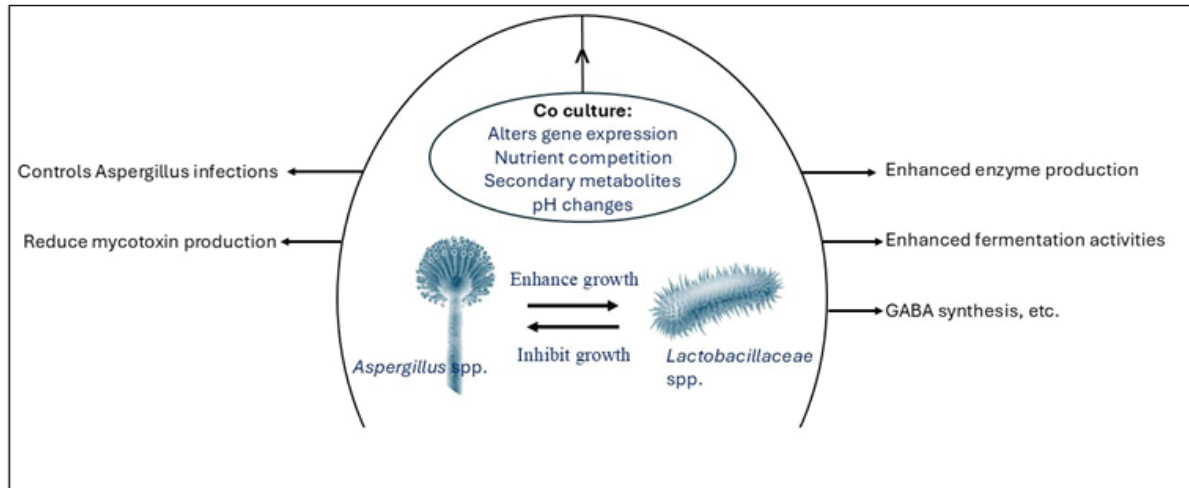


REVIEW ARTICLE

Current Knowledge on the Polymicrobial Interaction and Biofilm between *Aspergillus* and *Lactobacillaceae*: Regulatory Mechanisms and Applications

M. Premarathna*, R. Pathirana, U. Jayasundara, and G. Seneviratne



Highlights

- Lactobacillaceae includes over 300 species vital for fermentation and probiotics.
- They enhance the gut health, immune responses, and reduce inflammation
- *Lactobacillaceae* inhibit *Aspergillus* growth and aflatoxin production
- Co-cultures of *Aspergillus* and *Lactobacillus* enhance enzyme activities
- They reduce *Aspergillus* mycotoxins in food, improving quality

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Current Knowledge on the Polymicrobial Interaction and Biofilm between *Aspergillus* and *Lactobacillaceae*: Regulatory Mechanisms and Applications

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Abstract: The review aimed to evaluate the polymicrobial interactions between *Lactobacillaceae* and *Aspergillus* species, with a focus on their implications for food quality, fermentation enhancement, and biocontrol of fungal pathogens. We conducted a comprehensive literature search using PubMed, Google Scholar, and Scopus, covering publications from 1980 to 2025. More than 100 publications were screened, focusing on studies reporting direct interactions between *Lactobacillaceae* and *Aspergillus* species, and was analyzed and structured according to microbial strains, growth mode, mode of action, and applications. The *Lactobacillaceae* family consists of over 300 bacterial species, which metabolize carbohydrates to produce acids, aiding in food preservation. They also produce bioactive compounds with antifungal, antibacterial, and anti-inflammatory properties. *Lactobacillaceae* species, like *L. delbrueckii* and *L. johnsonii*, are used in dairy production and as probiotics, promoting gut health, immune responses, and inflammation reduction. *Lactobacillus plantarum*, *L. fermentum*, *L. buchneri*, *L. casei*, and *L. acidophilus* exhibit antagonistic effects on *Aspergillus* species such as *A. flavus*, *A. parasiticus*, *A. fumigatus*, and *A. carbonarius*. These *Lactobacillaceae* inhibit fungal growth and aflatoxin production by producing biofilms and antifungal metabolites, altering gene expression, nutrient competition, and pH changes. However, *Aspergillus* can enhance *Lactobacillaceae* growth in co-cultures. Co-cultures of *Aspergillus* species with *Lactobacillus*, such as *A. oryzae* with *L. plantarum* or *L. brevis*, enhance enzyme production, GABA synthesis, and fermentation activities in soy sauce and soybean pastes. Co-inoculation of *A. niger* and *Lactobacillus* sp. also improves lactic acid fermentation. Moreover, *Lactobacillaceae* controls *Aspergillus* infections in food, reducing mycotoxin production in grapes, olives, and peanuts. As such, polymicrobial interactions between *Aspergillus* and *Lactobacillaceae* have various applications in increasing food quality, enhancing fermentation, and biocontrolling of pathogens in agriculture.

