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# Lactic acid bacteria: A bio-green preservative against mycotoxins for food safety and shelf-life extension

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**REVIEW ARTICLE**

## Abstract

Mycotoxins produced from *Aspergillus*, *Penicillium*, and *Fusarium* cause food spoilages during handling and storage, owing to immense economic losses and serious human health concerns including immunosuppression and carcinogenic effects. Furthermore, these species are also known to produce mycotoxins. Aflatoxin B1 ($AFB_1$), zearalenone (ZEA), ochratoxin A (OTA), and deoxynivalenol (DON) are the most commonly occurring mycotoxins. The removal of mycotoxins from the contaminated food using lactic acid bacterias (LABs) has been proposed as a green, inexpensive, safe, and promising mycotoxin decontamination strategy. LABs can control the mycotoxin production following a series of steps, including, adsorption, metabolite interaction, and biodegradation. This article provides systematic review of LABs as bio-green preservative with anti-mycotoxin potential for sustainable food safety. This consolidated review may be of technical importance to understand detoxification mechanisms and potential interaction of compounds originated with mycotoxin degradation for target food before incorporation by the food industry.

*Keywords*: anti-mycotoxin; food safety; lactic acid bacteria; metabolite interaction; shelf-life

## Introduction

Fungal spoilage is a *major challenge* for food industries, leading to food sensory defects, food waste, economic losses, and public health concerns due to their toxins. Plant-pathogenic fungi are responsible for up to 20% loss of the global harvest yield, which is sufficient to take care of about 600 million individuals every year. In addition, fungal diseases of the five most cultivated food crops worldwide were assessed to annihilate about 125 million tons of produce annually (Almeida *et al.*, 2019). Certain fungal species secrete toxic secondary metabolites (mycotoxins), such as aflatoxins, ochratoxins, fumonisins, etc., which cause a major food safety issue for humans and livestock. According to the Food and Agriculture Organization report, 25% of the world's food crops are badly affected by mycotoxins during cultivation or storage (USDA, 2016). Thus, fungal mycotoxins in food are major concerns for producers, purchasers, researchers, and regulatory agencies. Various food products such as fruits, cereals, nuts, pulses, etc., have demonstrated the prevalence of mycotoxins as shown in Table 1.

Owing to the grave concerns over mycotoxins, there is an urgent need to establish alternative, eco-safe, and cost-effective approaches to overcome food mycotoxin contamination. As of late, the utilization of bio-preservatives, microorganisms, or their antimicrobial components for

**Table 1. Mycotoxins found in foods.**

| Fungus | Positive samples (%) | Mycotoxins | Detected foods | References |
|---|---|---|---|---|
| *Aspergillus flavus* *Aspergillus parasiticus* | 14.06 | Aflatoxins B1 | Dry nuts | Macri *et al.* (2021) |
| | 67.14 | Aflatoxins B1 | Vegetable oil | Poormohammadi *et al.* (2021) |
| | 41.1 | Aflatoxins M1 | Bovine milk | Pandey *et al.* (2021) |
| *Aspergillus niger*, *Aspergillus flavus*, and *Fusarium sp.* | 70 | Aflatoxins B1 | Dry fruits | Awan *et al.* (2021) |
| *Aspergillus niger*, *Aspergillus tubingensis*, and *Aspergillus flavus* | 5.26 | Ochratoxin A | Palm dates | Nikolchina and Rodrigues (2021) |
| | 0–100 | Ochratoxin A | Salami | Tolosa *et al.* (2020) |
| | 7.61 | Ochratoxin A | Milk | Turkoglu and Keyvan (2019) |
| *Monascus* spp. | Raw = 69.0<br>Dietary supplements = 35.1<br>Processed products = 5.7 | Citrinin | Fermented red rice | Twarużek *et al.* (2021) |
| *Aspergillus* spp. *Penicillium* spp. | 0–62<br>0–69 | Citrinin<br>Ochratoxin A | Supermarket food samples | Meerpoel *et al.* (2021) |
| | 30.8<br>17.5<br>33.3<br>Not detected | Aflatoxin $B_1$,T-2 toxin, Ochratoxin A, Deoxynivalenol | Dried shrimp, dried fish, and dried mussel products | Deng *et al.* (2020) |
| *Penicillum expansum* *Penicillum cyclopium* | 9.0 | Patulin | Dried fruits | Przybylska *et al.* (2021) |
| | 40 | Patulin | Strawberry | A-Reda and Sahib (2021) |
| | 21.8 | Patulin | Mango | Hussain *et al.* (2020) |
| *Fusarium poae, Fusarium equiseti,* | 8.2–12.3 | Fumonisin B1 | Cornmeal | Massarolo *et al.* (2021) |
| *Fusarium acuminatum, Fusarium sporotrichioides,* | 63.0 | Fumonisin B1 | Whole wheat | Iqbal *et al.* (2020) |
| *Fusarium graminearum, Fusarium cerealis, Fusarium culmorum* | Wheat/wheat flour = 4<br>Maize = 20<br>Paddy rice = 55 | Deoxynivalenol | Wheat, maize, paddy rice, wheat flour | Golge and Kabak (2020) |

