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Zhenbo Xu, Mahesh Premarathna, Junyan Liu & Gamini Seneviratne

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REVIEW ARTICLE

Current knowledge on the dual species interaction and biofilm between *Aspergillus* and *Bacillus*: exploiting molecular understanding toward applications

Zhenbo Xu[a], Mahesh Premarathna[b,c], Junyan Liu[c,d,e] and Gamini Seneviratne[c]

[a]Department of Laboratory Medicine, The Second Affiliated Hospital of Shantou University Medical College, Shantou, Guangdong, China; [b]School of Food Science and Engineering, South China University of Technology, Guangzhou, China; [c]Microbial Biotechnology Unit, National Institute of Fundamental Studies, Kandy, Sri Lanka; [d]College of Light Industry and Food Science, Guangdong Provincial Key Laboratory of Lingnan Specialty Food Science and Technology, Academy of Contemporary Agricultural Engineering Innovations, Zhongkai University of Agriculture and Engineering, Guangzhou, China; [e]Ministry of Agriculture, Key Laboratory of Green Processing and Intelligent Manufacturing of Lingnan Specialty Food, Guangzhou, China

ABSTRACT

The complex interaction between *Aspergillus* and *Bacillus* has been gaining attention with the evolution of their co-culture applications. Information reported on this interaction from different points of view including both synergistic and antagonistic mechanisms necessitates a review for better understanding. This review focuses on the interaction, biofilm formation, and the diverse biotechnological applications of *Aspergillus* and *Bacillus*, giving special attention to *Aspergillus niger* and *Bacillus subtilis*. The review demonstrates that co-cultivation of *Aspergillus* and *Bacillus* exhibits significant transcriptional changes, impacting metabolism and secondary metabolite production in both organisms. Signaling from living fungal hyphae, EPS production, TasA fibrils, and regulators like Spo0A are essential in forming biofilm communities. Nutrient availability and pH levels, species type, and mutations in EPS-producing genes may also influence whether *Bacillus* will act antagonistically or synergistically with *Aspergillus*. This dual-nature complex interaction activates silent genes synthesizing novel compounds mainly with antifungal and medicinal properties, showcasing its potential for diverse applications in various fields such as agriculture and crop protection, bioremediation, environmental biotechnology, food science and fermentation, industrial biotechnology, and medical biotechnology and health. The use of *Aspergillus* and *Bacillus* species has evolved from simple monoculture applications to more sophisticated co-cultures and has been trending toward their synergy and metabolic optimization.

HIGHLIGHTS

- *Bacillus* can either inhibit growth or engage in biofilm with *Aspergillus*
- *Aspergillus–Bacillus* co-cultivation produces novel secondary metabolites
- The metabolites can inhibit or promote *Aspergillus* depending on the environment
- Cross-feeding of *Aspergillus* and *Bacillus* alters their growth and gene regulation
- Their interaction offers applications in food science, environment, medicine, etc.

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1. Why it is important to review literature on the interactions and biofilm between *Aspergillus* sp. and *Bacillus* sp.

In nature, microbes rarely exist as planktonic or single cells/species. They (for bacteria, it is ca. 40–80%) live in complex communities called polymicrobial biofilms (Xu et al. 2022). The resident microbes in these biofilms work together with each other by division of metabolic labor leading to more productive outcomes over the planktonic stage (Lindemann et al. 2016). In addition, the genetic diversity of biofilm communities and microbial interactions play a crucial role in regulating the growth, metabolism, and differentiation of community members. Although competitive behaviors like antagonism and resource depletion tend to suppress certain populations, microorganisms have developed mechanisms to not only resist but also cooperate under specific conditions, thereby enhancing community fitness. In environments where both bacterial and

CONTACT Zhenbo Xu ✉ zhenbo.xu@hotmail.com Department of Laboratory Medicine, The Second Affiliated Hospital of Shantou University Medical College, Shantou, Guangdong, China.

fungal species coexist, these interactions often manifest as mutualistic relationships.

Aspergillus species are key producers of enzymes and organic acids, and *Bacillus* species are known for their use as probiotics, and producers of antibiotics, and enzymes. The interaction of *Aspergillus* and *Bacillus* is complex, and it has been reported from different points of view, making it even more complex. In addition, even though their diverse applications are spreading in various disciplines, that information has not been sufficiently reviewed thus far. Therefore, a thorough literature review on their interactions and ecological/industrial uses is an urgent need for staying updated on emerging trends like microbial co-cultivation and addressing innovative applications in biotechnology.

1.1. Introduction to the genus Aspergillus

Aspergillus is one of the most familiar genera of filamentous fungi in the phylum *Ascomycota*, known for its asexual reproduction through conidiophores, structures bearing spores. In 1729, spore heads that resembled the shape of an Aspergillum, a device used in Roman Catholic rituals described by Italian priest and botanist Pietro Antonio Micheli (Scazzocchio 2009). *Aspergillus* thrives in diverse environments, from nutrient-poor to extreme temperature, pH, and salinity conditions (El-Hawary et al. 2020) and has over 250 known species (Geiser et al. 2008). The soil remains the primary habitat for most of the *Aspergillus* species, and they have been isolated from almost all major biomes. Some species of the genus have been isolated from litter and play a major role in the degradation of organic matter and nutrient recycling in ecosystems (Klich 2002; Embacher et al. 2023).