Keywords: *Aspergillus*; Fermentation; Food quality; *Lactobacillaceae*; Polymicrobial interaction

INTRODUCTION

Introduction to the family *Lactobacillaceae*

The family *Lactobacillaceae* consists of over 300 species of bacteria belonging to 33 genera (Walter & O'Toole, 2023). In addition to genera such as *Pediococcus*, *Oenococcus*, and *Weissella*, the genus *Paralactobacillus*, and the family *Leuconostocaceae*, 25 genera were included in the *Lactobacillaceae* family in 2020 because

of the division of the former genus *Lactobacillus* due to the extraordinarily high level of genomic diversity in over 260 bacterial species (Zheng et al., 2020). Predominantly non-pathogenic Gram-positive bacteria in the *Lactobacillaceae* family colonize nutrient-rich environments, such as plants, food, feed, animals, and humans. They are non-spore-forming coccoid or rod-shaped cells that can be strictly or facultatively anaerobic (Biavati & Santini, 2007; Zheng et al., 2020). Their cell sizes and colony morphologies vary among species, with some forming smooth, creamy colonies on selective media like de Man, Rogosa, and Sharpe (MRS) agar, which is commonly used for their cultivation under anaerobic or facultatively anaerobic conditions (Kanak & Yilmaz, 2023). Identification of *Lactobacillaceae* species often involves a combination of phenotypic characterization, biochemical assays, and molecular methods such as 16S rRNA gene sequencing and Matrix Supported Laser Desorption/Ionisation Flight Time mass spectrometry (MALDI-TOF), enabling accurate differentiation of closely related genera and species (Kanak & Yilmaz, 2023). This diversity is fundamental to their adaptability and functionality in various environments, including fermented foods, human and animal microbiota, and industrial applications, and therefore, these microorganisms have a significant economic value (Ibrahim et al., 2016; Walter & O'Toole, 2023).

The fermentation of carbohydrates to produce lactate, acetate, and ethanol involves the metabolism of *Lactobacillaceae*, leading to their key traits, including acid production, rapid pH reduction, and competitive growth under acidic and saline conditions, which are crucial for food preservation through fermentation (Abedi & Hashemi, 2020; Walter & O'Toole, 2023). Moreover, the ability of *Lactobacillaceae* to acidify the microenvironment together with its bacteriocin production (Zhang et al., 2023) inhibits the proliferation of pathogenic microorganisms in the gut (Servin, 2004; Spinler et al., 2008) and vagina (Liu et al., 2023) of animals, potentially shaping microbiomes (Zhang et al., 2023). Beyond fermentation, *Lactobacillaceae* exhibit diverse metabolic processes, including proteolysis (Kieliszek et al., 2021), lipolysis (Coelho et al., 2022), bile acid hydrolysis (Begley, 2006), production of secondary metabolites (Zhang et al., 2023), and synthesis of bioactive compounds such as vitamins (LeBlanc et al., 2011). Owing

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to these varied actions, *Lactobacillaceae* have a unique role in microbiology and are considered the most extensively domesticated bacterial group.

An important aspect of studying *Lactobacillaceae* involves culturing techniques that allow for understanding microbial interactions in both isolated and combined environments. Coculturing techniques, where two or more microbial species are grown together either in direct interaction or as mixtures, are widely used to mimic natural microbial communities and explore synergistic metabolic functions (Selegato & Castro-Gamboa, 2023). In coculture, microbes may form structured communities known as biofilms, which involve surface attachment and secretion of extracellular polymeric substances, promoting cooperative survival and enhanced stress resistance. Biofilm formation by *Lactobacillaceae* and other microbes is a complex, multi-step process crucial in natural niches and industrial applications, influencing microbial stability and activity (Rather et al., 2021).

However, microbes can also coexist as free-living populations in coculture without forming biofilms, maintaining independent but simultaneous growth while potentially exchanging metabolites or signals. Such co-living states expand metabolic diversity, improve nutrient cycling, and can enhance bacteriocin production and other beneficial bioproducts. The interplay between biofilm and free-living growth modes in coculture impacts the ecological behavior and technological applications of *Lactobacillaceae*, including food fermentations, probiotics development, and bioremediation processes (Kaboré et al., 2018).

Lactobacillaceae are among the most common and economically significant bacterial taxa used as probiotics, particularly as ingredients in foods with claimed health benefits (Widyastuti et al., 2021). The health benefits of *Lactobacillaceae* have been studied in model systems, from insects to mammals, and through clinical research in humans (Walter & O'Toole, 2023). The *Lactobacillaceae* family, with its proven safety profile, health benefits, and metabolic flexibility, has significant potential for advancing food systems to promote sustainable, resilient, and healthy societies.

The *Lactobacillus* spp. are members of the family *Lactobacillaceae*. They are psychrophilic, non-spore-forming, rod-shaped, non-motile, Gram-positive, and facultative anaerobic (Feiner, 2006). Their nutritional needs are intricate, and they require a supply of carbohydrates, fatty acids or their esters, nucleic acid derivatives, vitamins, and salts (de Angelis & Gobbetti, 2016). The members of the genus *Lactobacillus* were historically characterized based on physiological characteristics (Salveti et al., 2022), however, the comparison of 16S rRNA gene similarity revealed that the diversity of lactobacilli is comparable to the diversity of an order rather than a genus (Zheng et al., 2020). In March 2020, the re-assignment of lactobacilli to an emended genus *Lactobacillus* (with *Lactobacillus delbrueckii* as a type species of the genus), *Pediococcus*, the revived genus *Paralactobacillus*, and 23 new genera was made (Zheng et al., 2020), indicating a

clear phylogenetic position of the microbes.