food preservation, has received a flood of interest due to increasing demands from consumers to embrace more natural food preservation approaches instead of depending on manufactured synthetic compounds. Lactic acid bacteria (LABs) are ideal probiotic candidates for food as fungal antagonists (Nielsen *et al.*, 2021). LABs are utilized in traditional food fermentations and are considered as Generally Regarded as Safe (GRAS) and Qualified Presumption of Safety (QPS) by the American Food and Drug Agency (FDA) and the European Food Safety Authority (EFSA), respectively (Mora-Villalobos *et al.*, 2020). LABs are considered as "green preservatives" due to their potential to inhibit fungal growth in foods. Organic acids, diacetyl, bioactive anti-mycotic peptides, fatty acids, carboxylic acids, bacteriocins, hydrogen peroxide ($H_2O_2$), lactones, alcohols, and reuterin are the reported antifungal compounds produced by LABs (Sadiq *et al.*, 2019). This review provides a concise overview of the anti-mycotoxin potential of LABs as green biopreservative, along with its application in various food products.

## LABs

In order to address the two consumer health concerns caused by (1) fungal growth and mycotoxin release in foods and (2) use of chemical preservative in foods, there is a great demand to develop safe and effective antifungal methods to improve or replace the current chemical and physical treatments. Biological control is a strategy that uses microorganisms or their metabolites to inhibit the growth and proliferation of pathogens. Using LAB as a green preservative is one of the most effective alternative owing to their potential to release antifungal metabolites against various fungal species.

LABs is a term given to a group of gram-positive bacteria that are characterized as catalase-negative, non-motile, and non-spore forming. The main fermentation products obtained from species LAB homofermentatives is lactic acid, while LAB heterofermentatives produce lactic acid along with carbon dioxide and ethanol/acetate. Various studies have promoted the use of LAB as a natural preservative that can effectively replace chemical preservatives in foods, and can also provide health-promoting and probiotic properties (Nasrollahzadeh *et al*., 2022a). Owing to the GRAS and QPS status of LAB, further exploring their potential as a biopreservative is now greatly appealing researchers over any other microorganism (Nasrollahzadeh *et al*., 2022b). Also, the LABs are easy to culture and maintain, and since they are naturally present in the gut they are more effective against mycotoxins (Muhialdin *et al*., 2020).

The LABs comprise genera, for example, *Lactobacillus*, *Lactococcus*, *Streptococcus*, *Leuconostoc*, *Pediococcus*, *Enterococcus*, *Oenococcus*, and *Weissella*. Different LAB strains with antifungal activity can be obtained from multiple sources, including *Lactobacillus kefiri* M4 and *Pediococcus acidilactici* MRS-7 from kefir; *Pediococcus acidilactici*, *Limosilactobacillus fermentum*, and *Lactiplantibacillus plantarum* from traditional fermented milk; *Lactobacillus sucicola*, *Weissella paramesenteroides*, *Pediococcus acidilactici* from citrus; and *L. plantarum*, *Lacticaseibacillus paracasei*, and *Lactiplantibacillus pentosus* from fermented beverages. These strains have been proved to be a promising tool to enhance the shelf-life of cereals, fruits and vegetables, nuts and seeds, bakery products, etc. An elaborate and latest prior-art of several LABs well acknowledged for their antifungal potential is given in Table 2.