Certain species within the *Aspergillus* genus are known agricultural pests and producers of various metabolites, which pose risks to global food security (Nji, Babalola, and Mwanza 2023). The *Aspergillus* spp. are capable of adjusting to different environments due to their structural constituents like the rodlet layer in their surfaces, functions in spore dispersion and fixation, production of aerial hyphae, and nutritional versatility (Kwon-Chung and Sugui 2013; Gresnigt et al. 2014). Moreover, their ability to produce numerous degrading enzymes allows the fungus to saprotrophically infect diverse hosts (Mellon, Cotty, and Dowd 2007). Five *Aspergillus* sections, viz., *Flavi*, *Fumigati*, *Nigri*, *Nidulante*, and *Terrei* have been reported to cause diseases in humans (Sugui et al. 2014), and they have been reported to induce host immune responses associated with a diverse range of fungal–bacterial interactions, especially in the respiratory tract (Santos-Fernandez et al. 2023). Those interactions influence microbiome colonization in lungs and the immunopathogenesis of chronic pulmonary aspergillosis, which has been acknowledged as a serious lung disease (Rozaliyani et al. 2023). *Aspergillus fumigatus* is a significant cause of these infections in people with weakened immune systems (MacAlpine, Robbins, and Cowen 2023). Here, *A. fumigatus* shows an interesting interaction with *Pseudomonas aeruginosa*. When in direct contact, *P. aeruginosa* secretes antifungal compounds and inhibits *A. fumigatus* biofilm formation. However, *P. aeruginosa* produces volatile compounds that promote *A. fumigatus* to invade the lung parenchyma when the two organisms are physically separated (Briard, Heddergott, and Latgé 2016). In various other mucosal areas of the human body, similarly to *P. aeruginosa*, *S. aureus* inhibits conidiation, filamentation, and biofilm maturation in *A. fumigatus* in polymicrobial biofilm formation (Ramírez Granillo et al. 2015).

Aspergillus spp. are important in natural ecosystems and biotechnology due to their production of extracellular enzymes, organic acids, and secondary metabolites. Traditionally identified through morphology and biochemical methods, modern techniques like DNA sequencing have refined *Aspergillus* classification. Co-cultivation of *Aspergillus* spp. with other microorganisms is a source of novel bioactive products (Alanzi et al. 2023). *Aspergillus flavipes* (Wang, Huang, et al. 2024a), *A. fumigatus* (Kumar et al. 2019; Wang, Cao, et al. 2024b), *A. protuberus* (Kato et al. 2017), and *A. alliaceus* (Mandelare et al. 2018) have been reported to produce medicinally important bioactive compounds such as cytochalasans, taxols and pentapeptides, notamides, and allianthrones, respectively.

1.2. Introduction to the genus Bacillus

The genus *Bacillus* is comprised of 435 species and 12 subspecies of low G+C Gram-positive bacteria (Kingdom Bacteria; Phylum Firmicutes; Class Bacilli; Order Bacillales; Family Bacillaceae) (Maughan and Van der Auwera 2011; Blanco Crivelli et al. 2024), known for their ability to form dormant endospores under unfavorable conditions, allowing them to survive extreme environments such as radiation, drought, and heat (Zeigler and Perkins 2021; Xu and Kovács 2024). These bacteria are widely distributed in natural environments like soil, air, and ocean sediments. Moreover, they are found in human-made environments, including public places such as homes, hospitals, schools, markets, offices, trains, and restaurants. *Bacillus* species play crucial ecological roles, especially in soil, where they aid in nutrient cycling, plant growth, and stress tolerance (Saxena et al. 2020). In addition, *Bacillus* spp. are recognized for their ability to produce lytic enzymes, antimicrobial agents, and volatile organic compounds, which have diverse applications (Blanco Crivelli et al. 2024). Certain species are also utilized as probiotics, highlighting their significant role in biotechnology and industrial processes (Blanco Crivelli et al. 2024; Payne et al. 2024).

1.3. Interaction between Bacillus spp. and Aspergillus spp.: co-growth and metabolism

Aspergillus and *Bacillus* co-culturing has been reported to produce novel secondary metabolites by activating silent genes (Sun et al. 2023). In co-culture, 10-deoxygerfelin produced by *A. sydowii* has induced *B. subtilis* to synthesize benzoic acid, which is subsequently converted by *A. sydowii* into 3-hydroxybenzoic acid. Using this 3-hydroxybenzoic acid, *A. sydowii* has produced five new compounds. Here, the bacteria have inhibited the fungal growth causing a stress response of the fungus, which has activated the silent secondary metabolic pathways of the microorganism to produce new secondary metabolites. Similarly to *A. sydowii*, co-culturing of *A. versicolor* with *B. subtilis* has led to producing a new cyclic pentapeptide, cotteslosin C, a new aflaquinolone, 22-epi-aflaquinolone B, and two new anthraquinones, along with 30 known compounds, some of which have been identified with antibiotic and anticancer properties (Abdel-Wahab et al. 2019). It is not yet clear which species were the source of the novel metabolites produced in the co-culture.