Lactobacillus spp. are key organisms in the production of dairy products (Salveti et al., 2022), especially they play a vital role in primary events during cheese ripening, that is, lactate, lactose, and citrate metabolism, lipolysis, and proteolysis (de Angelis & Gobbetti, 2016). These bacteria are unique producers of biosurfactants with industrial applications (Mouafo et al., 2022). Recent research has increasingly focused on *Lactobacillus* spp., driven by the discovery of new species and their diverse metabolites, including organic acids, bacteriocin, amino acids, exopolysaccharides, and vitamins (Tang et al., 2023a), which exhibit various properties such as antibacterial (Morais et al., 2017), antifungal (Bukhari et al., 2020; Li et al., 2024), antibiofilm (Morais et al., 2017), antioxidant (Mouafo et al., 2021), anticancer, and anti-inflammatory (Werning et al., 2022) activities.

Meanwhile, among the *Lactobacillus* spp of *Lactobacillus delbrueckii*, *Lactobacillus johnsonii*, *Lactiplantibacillus plantarum*, and *Lacticaseibacillus casei*, *Lactobacillus delbrueckii*, which belongs to the genus *Lactobacillus*, consists of six subspecies: *L. delbrueckii* subsp. *delbrueckii*, *L. delbrueckii* subsp. *bulgaricus*, *L. delbrueckii* subsp. *jakobsenii*, *L. delbrueckii* subsp. *lactis*, *L. delbrueckii* subsp. *indicus*, and *L. delbrueckii* subsp. *sunkii* (Baek et al., 2023). Strains of this species can be isolated from different ecological sources, such as dairy products, fermented foods, vegetables, and the human urogenital and intestinal tract (George et al., 2018). *Lactobacillus delbrueckii* is widely used in the fermented milk industry (de Jesus et al., 2024), in which *L. delbrueckii* subsp. *bulgaricus* is considered one of the most acid-producing lactic acid bacteria because of its ability to ferment sugars, such as glucose, fructose, and lactose, to produce lactic acid via homolactic fermentation (Jan et al., 2022; Yamamoto, 2024). In addition to its significant role in fermentation, *L. delbrueckii* is commercially used for a variety of probiotic functions (de Jesus et al., 2022; Tang et al., 2023b) and is considered safe for consumption. Moreover, *L. delbrueckii* can reduce the adhesion of pathogenic bacteria to the gut (Banerjee et al., 2009). *L. delbrueckii* treatment has been reported to reduce anxiety-like behavior and increase gut and brain glutamic acid decarboxylase (*gad*) gene expression in zebrafish (Olorocisimo et al., 2023). The importance of its industrial production and probiotic function has led *L. delbrueckii* to receive a great deal of attention from researchers (Song et al., 2021).

The other *Lactobacillus* spp of *Lactobacillus johnsonii* can be isolated from the gastrointestinal and vaginal tracts of vertebrates including poultry (Dec et al., 2018; Reed et al., 2022), rodents (Ravi et al., 2023; Wu et al., 2016), and humans (Guerrero-Preston et al., 2017; Leonard et al., 2014;). The prevalence of this bacterium across different environments is influenced by external factors, including dietary habits (Antonissen et al., 2016; Thompson et al., 2023), antibiotic use, and interactions with other microbes (Mason et al., 2012). Like other prominent *Lactobacillus* species, *L. johnsonii* is notable for its potential health benefits in regulating immune responses, pathogen

antagonism, reducing inflammation, and enhancement of the epithelial barrier, making it a strong candidate for probiotic applications (Arzola-Martínez et al., 2024; Zhao et al., 2024). To survive in the gut environment, *L. johnsonii* competes with other indigenous microbes and exhibits tolerance mechanisms against stressors (Bagon et al., 2021; Stavropoulou & Bezirtzoglou, 2020). *L. johnsonii* is enveloped by a protective outer protein layer known as the S layer (surface layer), a regularly arranged crystalline layer of proteins or glycoproteins that covers the bacterial cell wall and acts as a barrier against environmental stress while mediating host microbe interactions (Hynönen & Palva, 2013). Additionally, components such as teichoic acids, extracellular peptidoglycan, and capsular and exopolysaccharides provide protection, maintain cellular integrity, and facilitate adhesion to the host. Stress resistance is further enhanced by mechanisms involved in stress-sensing and export systems (Lebeer et al., 2008). It has been reported that *L. johnsonii* can produce higher levels of short-chain fatty acids (e.g., acetic acid and butyric acid) and lactic acid, which promotes the maturation of the host immune system while affecting the gut microbiota and metabolic profile (Arzola-Martínez et al., 2024; He et al., 2019; Richards et al., 2016).

The *Lactiplantibacillus plantarum* is a facultative heterofermentative bacterial species classified under *Lactiplantibacillus*, a genus established following the recent reclassification of the former *Lactobacillus* genus (Zheng et al., 2020). It is one of the most widespread and versatile species of lactic acid bacteria that can be found in dairy products, fish, meat, vegetables, wine, silage, gastrointestinal, urogenital, and vaginal tracts. Several studies carried out in the past few decades have reported the beneficial effects of *L. plantarum*, primarily on gastrointestinal health (García-González et al., 2021; Nordström et al., 2021). It is safe for human consumption and does not possess antibiotic resistance. Compared to other lactic acid bacteria species, *L. plantarum* has a larger genome, consisting of numerous genes responsible for its robust adaptability, versatility, and massive diversity in phenotypic properties (Seddik et al., 2017). This genetic makeup supports its broad metabolic capacity and a wide range of industrial applications. As a lactic acid bacteria species, *L. plantarum* is usually applied in fermented foods, including cheese, yogurt, cakes, and bread, and it plays a crucial role in enhancing food safety during the fermentation process (Zapašnik et al., 2022). In addition to the fermentation industry, *L. plantarum* produces peptides, organic acids, and volatile compounds that play crucial roles in fungal growth inhibition and mycotoxin removal via binding or biodegradation mechanisms (García-González et al., 2021; Li et al., 2023). The continuous increase in the number of publications in recent years reflects the significance of *L. plantarum* in fungal antagonism and biodegradation.