## Mycotoxin Detoxification Using LAB

Mycotoxin detoxification in foods by LABs can be achieved either through viable cells and their metabolites, or by particular enzymes obtained by certain LAB strains. It has been hypothesized that the development of fungal mycotoxins is encouraged under unfavorable environmental conditions and can be arrested by observing competition for available space and nutrients by the viable cells of LABs (Sadiq *et al*., 2019). These viable cells of LABs are capable of releasing acids and antifungal bioactive metabolites, such as lactic acid, benzoic and propionic acid, formic acid, butyric acid, hexanoic and caproic acid, phenyllactic acid, hydrogen peroxide, monohydroxy octadecenoic acid, carbon dioxide, cyclic dipeptides, phenolic compounds, bacteriocins, fungicins, reuterine, ethanol, diacetyl, and hydroxyl fatty acids (Ruggirello *et al*., 2019), all of which are associated to arresting the fungal activity. On the other hand, certain strains of LABs produce proteolytic enzymes that hydrolyze cell wall proteinases into polypeptides, peptide transporters (that carry peptides in the cell), and intracellular peptidases (that degrade peptides into amino acids) (Muhialdin *et al*., 2020). However, the mechanisms of reduction in mycotoxins have certain uncertainties; for example, the same phenomena of decrease in toxin concentration is ambivalent, as the conventional analytical methods cannot determine whether the mycotoxins have been adrift or have been masked by being temporarily bound to other elements in food (du Plessis *et al.*, 2020). Therefore, in order to understand the reduction in fungal growth and mycotoxin levels, this section reviews the possible mechanisms reported for various mycotoxins. As the literature suggests, the possible reduction in mycotoxins is mainly due to a series of steps, including, adsorption, metabolite interaction, and biodegradation (Figure 1).

### *Binding/adsorption, interaction, and degradation of*

***(1) Ochratoxin A (OTA):*** Some authors have reported the adsorption of mycotoxins onto LAB cell walls as a probable mechanism for their anti-mycotoxin potential. OTA degradation was observed by binding OTA to LAB strains cell wall components, owing to the surface hydrophobicity, electron donor–acceptor association, and Lewis acid–base interaction. This binding capacity can be further increased through mutagenesis/genetic manipulation or supplementation with binding promoting compounds (Sadiq *et al.*, 2019). The most common LAB species known to adsorb OTA are *L. plantarum* (Hashemi and Gholamhosseinpour, 2019) and *Lactobacillus brevis*. However, the effect of *L. plantarum* against OTA produced from *Aspergillus parasiticus* depended on the medium pH, as the maximum OTA reduction was observed at pH 3.0 compared to pH 6.5 (Møller *et al.*, 2021). Similar results were observed by Taheur *et al.* (2021), where LAB species *Lactobacillus kefiri* diminished the OTA content produced from *Aspergillus flavus* and *Aspergillus carbonarius* in agar medium by 75% in bacteria supernatant (CFS), which was significantly affected and reduced to 17% when the pH was neutralized to 7. The authors inferred that the residual OTA amount in culture media was directly influenced by the pH, fungal strain, and bacterial species. Taheur *et al.* (2021) also examined the *in vitro* OTA degradation and absorption by LAB. They demonstrated that the decrease in the mycotoxins was mainly due to the inhibition of fungal growth, followed by adsorption. Du *et al.* (2021) also suggested the involvement of microbial catabolism and adsorption as potential mechanisms for the anti-mycotoxigenic activity of LABs, in Tibetian kefir grains, with the dominant LAB species of *Lactobacillus kefiranofaciens.*