Cross-feeding *A. oryzae* metabolites affected higher growth and biofilm formation in *B. amyloliquefaciens* (Singh, Lee, and Lee 2022). On the contrary, *Bacillus* extracts cross-fed to *Aspergillus* reduced its mycelial growth and conidiation indicating an ammensalic interaction. Similar results were observed when *A. flavus* interacted with *B. tequilensis* and *B. velezensis* (Wu et al. 2022). The two bacterial species may have emitted secondary metabolites that regulate the related gene transcription of *A. flavus* to inhibit growth and aflatoxin production. Another similar effect of metabolites produced by *B. subtilis* on *A. carbonarius* growth has been reported by Jiang et al. (2020). In addition, *B. velezensis* and *B. subtilis* have been reported to reduce ochratoxin production in *A. carbonarius* and *A. niger*, respectively, while decreasing the growth of the fungus (Yassein and Elamary 2021; Silveira et al. 2022). Furthermore, volatile compounds produced by *B. sporothermodurans* and *B. megaterium* have been reported to inhibit spore germination and mycelial growth in *A. fumigatus* (Mannaa and Kim 2018; Osaki et al. 2021).

1.4. Regulatory mechanisms of Aspergillus spp. and Bacillus spp.

The process of exchanging and utilizing secondary metabolites between *A. sydowii* and *B. subtilis* to produce new compounds is facilitated by the upregulation of key enzymes such as hydroxylase, hydrolase, and acyltransferase (Sun et al. 2023). Many of those compounds exhibit antifungal properties as explained above. Li et al. (2022) have identified some of the antifungal secondary metabolites produced by *Bacillus* spp. as fengycin and iturins, which could inhibit the spore germination, and abnormal expansion of hyphae and cell rupture by downregulating genes involved in ribosome biogenesis (NOG1, KRE33) and aflatoxin biosynthesis (aflK, aflR, veA, omtA) pathways in *A. flavus*. Moreover, the differential transcriptomic analysis showed that the iturin A produced by *B. subtilis* has downregulated the expression of genes related to the cell membrane, osmotic pressure, transport, energy metabolism, and oxidation-reduction processes, which led to swelling of the cells, thinning of the cell wall and membranes, and inhibiting spore germination in *A. carbonarius* (Jiang et al. 2020). As such, iturin A produced by *B. subtilis* performs a crucial role in inhibiting *A. carbonarius* by changing the fungal cell structure and disturbing osmotic pressure, transport, and energy metabolisms.

El-Sayed et al. (2021) reported that the release of antifungal compounds by *B. subtilis* not only inhibits *A. flavipes* growth but also triggers its Taxol biosynthesis through intimate bacterial–fungal interaction. Here, proteomic analysis identified 106 proteins with notable upregulation and downregulation in key metabolic processes. Except for *B. subtilis*, *B. megaterium* shows a similar inhibitory effect on *A. flavus* and *A. candidus* as well by producing mainly 5-methyl-2-phenyl-1H-indole as the active antifungal volatile compound (Mannaa, Oh, and Kim 2017; Mannaa and Kim 2018), and down-regulated the expression of aflatoxin pathway gene cluster (aflF, aflT, aflS, aflJ, aflL, and aflX) in *A. flavus* (Kong et al. 2014).

2. *Aspergillus niger* and *B. subtilis*

Aspergillus niger and *B. subtilis* are key index species in their respective genus due to their widespread applications in biotechnology and research. Therefore, those two species have been selected in this review to analyze their interaction in depth.

2.1. Introduction to A. niger

Aspergillus niger, a filamentous fungus known as a prominent cell factory, is extensively used in industrial biotechnology to produce enzymes like cellulases, pectinases, and xylanases, as well as organic acids such as citric acid (Kumar, Sharma, and Sarkar 2011; Krijgsheld et al. 2012; Oyeleke et al. 2012; Behera 2020; Li et al. 2020). In 1917, James Currie discovered that *A. niger* could create citric acid from sugar using the surface fermentation method. This finding served as the foundation for *Aspergillus*'s application in industrial production (Cairns, Nai, and Meyer 2018; Corbu et al. 2023). *A. niger* produces higher citric acid yields than other microorganisms by fermenting diverse inexpensive materials (Show et al. 2015). As such, the ability of *A. niger* to produce enzymes that aid in the digestion of complex carbohydrates and fibers could facilitate recycling of nutrients in ecosystems (Kržišnik and Gonçalves 2023). In addition, *A. niger* can form biofilms, particularly in response to nutrient limitations or environmental stress. These biofilms have been shown to enhance the degradation of organic substrates and plastic waste, making them highly effective in waste management and bioprocessing applications (Mathur, Mathur, and Prasad 2011).