The *Lacticaseibacillus*, formerly known as *Lactobacillus casei*, is a representative genus of lactic acid bacteria. The members of *Lacticaseibacillus* are considered probiotics and they have many applications in the food industry, especially in fermentation (Bellaver et al., 2024; Sultana et

al., 2023). It has been reported that *L. casei* shows several nutritional and health-promoting functions, including intestinal pathogen inhibition, immune system regulation, microbiota-gut-brain axis modulation (Balasubramanian et al., 2024; Hill et al., 2018), obesity treatment, cardiovascular disease prevention (Ibrahim et al., 2023; Pimentel et al., 2021), and antihypertensive actions (Pimentel et al., 2021), contributing to a gradual increase in consumer demand for *L. casei* (Ma et al., 2024).

Introduction to the genus *Aspergillus*

In 1729, Italian botanists and priests Pietro Antonio Micheli observed fungal spore heads resembling a device used in Roman Catholic rituals, called an *Aspergillum* (Scazzocchio, 2009). *Aspergillus* is one of the most common genera with more than 250 known species of filamentous cryptic fungi in the *Ascomycetes* family, which is known for its asexual reproduction through conidiophores, that is, structures bearing spores (Geiser et al., 2008). *Aspergillus* succeeds in diverse and extreme environments, especially in those with poor nutrient levels and extreme pH, salinity, and temperature conditions (El-Hawary et al., 2020). They can adjust to different environments by having special structural components such as aerial hyphae, rodlet layer on their surfaces, functions in spore dispersion and fixation, and nutritional versatility (Gresnigt et al., 2014; Kwon-Chung & Sugui, 2013). Most *Aspergillus* species have been isolated from almost all major biomes, but soil remains their primary habitat. Some species of *Aspergillus* have been isolated from litter and play a vital role in organic matter degradation and nutrient recycling in ecosystems (Embacher et al., 2023; Klich, 2002). However, some species are recognized as agricultural pests that accompany risks to global food security (Nji et al., 2023).

The ability of *Aspergillus* to produce various degrading enzymes allows them to saprotrophically infect diverse hosts (Mellon et al., 2007). It has been reported that the *Aspergillus* sections i.e. *Fumigati*, *Flavi*, *Nigri*, *Terrei*, and *Nidulante* can cause diseases in humans (Sugui et al., 2015). Particularly in the respiratory tract, they have been reported to maintain diverse fungal-bacterial interactions that cause host immune responses (Santos-Fernandez et al., 2023). This could influence microbiome colonization and immunopathogenesis, leading to serious diseases such as chronic pulmonary aspergillosis (Rozaliyani et al., 2023), especially in people with weakened immune systems (MacAlpine et al., 2023). *Aspergillus fumigatus* is a well-documented candidate in this context. However, studies have shown that biofilm formation in *A. fumigatus* is inhibited when it comes into direct contact with *P. aeruginosa* due to antifungal compounds released by the latter (Briard et al., 2016). However, when the two organisms are physically separated, *P. aeruginosa* produces compounds that facilitate *A. fumigatus* to invade the lung parenchyma. Like *P. aeruginosa*, *Staphylococcus aureus* has also been reported to inhibit filamentation, conidiation, and biofilm maturation in *A. fumigatus* in various other mucosal areas of the human body (Ramírez Granillo et al., 2015).

Aspergillus can produce diverse biochemicals, including

organic acids, extracellular enzymes, and secondary metabolites, which play vital roles in ecosystems. In biotechnology, these biochemicals have been produced by co-cultivating *Aspergillus* with other microorganisms and are being used as novel bioactive products in diverse fields (Alanzi et al., 2023). In medicine, bioactive compounds such as cytochalasans, taxols, pentapeptides, notamides, and allianthrone are produced by *Aspergillus flavipes* (Wang et al., 2024a), *A. fumigatus* (Kumar et al., 2019; Wang et al., 2024b), *A. protuberus* (Kato et al., 2017), and *A. alliaceus* (Mandelare et al., 2018), respectively. In the food industry, *A. oryzae* is extensively used to produce amylases, proteases, and lipases for sake, soy sauce, and miso fermentation (Machida et al., 2008; Tanaka & Gomi, 2021). Beyond its role as a contaminant and producer of harmful mycotoxins, *Aspergillus* species play a pivotal role in food biotechnology, especially in fermentation processes that improve food quality and nutritional value (Tanaka & Gomi, 2021). Species such as *A. oryzae* and *L. plantarum* in co-culture are widely utilized in traditional, Asian fermentation for producing soy sauce, miso, sake, and other fermented foods (Zhang et al., 2022). In addition, *A. niger* is widely applied for citric acid production and in pectinase manufacturing for juice clarification (Dhillon et al., 2007). In horticulture, *A. niger* derived gibberellic acid and organic acids have been reported to enhance seed germination and plant growth (Mathur et al., 2022).

