Decomposition and mycelial growth are accelerated when bacteria and yeasts are combined with wood decay fungi. The effect of basidiomycetes and compound inoculums can result in up to 10% additional weight loss compared to basidiomycetes alone. Glucosamine studies show that at the end of five months, as much as 5–10% of the total dry weight may be mycelium, and the mycelium content of the combined inoculant treatments may be 10–200% higher than that of the basidiomycetes alone (Blanchette, Shaw, 1978).

Antagonistic Interactions between fungi and microorganisms

Interactions between microorganisms can be antagonistic as well and more than often are. As already mentioned above, actinomycetes act exclusively as antagonists for fungi, including wood decomposers, by inhibiting their growth (Blanchette et al., 1981) and they are even studied as biocontrol agents for brown and white rot fungi (Roussel et al., 2000). There are also numerous examples of antagonistic reactions between fungal species, which are expressed by various morphological, physiological and biochemical changes occurring during interactions, such as rapid cell division, branching, hyphal aggregation, aerial growth, autolysis, pigment production, release of volatile organic compounds, diffusible enzymes, toxins and antifungal metabolites (Woodward, Boddy, 2008). For example, Yao et al., 2016 developed 136 symbiotic systems using 17 basidiomycetes in order to observe macrofungal interactions and found that *Trametes versicolor* and *Ganoderma applanatum* showed the strongest antagonistic effects among them. However, type of interactions between fungi may depend on the decay class of their substrates. Fukasawa, Matsukura, 2021 found that *Phlebia livida* and *Gloeophyllum sepiarium* may show both positive and negative associations in differently decayed substrates. Bacteria may also demonstrate varying impact on fungi. Orban et al., 2023 co-cultivated bacterial isolates, that were previously obtained from *Pleurotus ostreatus* with *P. ostreatus*, *Pleurotus eryngii*, *Pleurotus sapidus*, *Pleurotus citrinopileatus*, *Cyclocybe aegerita*, *Lentinula edodes*, and *Kuehneromyces mutabilis* during eight days and found that bacterial isolates only showed significant mycelial growth-promoting effects when co-cultivated on Petri dishes with *Pleurotus* species, except for *P. citrinopileatus*. Among the bacterial isolates, *Paenibacillus peoriae* showed strong positive impact on the mycelial growth in *P. ostreatus*, *P. eryngii*, and *P. sapidus*, but only during the early cultivation stages, meanwhile in later cultivation stages this strain inhibited the growth of all fungi. Antagonistic effect of bacteria on fungi may have positive effect as well: some bacteria act as antagonists against pathogens that can damage fungal mycelium. Fluorescent *Pseudomonads* and *Bacillus* species, which can protect fungi against diseases caused by pathogenic fungi or bacteria, can serve as such examples (Haidar et al., 2016).

DISCUSSION

To achieve the desired quantity and quality of fungal cultivation products, several points are to be applied in the co-culture strategies. First and foremost, it is important to identify possible synergies, i.e., select most suitable micro-organisms and their strains. Another point is to understand physicochemical conditions under which the synergy will work most effectively. Environmental pH, for example, may play an important role in promoting or suppressing the activity of one or all micro-organisms involved in a synergy. Although some microorganisms tolerate a broad range of pH conditions in their environments, most are susceptible to a pH below 4 (O'May et al., 2005), therefore lowering the pH can promote the growth of acid-tolerant microorganisms or inhibit acid-sensitive organisms. For example, fungi can rapidly lower the pH by releasing organic acids such as oxalic acid. A rapid decrease in pH can be detrimental to many bacteria, especially in the presence of undissociated forms of weak organic acids (Booth, 1985). Trophic competition between fungi and bacteria may also play the role in bacterial-fungal interactions and in their co-cultivation, especially the competition for carbon substrates, which was shown by Moller et al. in the study of leaf decomposition (1999). Competition for other elements, such as iron (Marshall, Alexander, 1960) or nitrogen (Lemanceau et al., 1993) may also affect bacterial-fungal interactions.

CONCLUSIONS

The literature search identified a number of economically important interactions between fungi and various micro-organisms. Many of these are synergistic, enhancing economically important properties of the fungi: fruiting body formation, mycelial growth and chemical efficiency. Antagonistic interactions, which may inhibit the functioning of target fungal species, have also been revealed. Both positive and negative interactions, as well as environmental conditions need to be taken into account to obtain better results in fungal produce. In addition, a better understanding of micro-organism interactions and their mechanisms would require a wider range of co-culture experiments, such as 13C labelling, proteomic analysis, and genetic engineering, in order to obtain more comprehensive results that can be applied to obtaining fungal products.

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Matas Gavenauskas, Reda Iršėnaitė,
Jurga Motiejūnaitė

GRYBŲ IR KITŲ MIKROORGANIZMŲ SĄVEIKA GRYBINIŲ PRODUKTŲ PAGERINIMUI

Santrauka

Gamtinėmis sąlygomis substratus kolonizuoja grupės įvairių mikroorganizmų, kurie tarpusavyje sąveikauja sinerginiais arba antagonistiniais ryšiais. Šios sąveikos gali daryti poveikį ekonomiškai svarbių grybų augimui, vystymuisi ir biochemijai, sustiprinti jų naudingąsias savybes, paskatinti vaisiakūnių augimą arba pagreitinti augimą grybienos, naudojamos įvairių produktų gamybai ir biotechnologiniams procesams, kuriuose dalyvauja grybai. Čia pateikiame literatūros apžvalgą, apimančią žinomas grybų ir bakterijų, grybų ir aktinomicetų bei skirtingų grybų sąveikas, kurios gali būti panaudotos grybinių produktų gamybai skatinti arba į kurias reikia atsižvelgti siekiant išvengti produkcijos nuostolių. Taip pat trumpai apžvelgiamos grybų ir mikroorganizmų kultivavimo drauge strategijos.

Raktažodžiai: bazidiomicetai, askomicetai, bakterijos, aktinomicetai, sinergija, antagonizmas