2.2. Introduction to *Bacillus subtilis*

Bacillus subtilis is a well-known Gram-positive, rod-shaped model bacterium with outstanding capabilities as a probiotic, biofertilizer, and enzyme producer. Its role in promoting plant growth highlights its biotechnological importance (Gómez-Godínez et al. 2023; Mourouzidou et al. 2023). Moreover, it is widely recognized for producing antibiotics (Miao et al. 2024) and extracellular enzymes such as proteases, amylases, and lipases (Kumari and Rajas 2023; Lee and Moon 2023), which have significant industrial applications (Chen et al. 2019). Furthermore, *B. subtilis* is well-known for forming biofilms, that play a crucial role in environmental adaptation, stress resistance, and host interaction (Vlamakis et al. 2013). On a molecular level, the biofilm matrix comprises polysaccharides, proteins, and extracellular DNA (eDNA), which provide structural integrity and protect the cells within hostile environments.

2.3. Interaction between *Aspergillus niger* and *Bacillus subtilis*: co-growth and metabolism

Bacillus subtilis produces antifungal compounds (Mohammadipour et al. 2009; Meena and Kanwar 2015), but interestingly, it also forms biofilms on fungal hyphae (Benoit et al. 2015). When *B. subtilis* co-inoculated with *A. niger*, the bacteria adhere and colonize the surface of the fungal mycelium, damaging the cell wall, leading to its lysis (Podile and Prakash 1996). At 0, 6, and 12 h of the co-inoculation, *B. subtilis* has reported to significantly suppress *A. niger* growth achieving over 90% inhibition, with lower inhibition for older fungal cultures (Podile and Prakash 1996). On the contrary, it has also been reported that *B. subtilis* proliferates on *A. niger*'s hyphae while facilitating co-growth (Benoit et al. 2015). Currently, an increasing interest can be seen in the scientific world in studying these astonishing interactions between *B. subtilis* and *A. niger*, especially when they form biofilms.

2.4. Regulatory mechanisms of *Bacillus subtilis* in co-culture with *Aspergillus niger*

In co-culture, *B. subtilis* is capable of secreting various lipopeptides such as surfactins, iturins, and fengycins regulated by several genes, viz., *srf*, *sfp*, *degQ*, *aspAT*, and *yczE* (Kim et al. 2017; Gao et al. 2022; Yaraguppi et al. 2023; Yin et al. 2023). These lipopeptides have been reported to inhibit fungal growth, reduce fungal-mediated acidification, or even kill fungal cells (Mohammadipour et al. 2009; Meena and Kanwar 2015; Richter et al. 2024). Some *B. subtilis* strains block fungal-mediated acidification of the medium during co-cultivation with several *Aspergillus* species including *niger*, indicating an advantage of increased spreading by *B. subtilis* during competition for space and nutrients on a surface (Richter et al. 2024). In nutrient-poor environments, *B. subtilis* may switch to the biofilm-forming mode as a survival strategy, using the fungal hyphae as a surface to establish biofilms and enhance resource acquisition. The microhabitat created by the mycelium network of *A. niger* has been reported to maintain a water layer surrounding fungal hyphae and facilitates *B. subtilis* to cover a larger area, reaching more nutrients (Abeysinghe et al. 2020; Richter et al. 2024). *Bacillus subtilis* uses quorum sensing to regulate biofilm formation. In response to signals, particularly from fungal hyphae, that is, molecules that can act as signals to bacteria (Wang, Zeng, et al. 2024c) or external stresses, the bacteria can change their gene expression, leading to biofilm formation (Benoit et al. 2015). Interestingly, it has been reported that the attachment of *B. subtilis* cells on *A. niger* mycelium is possibly dependent on living *A. niger* mycelium or on specific cell wall components, and this process could also be facilitated with the proteins produced by *A. niger* (Benoit et al. 2015; Fifani et al. 2022). Moreover, *B. subtilis* produces an extracellular matrix, which consists of proteins like TasA and extracellular polymeric substances (EPS), which allows the bacteria to adhere to fungal hyphae, providing a stable environment for the bacteria and enabling the colonization of fungal structures (Romero et al. 2010; Arnaouteli et al. 2021).

In addition, *A. niger* and *B. subtilis* exhibit significant transcriptional changes. For *A. niger*, ca. 5.4% (786 genes) of its genome has reported to show altered expression when exposed to *B. subtilis* (Benoit et al. 2015). Among these, 47% were upregulated, and 53% were downregulated, particularly genes involved in detoxification/secondary metabolite production (15%) and carbon metabolism (10%). Notably, genes related to fungal cell wall biosynthesis, such as those for chitin synthesis, are upregulated, suggesting enhanced structural support. About 25% of the altered genes encode hypothetical proteins of unknown function, and some are linked to fungal defense mechanisms. For *B. subtilis*, the interaction has reported to trigger expression changes in around 7% (279 genes) of its genome, particularly genes involved in late sporulation and anaerobic metabolism, indicating a shift toward a sessile lifestyle (Benoit et al. 2015). Genes related to motility, autolysis, and stress response are downregulated. Interestingly, surfactin, a key antibiotic and biosurfactant produced by *B. subtilis* are reduced in the presence of *A. niger*, possibly due to downregulation of the srfA operon: However, Richter et al. (2024) showed that some of the *B. subtilis* strains enhance surfactin production leading to inhibiting fungal growth and acidification of the environment. These characteristics were explained by specific mutations in the DegS–DegU two-component system. Co-evolutionary dynamics of *B. subtilis*–*A. niger* interaction have led to mutual adaptation, including secondary metabolite production and inhibition of *A. niger* growth. These transcriptional changes reflect the complex and multifaceted nature of microbial interaction, impacting both metabolism and secondary metabolite production in both organisms.