Among the secondary metabolites produced by *Aspergillus* species, aflatoxins are some of the most toxic and carcinogenic compounds, posing a severe threat to global food safety and public health (Wu & Khlangwiset, 2010). Aflatoxins, particularly produced by *Aspergillus flavus* and *Aspergillus parasiticus*, contaminate important agricultural products such as peanuts, maize, and tree nuts, leading to significant economic losses and health risks including acute poisoning and hepatocellular carcinoma. Therefore, mitigating aflatoxin contamination remains a critical focus in food microbiology and biotechnology. The antagonistic interactions of *Lactobacillus* species with *Aspergillus* are especially significant in this context, as these bacteria inhibit fungal growth and suppress aflatoxin biosynthesis through multiple mechanisms, including metabolite production and biofilm formation (Zhao et al., 2019).

This review evaluates the polymicrobial interactions between *Lactobacillaceae* and *Aspergillus* species, emphasizing their impact on food quality, fermentation enhancement, and biocontrol of fungal pathogens. A comprehensive literature search was conducted across PubMed, Google Scholar, and Scopus, covering publications from 1980 to 2025. Over 100 studies were screened, focusing on direct interactions between *Lactobacillaceae* and *Aspergillus* species. The findings were analyzed and organized by microbial strains, growth modes, modes of action, and applications.

Polymicrobial interactions between *Aspergillus* and *Lactobacillaceae*

The antagonism between *Lactobacillaceae* and *Aspergillus* species in co-culture is characterized primarily by suppression of fungal growth and toxin production,

which is a critical feature underlying their technological applications in food safety and biocontrol. This antagonistic interaction involves multiple mechanisms: *Lactobacillaceae* species outcompete *Aspergillus* for essential nutrients, lowering fungal biomass significantly (Magnusson et al., 2003). They produce diverse antifungal metabolites, including organic acids like lactic acid, cyclic dipeptides, and fatty acid derivatives, which disrupt fungal cell wall integrity, cause cytoplasmic leakage, and impair metabolic functions, resulting in reduced hyphal growth and spore germination (Crowley et al., 2013; Salman et al., 2022; Zhao et al., 2019). Additionally, the acidification of the microenvironment by *Lactobacillaceae* lowers pH to unfavorable levels for *Aspergillus* development, further inhibiting fungal proliferation (Nateghi et al., 2016). Biofilm formation by *Lactobacillaceae* on surfaces provides a physical barrier to *Aspergillus* colonization, limiting oxygen availability and space, thereby reducing fungal growth (Kachouri et al., 2014). These combined antagonistic features make *Lactobacillaceae* effective biological control agents against *Aspergillus* contamination and aflatoxin production, highlighting their utility in food fermentation and bio-preservation practices.

Aspergillus and *Lactiplantibacillus plantarum*

Lactiplantibacillus plantarum (previously known as *Lactobacillus plantarum*) completely inhibits *A. flavus* growth, decreases aflatoxin production by 93%, and destroys the cellular structure of hyphae and spores (Zhao et al., 2019). Here, *A. flavus* aflatoxin biosynthetic genes were downregulated, whereas genes implicated in the synthesis and organization of cell wall polysaccharides were upregulated. In another study, *L. plantarum* reduced *A. flavus* growth by up to 86% and aflatoxin production (Kachouri et al., 2014). The same study showed that *L. plantarum* formed biofilms on surfaces that inhibited the growth of *A. flavus* through oxygen competition. Moreover, Ahlberg et al. (2017) reported that *L. plantarum*'s biomolecules production with antifungal activity contributes to its strong antifungal activity against *A. flavus*. Similarly, cell-free supernatants from *L. plantarum* have been reported to inhibit the growth of *A. parasiticus* (Poornachandra Rao et al., 2019). The major antifungal compounds in the cell-free supernatants from *L. plantarum* were octanoic acid, butanamide, oleic acid, and decanoic acid derivatives. The cell-free supernatants from *L. plantarum* have been reported to cause significant damage to the hyphal wall of *A. parasiticus*, resulting in cytoplasmic leakage and the eventual destruction of the fungal structure. In addition, cell-free supernatants from *L. plantarum* inhibit the growth of *A. fumigatus* (Crowley et al., 2013). Here, antifungal cell-free supernatants from *L. plantarum* altered the expression of *A. fumigatus* genes, leading to metabolic shutdown and subsequent cell death. Ström et al. (2005) reported that *L. plantarum* produces antifungal metabolites such as cyclo (1-Phe-1-Pro), lactic acid, and 3-phenyllactic acid, which strongly affect the morphology of the *A. nidulans* mycelium and decrease the biomass up to 36% of the control. Here, the amount of several *A. nidulans*-proteins was also increased during co-cultivation and by all the inhibiting substances. Another

study reported that *L. plantarum* metabolites acted against conidiospore germination and mycelial growth in *A. carbonarius* (Djossou et al., 2011). Lappa et al. (2018) also reported that *L. plantarum* inhibited the growth of *A. carbonarius* by up to 88% while significantly reducing toxin production by up to 100%. Exposure to co-cultivation has resulted in differential expression of genes such as AcOTApks (*Aspergillus carbonarius* OTA polyketide synthase), AcOTAnrps (*Aspergillus carbonarius* OTA nonribosomal), and laeA, highlighting the impact of strain variability (Lappa et al., 2018). Here, laeA and AcOTAnrps were most influenced by the presence of *L. plantarum*.