Transcriptomic analyses during biofilm development have identified regulatory pathways controlled by master regulators like Spo0A, which coordinate the transition of *B. subtilis* from planktonic growth to biofilm formation (Hamon and Lazazzera 2001; Verhamme, Murray, and Stanley-Wall 2009; Vlamakis et al. 2013). It has been reported that the Spo0A enables *B. subtilis* to make an attachment to the fungal hyphae (Kjeldgaard et al. 2019), possibly regulating genes that encode proteins that contribute to attachment.

TasA, a protein in *B. subtilis* biofilms, assembles into ordered fibrils that contribute to the biofilm's extracellular matrix (ECM) (Chai, Zaburdaev, and Kolter 2024). Its assembly is triggered by environmental factors like pH reduction or the presence of hydrophobic surfaces. TasA interacts with TapA, a chaperone-like protein, to accelerate fibril formation. Depending on the ratio of TasA to TapA, the fibrils can vary in structure ranging from TasA-rich fibrils to branched or capped forms. This regulated assembly of TasA fibrils helps organize the ECM, providing structure and stability to biofilms. Recently, it has been reported that the N-terminal tail of TapA is necessary for the structured biofilm formation, suggesting that the strand-exchange fibrils are the active form in the biofilm matrix (Arnaouteli et al. 2021; Bamford et al. 2024). Furthermore, TasA interacts with other biofilm matrix proteins and modulates biofilm development, especially when colonizing fungal hyphae (Kjeldgaard et al. 2019). The hyphal biofilm formation by *B. subtilis* was diminished by deletion of spo0A, epsA-O, or TasA genes (Kjeldgaard et al. 2019) and mutations to TapA genes (Arnaouteli et al. 2021).

Dual-species biofilms can gain unique characteristics as compared to their respective monoculture colonies, altering their metabolism during interaction (Benoit et al. 2015; Duanis-Assaf et al. 2018). Kjeldgaard et al. (2019) demonstrated that the biofilm matrix components of *B. subtilis* are essential for colonization on the hyphae of *A. niger*. In addition, the secretion of these matrix components is sufficient to rescue biofilm formation of matrix deficient strains suggesting that social interaction shapes the co-evolution of fungi and bacteria in the environment.

An overview of the complex interactions explained above is depicted in Figure 1.

3. Applications of *Bacillus subtilis* and *Aspergillus niger*

Bacillus subtilis and *A. niger* have been explored for their potential in biofertilizers, where they promote nutrient solubilization and root colonization (Sivasakthi, Usharani, and Saranraj 2014; Escobar Diaz et al. 2021). Studies have shown that their biofilms enhance plant growth by improving the uptake of minerals such as phosphorus and iron (Kalayu 2019). Moreover, *B. subtilis* and *A. niger* have demonstrated long-lasting effects on crop protection (Sivasakthi, Usharani, and Saranraj 2014), as the biofilm matrix provides a stable environment for these microorganisms to exert biocontrol over plant pathogens (Rafique et al. 2015).

In biotechnology, *B. subtilis* is widely used for its ability to express and secrete heterologous proteins, making it a model organism for industrial enzyme production (Das and Prasad 2010). Its biofilm-forming ability enhances its role as a biocontrol agent, as biofilms enable robust root colonization and long-term protection against pathogens in agricultural applications (Khezri et al. 2011; Wang et al. 2018).

In the human gut, *B. subtilis* biofilms act as a potential probiotic strategy, helping maintain gut health by improving colonization and protecting

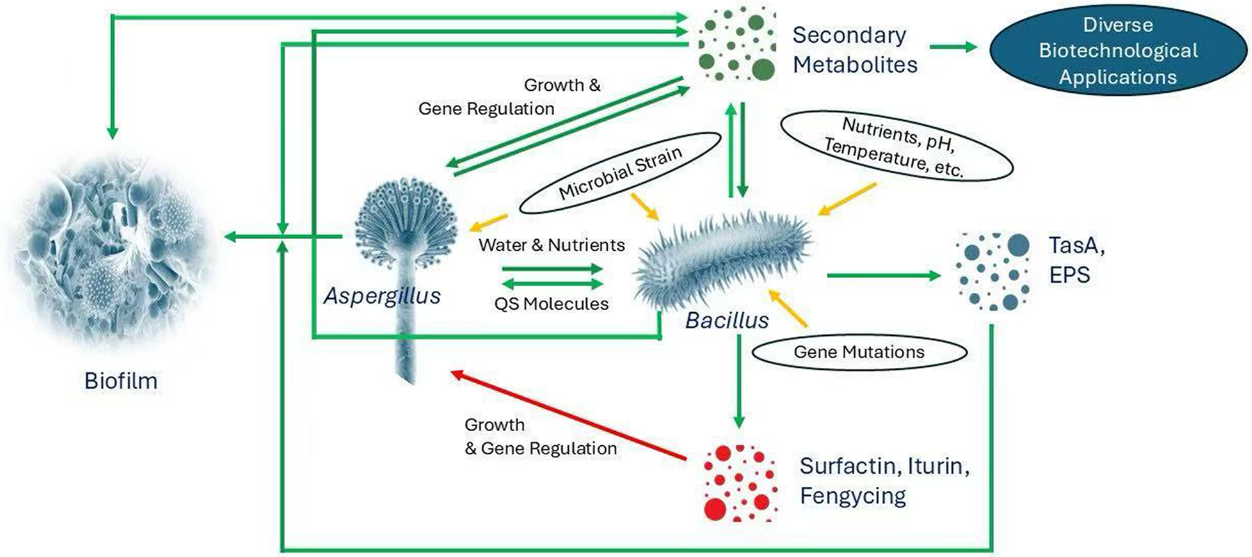

Figure 1. An overview of the complex interactions between *Aspergillus* and *Bacillus*. Arrows: Red—inhibition, green—promotion/production, and orange—affect.

beneficial microbes from gastrointestinal stresses. *Bacillus subtilis* biofilms shield the cells from low pH and bile salts, thereby enhancing their persistence in the gut environment (Elshaghabee et al. 2017; Larsen et al. 2014). Moreover, the biofilm matrix has been found to modulate immune responses, protect the intestinal barrier, and prevent the colonization of pathogenic bacteria, suggesting potential therapeutic uses in treating inflammatory bowel disease (Palkovicsné Pézsa et al. 2022).

3.1. Applications of Aspergillus spp. and Bacillus spp. in diverse fields

Diverse applications of *Bacillus* species*: B. subtilis*, *B. velezensis*, *B. licheniformis*, *B. pumilus*, *B. cereus*, *B. amyloliquefaciens*, *B. megaterium*, and *B. circulans*, and *Aspergillus species: A. brasiliensis*, *A. sydowii*, *A. violaceofuscus*, *A. niger*, *A. versicolor*, *A. flavipes*, *A. oryzae*, *A. flavus*, *A. fumigatus*, and *A. kawachii* are depicted in Table 1.

The use of monocultures and co-cultures of numerous *Aspergillus* and *Bacillus* species is highlighted in the fields of agriculture and crop protection, bioremediation, environmental biotechnology, food science and fermentation, industrial biotechnology, and medical biotechnology and health (Table 1). Most of the applications have focused on synergy and metabolic optimization of the microbes to achieve more productivity.

4. Future perspectives

Understanding the interaction of *Aspergillus* and *Bacillus* species has facilitated to evolution of their applications from use in agriculture for pathogen inhibition and plant growth promotion to novel applications such as complex biocontrol strategies and stress resilience, pollutant degradation, bio-catalytic approaches, producing bioactive compounds, nanoparticles, and enzymes, optimizing processes in wastewater treatment and fermentation, improving nutrient content and fermentation quality, and generating health-promoting bioactive molecules. Overall, the trend reveals increasing reliance on microbial synergy and metabolic engineering to enhance sustainability and efficiency in agriculture, environment, food, and health industries. In addition, challenges remain in optimizing biofilm formation conditions, and *in silico* animal and human models would be beneficial for ensuring that the developed/engineered biofilms are stable and safe for use in health-related applications.

5. Conclusion

Cross-feeding mechanisms play a crucial role in shaping growth and biofilm formation in *Aspergillus* and *Bacillus*, indicating that the metabolic exchanges between these two organisms are vital for their survival and ecological success. The production of EPS, fibrils like TasA, and signaling from living fungal hyphae seem to be essential in forming syntrophic biofilm communities. Environmental conditions, such as nutrient availability and pH levels, species type, and gene mutations, especially in EPS-producing genes may influence whether *Bacillus* will act antagonistically or synergistically with *Aspergillus*. This flexibility in behavior features the adaptive strategies that these microbes

Table 1. Biotechnological applications involving both *Aspergillus* spp. and *Bacillus* spp. across diverse fields.