***Aspergillus* and other *Lactobacillaceae* spp.**

During cogrowth, *Lactobacillaceae* spp. showed antagonistic effects on *Aspergillus* spp. It has been reported that *L. fermentum* reduced mycelial mass and total aflatoxin production in *A. parasiticus* by 77% and 99.9%, respectively, compared to controls ($p \leq 0.05$) (Ghazvini et al., 2016). Various factors, including nutritional competition, secondary metabolites, pH, and their combinations, have been proposed for the inhibition of *A. parasiticus* growth by *L. fermentum* (El-Nezami et al., 2002; Magnusson et al., 2003). Similarly, the diameter of *A. westerdijkiae* colonies was reduced by approximately 26-38% by *L. buchneri* (Iacumin et al., 2020). Reduction in fungal growth has also limited ochratoxin A production. *A. westerdijkiae* has been reported to depend on competition for nutrients and antimycotic factor production. Moreover, it has been reported that the mycelial growth and Aflatoxin B1 biosynthesis of *A. flavus* were inhibited by *L. casei* (Chang et al., 2007). This inhibitory activity was due to antiaflatoxinogenic extracellular metabolites produced in cell-free supernatant fluids of the culture broth of *L. casei*. Similarly, cell-free supernatants consisting of cyclic dipeptides from *L. coryniformis* with antifungal properties inhibited the growth of *A. flavus* (Salman et al., 2022).

A similar effect of *L. casei* on *A. flavus* was reported by Bueno et al. (2006). In this study, the mycelial dry weight of *A. flavus* was reduced to 85% and 73% by *L. rhamnosus* and *L. casei*, respectively. The pH decreases in mixed cultures when the *A. flavus* mycelial dry weight is reduced may play an important role in the inhibition. Additionally, *L. acidophilus* and *L. casei* have been reported to inhibit the growth of *A. parasiticus* by 86% and 70%, respectively, while downregulating aflR by up to 99.7% and 98%, respectively (Nateghi et al., 2016).

Although *Lactobacillaceae* spp. exhibit antagonistic effects on *Aspergillus* spp., in some instances *Aspergillus* spp. have been reported to contribute for the improved growth of *Lactobacillaceae* spp. In a co-culture, *A. parasiticus* has been reported to support the growth of *L. casei* (El-Gendy et al., 1981). In this study, reduced aflatoxin production by *A. parasiticus* was observed compared to that by monoculture. Elevated pH in the co-culture environment has favored the growth of *L. casei*. Additionally, the limited nutrient availability, influenced by the proliferation of *L. casei*, might have contributed to reduced aflatoxin synthesis. Moreover, other *Lactobacillaceae* members, including *L. coryniformis* and *L. fermentum*, show potent antiaflatoxinogenic activity through unique mechanisms like cyclic dipeptide production and strong suppression of fungal biomass. In addition to these antagonistic mechanisms, some co-cultures exhibit unexpected outcomes, such as *A. parasiticus* supporting the growth of *L. casei* while reducing its own aflatoxin synthesis. These findings are consolidated in Table 1.

Applications of the co-cultures of *Aspergillus* sp. and *Lactobacillaceae* sp.

In Table 2, we summarize the diverse applications and the related polymicrobial interactions between the different species of *Lactobacillaceae* and *Aspergillus* in co-culture/biofilm mode.

Table 1: Antifungal and antiaflatoxinogenic activities of different *Lactobacillaceae* sp. on *Aspergillus* sp.

Microbial species	Growth mode	Mode of Action (Gene Expression/Protein and Metabolic Changes)	Results	Reference
<i>A. Parasiticus</i> PTCC 5286 and <i>L. fermentum</i> PTCC 1744	Co-culture	Nutritional competition, secondary metabolites, and pH inhibit fungal growth. LAB metabolites reduced aflatoxins.	Reduced mycelial mass by 77% and aflatoxin by 99.9% compared to controls.	Ghazvini et al. (2016)
<i>A. flavus</i> ACCC 32656 and <i>L. plantarum</i> IAMU80070	Co-culture	Downregulated aflatoxin biosynthetic genes; upregulated cell wall polysaccharide genes.	Inhibited fungal growth, decreased aflatoxins by 93%, and damaged hyphae and spores.	Zhao et al. (2019).
<i>A. carbonarius</i> Ac29a, Ac33a, Ac47a, and ITEM5010, and <i>L. plantarum</i> T571c, 1645d, 345a, and 195a	Co-culture	Differential expression of AcOTAnrps, AcOTApks, and laeA genes.	Inhibited fungal growth (88%) and mycotoxin production (32-92%) in grapes.	Lappa et al. (2018)