Field of application	Microbial species	Growth mode	Application/outcome	References
Agriculture and crop protection	*Bacillus subtilis* MZ133755, *Bacillus subtilis* MZ133476, *Bacillus velezensis* MZ133757, *Aspergillus brasiliensis* MZ133758, *Aspergillus sydowii* MZ133759, and *Aspergillus* sp. MZ133456	Co-culture	Enhanced cotton growth through optimized concentrations of microbial species.	Escobar Diaz et al. (2021)
	Aspergillus sydowii and *Bacillus subtilis*	Co-culture	Increased production of metabolites with antibacterial properties, useful for biocontrol.	Sun et al. (2022)
	Aspergillus violaceofuscus and *Bacillus licheniformis*	Co-culture	Enhanced tomato growth and potassium uptake in drought conditions, indicating effective biostimulation.	Muthuraja, Muthukumar, and Natthapol (2023)
	Aspergillus spp. and *Bacillus licheniformis*	Monoculture	Volatile compounds exhibited strong inhibition of *Aspergillus* and *Penicillium* pathogens.	Ul Hassan et al. (2019)
	Aspergillus carbonarius and *Bacillus velezensis*	Monoculture	Volatile compounds showed antifungal properties and could be used for biofungicide applications against *Aspergillus carbonarius* in grapes.	Silveira et al. (2024)
	Aspergillus flavus and *Bacillus* spp.	Monoculture	Significant inhibition of aflatoxin B1 production and growth of *Aspergillus flavus* in maize.	Bluma and Etcheverry (2006)
	Aspergillus flavus and *Bacillus* sp. R2	Monoculture	Inhibition of *Aspergillus flavus* growth and prevention of contamination in unhulled rice.	Wang, Zhang, et al. (2024d)
Bioremediation	*Aspergillus niger* and *Bacillus subtilis*	Monoculture	Effective degradation of Endosulfan.	Ahmad (2020)
	Aspergillus niger and *Bacillus subtilis*	Monoculture and co-culture	Combined culture enhanced 2-naphthol degradation efficiency, and reduced toxic metabolite accumulation.	Zang et al. (2010)
	Bacillus subtilis and *Aspergillus niger*	Co-culture	Improved growth and cadmium tolerance in wheat plants.	Bashir et al. (2022)
	Bacillus licheniformis and *Aspergillus violaceofuscus*	Co-culture	Improved tomato growth and potassium uptake under saline conditions.	Muthuraja and Muthukumar (2022)
	Bacillus subtilis, *Aspergillus niger* and *Aspergillus flavus.*	Co-culture	Demonstrated significant potential for bioremediation of Endosulfan.	Ahmad (2020)
	Aspergillus flavus complex and *Bacillus* cereus group.	Biofilm	Biofilm formation enhanced the degradation of hexadecane, showcasing collaborative effects between microbial communities.	Perera et al. (2019)
	Aspergillus oryzae M4 and *Bacillus licheniformis* B1	Co-culture	Co-culturing enhanced the degradation of beta-Cypermethrin and 3-Phenoxybenzoic acid.	Zhao et al. (2016)
	Bacillus subtilis YB1, *Aspergillus niger* YF1	Co-culture	Nicosulfuron is efficiently degraded by the combined action of the two species.	Lu et al. (2012)
	Aspergillus niger, *Bacillus circulans*	Co-culture	Up to 39% removal of alumina from iron ore slime.	Pradhan et al. (2006)
	Aspergillus sp. and *Bacillus* sp.	Biofilm	Biofilm with the two microbes reduced the lag in crude oil degradation.	Perera et al. (2021)
Environmental biotechnology	*Aspergillus niger* (Ch4/07) and *Bacillus subtilis*	Monoculture and Biofilm	Induced calcium carbonate and oxalate crystallization on calcite marbels.	Sazanova et al. (2020)
	Aspergillus niger and *Bacillus subtilis*	Monoculture	Biosynthesized Ag-doped ZnO nanorods show superior antifungal properties compared to commercial antibiotics.	Rilda et al. (2024)
	Aspergillus niger and *Bacillus subtilis*	Monoculture	Potential for lignocellulose degradation, improved biomass treatment.	Maryanty et al. (2021)
	Bacillus sp. (BK1) and *Aspergillus* sp. (BK2)	Co-culture	Successfully demonstrated in-situ bioremediation of nitrogen and phosphorus in wastewater management.	Bhambri, Karn, and Singh (2021)
	Aspergillus spp. and *Bacillus pumilus* (MSH)	Monoculture	An antifungal compound produced and showed activity against *Mucoraceae* and *Aspergillus* species.	Bottone and Peluso (2003)
Food science and fermentation	*Aspergillus niger* and *Bacillus subtilis*	Monoculture and co-culture	Improved digestibility, increased gas production, enhanced crude protein and fiber content in date palms.	Kouhsar et al. (2021)
	Aspergillus niger 2106 and *Bacillus subtilis* 10071	Monoculture and co-culture	Co-fermentation led to an increase in amino acids, fatty acids, and peptides in black soldier fly larvae.	Liu et al. (2022)
	Aspergillus niger ATCC 20345, *A. niger* ATCC 9142, *Bacillus subtilis* ATCC 21556	Monoculture	Improved protein, ether extract, and nutrient digestibility of pomegranate.	Güngör, Altop, and Erener (2020)
	Aspergillus flavus and *Bacillus subtilis* E11	Monoculture	Effective in inhibiting *Aspergillus flavus* growth in dried red chili.	Yuan et al. (2023)
	Aspergillus niger ATCC 9142 and *Bacillus subtilis* ATCC 21556	Monoculture	Improved crude protein and ash content and reduced crude fiber in the sweet cherry kernel.	Altop, Gungor, and Erener (2020)
	Aspergillus oryzae and *Bacillus amyloliquefaciens*	Co-culture	Significant alterations in metabolomic profiles that enhance sensory qualities in rice koji.	Lee et al. (2016)
	Aspergillus westerdijkiae fc-1 and *Bacillus* velezensis E2	Monoculture	Effective degradation of ochratoxin A and biocontrol against pathogenic fungi like *Aspergillus westerdijkiae* fc-1.	Zhang et al. (2022)
	Aspergillus oryzae and *Bacillus amyloliquefaciens*	Co-culture	Different inocula permutations significantly influenced enzyme activity and metabolite profiles during fermentation.	Gil et al. (2018)
	Bacillus subtilis KCCM 10673P and *Aspergillus oryzae* KCTC 10258BP	Monoculture	Found safe and effective as feed additives, enhancing animal health and performance.	Rychen et al. (2018)
	Bacillus subtilis X1 and *Aspergillus* fumigatus M1	Co-culture	Fermentation with these strains for 6 days produced quality values comparable to 35 days of natural fermentation in Qingzhuan brick tea.	Xu et al. (2019)
	Bacillus amyloliquefaciens and *Aspergillus oryzae*	Co-culture	Identified aroma compounds enhancing sensory quality in koji products.	Seo et al. (2018)
	Bacillus velezensis and *Aspergillus oryzae*	Co-culture	Fermentation enhanced amino-type nitrogen in Meju with separate inoculation, and glucose and fatty acids with co-inoculation.	Gil et al. (2021)
	Bacillus subtilis and *Bacillus amyloliquefaciens*	Co-culture	Both strains effectively inhibited aflatoxin production in pistachios.	Siahmoshteh et al. (2017)
	Aspergillus flavus, *Bacillus subtilis* UTBSP1	Co-culture	Reduced fungal contamination and aflatoxin levels on pistachio nuts.	Farzaneh et al. (2016)
	Aspergillus oryzae, and *Bacillus subtilis*	Monoculture	Enhanced proteolytic activity was observed in casein degradation.	López-Fandiño et al. (1991)
	Aspergillus spp. and *Bacillus* cereus	Monoculture	Produced diketopiperazines and inhibited the growth of *Aspergillus* species in peanut kernels.	Kumar et al. (2014)

(*Continued*)

Table 1. Continued.

Field of application	Microbial species	Growth mode	Application/outcome	References
Industrial biotechnology	*Aspergillus niger* and *Bacillus subtilis*	Monoculture	Enhanced α-amylase production.	Abd El Mageed et al. (2022)
	Aspergillus niger NCIM 1054 and *B. subtilis* NCIM 2439	Monoculture	Enhanced α-amylase production.	Khadse and Babar 2018
	Aspergillus niger GIO and *Bacillus megaterium*.	Co-culture	Synergistic xylanase production.	Fasiku, Bello, and Odeniyi (2023)
	Bacillus subtilis, *Aspergillus oryzae*	Co-culture	Lytic enzymes from *Bacillus* circulans act on *Aspergillus oryzae*.	Horikoshi and Iida (1959)
Medical biotechnology and health	*Bacillus subtilis* and *Aspergillus kawachii*	Co-culture	*B. subtilis* fermented silkworm powder reduced alcohol-induced hepatotoxicity and oxidative stress.	Cha et al. (2012)
	Bacillus species Msh-1 and *Aspergillus* fumigatus	Monoculture	Selenium nanoparticles produced showing antifungal activity against *Aspergillus fumigatus* and *Candida albicans*.	Shakibaie, Salari Mohazab, and Ayatollahi Mousavi (2015)
	Aspergillus sp. CO2 and *Bacillus* sp. COBZ21	Co-culture	Significant induction of bioactive compounds with antimicrobial and antioxidant properties.	Hamed et al. (2024)
	Bacillus subtilis and *Aspergillus oryzae*	Monoculture	Enhances immunity, stimulates the production of antibodies, and enhances resistance against *Aeromonas hydrophila* and *Streptococcus iniae* infections in juvenile tilapia.	Iwashita et al. (2015)
	Aspergillus versicolor and *Bacillus subtilis*	Co-culture	Production of new compounds with antibacterial and anticancer properties.	Abdel-Wahab et al. (2019)
	Aspergillus flavipes and *Bacillus subtilis*	Co-culture	Taxol biosynthesis.	El-Sayed et al. (2021)

employ in diverse settings. The dual-nature (both antagonistic and synergistic) complex interaction activates silent genes synthesizing novel compounds mainly with antifungal and medicinal properties. This showcases the potential of their co-cultivation for diverse applications in various fields providing innovative biotechnological solutions. The trend in using *Aspergillus* and *Bacillus* species has evolved from simple monoculture applications to more sophisticated co-cultures, increasingly focusing on synergy and metabolic optimization.

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Authors' contributions

ZX and MP: Conceptualization, writing—original draft, writing—review and editing. JL: Writing—review and editing. GS: Writing—review and editing.

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ORCID

Zhenbo Xu http://orcid.org/0000-0003-2865-2441

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