Microbial species	Growth mode	Mode of Action (Gene Expression/Protein and Metabolic Changes)	Results	Reference
<i>A. flavus</i> Ap, TR2, and CF80, <i>L. casei</i> CRL 431, and <i>L. rhamnosus</i> CRL 1224	Co-culture	pH decreases reduced fungal growth and mycelial weight.	Reduced mycelial dry weight by 85% and 73% with <i>L. rhamnosus</i> and <i>L. casei</i> , respectively.	Bueno et al. (2006)
<i>A. parasiticus</i> ATCC 1551117, <i>L. acidophilus</i> , and <i>L. casei</i>	Co-culture	Downregulated aflR gene by 99.7% (<i>L. acidophilus</i>) and 98% (<i>L. casei</i>).	Inhibited fungal growth by 86% (<i>L. acidophilus</i>) and 70% (<i>L. casei</i>).	Nateghi et al. (2016)
<i>A. flavus</i> and <i>L. plantarum</i>	Biofilm	<i>L. plantarum</i> adhered to olive surfaces, inhibiting fungal growth through oxygen competition.	Reduced fungal growth (by 86%) and aflatoxin in olives.	Kachouri et al. (2014)
<i>A. flavus</i> ATCC 46283 and <i>L. plantarum</i>	Co-culture	Produced antifungal biomolecules.	Inhibited fungal growth.	Ahlberg et al. (2017)
<i>A. parasiticus</i> MTCC 411 and <i>L. plantarum</i> MYS44	Monoculture	Antifungal compounds (oleic acid, octanoic acid, butanamide, and decanoic acid derivatives) in supernatants caused cytoplasmic leakage.	Inhibited fungal growth and reduced aflatoxins in peanuts.	Poornachandra Rao et al. (2019)
<i>A. flavus</i> subsp. p. NRRL 2999, <i>L. plantarum</i> , <i>L. bulgaricus</i> , and <i>L. acidophilus</i>	Co-culture	Low-molecular-weight bacterial metabolites interfered with aflatoxin synthesis.	Inhibited fungal growth and aflatoxin production.	Gourama et al. (1995)
<i>A. flavus</i> and <i>L. coryniformis</i> BCH-4	Monoculture	Supernatants containing antifungal cyclic dipeptides inhibited fungal growth.	Inhibited <i>A. flavus</i> effectively.	Salman et al. (2022)
<i>A. fumigatus</i> Af293 and <i>L. plantarum</i> 16	Monoculture	Antifungal metabolites altered fungal gene expression, causing metabolic shutdown and cell death.	Fungal growth inhibited.	Crowley et al. (2013)
<i>A. nidulans</i> J283, <i>L. plantarum</i> MiLAB 393, and <i>L. coryniformis</i> MiLAB 123	Co-culture	<i>L. plantarum</i> produced antifungal metabolites such as cyclo(l-Phe-l-Pro), lactic acid, and 3-phenyllactic acid.	Reduced fungal biomass to 36%.	Ström et al. (2005)
<i>A. parasiticus</i> and <i>L. casei</i>	Monoculture and Co-culture	Increased pH in the co-culture supported <i>L. casei</i> growth. <i>L. casei</i> competed with fungi for nutrients.	<i>A. parasiticus</i> supported the growth of <i>L. casei</i> . Lesser aflatoxin production of <i>A. parasiticus</i> was observed.	El-Gendy et al. (1981)
<i>A. carbonarius</i> Ac 162 and Ac 164, and <i>L. plantarum</i>	Co-culture	<i>L. plantarum</i> produced antifungal metabolites	Inhibited mycelial growth and conidiospore germination.	Djossou et al. (2011)
<i>A. flavus</i> ATCC 15517 and <i>Lactobacillus casei</i> KC-324	Co-culture	Antiaflatoxigenic metabolites in supernatants inhibited fungal growth.	Reduced aflatoxin biosynthesis and mycelial growth in <i>A. flavus</i> .	Chang et al. (2007)

Table 2: Applications of *Lactobacillaceae* and *Aspergillus* co-cultures/biofilms, and their related polymicrobial interactions

<i>Lactobacillaceae</i> sp.	<i>Aspergillus</i> sp.	Application	Polymicrobial interaction	Reference
<i>Pediococcus pentosaceus</i> and <i>Lactobacillus crustorum</i>	<i>Aspergillus flavus</i>	Bio-preservation (aflatoxin control)	Co-culture of these LAB strains inhibited <i>A. flavus</i> mycelial growth and markedly reduced aflatoxin B ₁ levels (antagonistic interaction).	Yun et al. (2024)
<i>Lactobacillus plantarum</i>	<i>Aspergillus oryzae</i>	Fermentation (soy sauce koji)	Mixed inoculation in koji-making significantly increased enzyme activities (acid protease, β -glucosidase, pectinase) and raised levels of phenolics, amino acids and antioxidants in the final moromi compared to <i>A. oryzae</i> alone.	Zhang et al. (2022)
<i>Lactobacillus plantarum</i>	<i>Aspergillus oryzae</i>	Fermentation (legume flour protein enrichment)	Co-cultivation on legume flours (pea, lentil) led to the highest yields of microbially-derived amino acids and increased protein content. LAB enhanced fungal saccharification and overall nutritional quality of the substrate (synergistic metabolic interaction).	Kryachko et al. (2025)

In koji production, co-inoculation of *A. oryzae* with *L. plantarum* was shown to effectively stimulate the production of active substances and increase β -glucosidase, pectinase, and acid protease activities in soy sauce (Zhang et al., 2022; Table 2). Beyond soy-based fermentations, co-cultivation on protein-rich legume flours such as pea and lentil markedly increased microbial amino acid yields and overall protein content, indicating the potential of *Aspergillus* and *Lactobacillaceae* interactions in nutritional enhancement of plant-based foods (Table 2). Moreover, the co-culture of *A. oryzae* and *L. brevis* produces gamma-aminobutyric acid (GABA) by fermenting soybean paste (Kim & Ji, 2015). Another study reported that GABA and Angiotensin-I Converting Enzyme (ACE) activity was enriched in soybean fermented with the co-culture of *A. oryzae* and *L. brevis* (Jang et al., 2015). Here, changing the pH by microbes affected enzymes, such as proteases and glutamate decarboxylase (GAD). Similarly, the co-culture of *A. niger* and *Lactobacillus* sp. improved l-lactic acid fermentation from Jerusalem artichoke tubers (Ge et al., 2009). Here, the synthesis of inulinase and invertase from *A. niger* was increased by co-inoculation with *Lactobacillus* spp. The use of a combination of *A. niger* and *L. plantarum* as starter cultures enhances the malt quality of barley (Hattingh et al., 2014). Here, cell-free culture supernatants of *Aspergillus* had a stimulatory effect on β -glucanase and α -amylase production during malting. The broader involvement of *Aspergillus* and *Lactobacillaceae*

co-cultures in food fermentation, enzyme production, and other industrial applications is summarized in Table 3.

In addition, *L. plantarum* controlled *A. carbonarius* infection in grape berries with up to 71% inhibition and reduced mycotoxin production ranging from 32% to 92% (Lappa et al., 2018). Moreover, *L. plantarum* reduces *A. flavus* growth by up to 86% and decreases aflatoxin production in olives (Kachouri et al., 2014). *L. plantarum* adheres to the olive surface and probably produces a biofilm that inhibits the multiplication of *A. flavus* via oxygen competition. Similarly, *L. buchneri* reduced *A. westerdijkiae* growth and limited ochratoxin A production in short-seasoned dry-cured ham (Iacumin et al., 2020). Here, the diameters of the *A. westerdijkiae* colonies were reduced by approximately 26-38%. Poornachandra Rao et al. (2019) reported a reduction in toxins in food. In this study, cell-free supernatants from *L. plantarum* inhibited the growth of *A. parasiticus*, leading to reduced aflatoxin production in peanuts. Beyond toxin reduction, these co-cultures are also utilized to improve food processing and functional quality. For instance, *L. buchneri* limited ochratoxin A production in ham during curing, while *A. niger* and *L. plantarum* combinations improved enzymatic activities critical for malt quality. Additionally, various *A. oryzae* and *L. brevis* co-cultures enriched γ -aminobutyric acid (GABA) and enhanced ACE-inhibitory activity, highlighting their potential in developing functional foods (Table 3).

Table 3: Applications of co-cultures of *Aspergillus* sp. and *Lactobacillaceae* sp. in different fields

Microbial species	Growth mode	Mode of Action (Gene Expression, Protein & Metabolic Changes)	Remarks/Results	Reference
<i>Aspergillus westerdijkiae</i> and <i>Lactobacillus buchneri</i>	Co-culture	Nutrient competition and antimycotic factor production inhibited mold growth.	Reduced colony diameter by 26-38%, limiting ochratoxin A production in ham.	Iacumin et al. (2020)
<i>Aspergillus niger</i> MH1 and <i>Lactobacillus plantarum</i> B.S1.6	Co-culture	Fungal supernatants stimulated β -glucanase and α -amylase production in malting.	Co-culture enhanced barley malt quality.	Hattingh et al. (2014)
<i>Aspergillus oryzae</i> HY-04 and <i>Lactobacillus plantarum</i> HY-01	Monoculture and Co-culture	Co-inoculation increased pectinase, β -glucosidase, and acid protease activities in koji making.	Improved active substance production in soy sauce.	Zhang et al. (2022)
<i>Aspergillus oryzae</i> FMB S46471 and <i>Lactobacillus brevis</i>	Co-culture	Fermentation	Generated GABA through co-culture fermentation.	Kim and Ji (2015)
<i>Aspergillus oryzae</i> FMB S46471 and <i>Lactobacillus brevis</i> GABA 100	Co-culture	pH changes influenced protease and GAD enzymes.	Enhanced GABA and ACE activity in soybean fermented with co-culture.	Jang et al. (2015)
<i>Aspergillus niger</i> SL-09 and <i>Lactobacillus</i> sp. G-02	Co-culture	Enhanced synthesis of inulinase and invertase by co-inoculation.	Improved lactic acid fermentation from Jerusalem artichoke.	Ge et al. (2009)

CONCLUSION

The *Lactobacillaceae* family, with its diverse species, plays a vital role in food fermentation, probiotics, and health-related applications. Importantly, their antagonistic interactions with *Aspergillus* species provide one of the most promising natural strategies for reducing aflatoxin contamination, which remains the most critical global challenge associated with *Aspergillus*. By producing antifungal metabolites, altering gene expression, and competing for nutrients and oxygen, *Lactobacillaceae* significantly suppress both fungal growth and aflatoxin biosynthesis. Beyond biocontrol, synergistic co-cultures with non-toxicogenic *Aspergillus* species, such as *A. oryzae*, enhance fermentation processes and improve the nutritional quality of foods. Therefore, while *Lactobacillaceae-Aspergillus* interactions have broad biotechnological applications, their most impactful role lies in aflatoxin mitigation and food safety, with synergistic benefits in fermentation serving as complementary industrial applications. Future research should focus on translating in vitro findings into scalable, consistent applications in food systems, while addressing

challenges such as the limited understanding of molecular mechanisms underlying *Lactobacillaceae-Aspergillus* interactions. Efforts to optimize co-culture conditions and establish standardized protocols will be crucial for advancing industrial applications.

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DECLARATION OF CONFLICT OF INTERESTS

The authors declare no competing interests.

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