***(2) Aflatoxins:*** Likewise, aflatoxins have also been observed to have binding potential to LAB cell walls

**Table 2. Anti-mycotoxin potential of LABs.**

| Fungal species | LAB species for mycotoxin removal | Substrate | Culture conditions | Detection and quantification technique | Percent mycotoxin reduction | Proposed mechanism | References |
|---|---|---|---|---|---|---|---|
| **Ochratoxin A** | | | | | | | |
| *Aspergillus niger, Aspergillus carbonarius* | *Pediococcus pentosaceus* | Grapes | Grape samples were diluted in sterile saline solution and then plated on MRS agar at 37°C for 48 h; ochratoxin removal potential assessed in both MRS and PBS | HPLC-FLD | 84% in MRS and 25% in PBS | Biodegradation; Various metabolic compounds and metabolites of LAB contributed to the antifungal activity. | Taroub *et al.* (2019) |
| *Aspergillus flavus, Aspergillus parasiticus, Aspergillus nidulans Aspergillus ochraceus* | *L. plantarum* | Table cream | Inoculation at a 5.2 log CFU/mL in MRS broth and incubation at 37°C for 4 days anaerobically | HPLC-FLD | 58% | Adsorption to bacterial cell wall components, especially to polysaccharides and peptidoglycans as well as teichoic and lipoteichoic acids | Hashemi and Gholamhosseinpour (2019) |
| *Aspergillus parasiticus* | *L. plantarum, L. brevis, Levilactobacillus* spp. | Brazilian artisanal cheese | LAB strains inoculated in MRS broth washed, resuspended culture was adjusted to 0.5 MCFarland (~ 108 CFU/mL) and diluted in 0.9% NaCl to obtain a final cell density of 5.0 $\log_{10}$ CFU×$g^{-1}$; mycotoxin removal potential assessed in PPB | Liquid chromatography with fluorescence detector | ≈ 50–90% | Adsorption to bacterial cell walls through ion exchange, complexation, and hydrophobic iterations | Møller *et al.* (2021) |
| **Aflatoxin** | | | | | | | |
| *Aspergillus flavus, Aspergillus parasiticus*, and *Aspergillus nomius* | *L. lactis ssp. cremoris, L. rhamnosus, L. ssp. lactis* | Skimmed milk | Bacterial cells re-activated in MRS broth and isolated in MRS agar; bacterial cell wall isolates | Ultraperformance liquid chromatography | 81.4, 56.8, and 50.8%, respectively. | Adsorption; Sequestering property of clays | Muaz *et al.* (2021) |
| *Aspergillus flavus and Aspergillus carbonarius* | *L. kefiri* | Kombucha beverage | LAB was isolated on MRS agar and incubated at 30°C under anaerobic conditions for 5 days. | HPLC-FLD | 97.22 and 95.27% of $AFB_1$ and $AFB_2$, respectively | Biodegradation and adsorption (mechanisms involving hydroxylation, epoxidation, reduction, and dehydrogenation) | Taheur *et al.* (2019) |
| Not known | *L. rhamnosus, L. lactis* | Frescal cheese | $1.0 \times 10^{10}$ cells/g of the starter culture as procured by the manufacturer | HPLC-FLD | ≈ 100% | Adsorption: Physical binding of the toxin to bacterial cell wall components, mainly peptidoglycans and polysaccharides | Gonçalves *et al.* (2020) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Aspergillus flavus*, *Aspergillus parasiticus*, and *Aspergillus nomius* | *L. fermentum*, *L. paracasei*, *L. plantarum* | Fruit processing by-products | Cultures were maintained aerobically on MRS agar at 4°C and transferred to a new media monthly. Before use in assays, each isolate was cultivated anaerobically in MRS broth at 37°C for 20–24 h, harvested by centrifugation, washed twice, and resuspended in PBS. | HPLC-FLD | ≈80% | Not known | Cruz *et al.* (2021) |
| *Aspergillus*, *Penicillium*, and *Fusarium spp.* | *L.s rhamnosus*, *Pediococcus acidilactici*, *Pediococcus pentosaceus* | Milk | Cryopreserved LABs were reactivated in MRS broth and incubated at 37°C and 5% $CO_2$ for 24 h. | HPLC-FLD | ≈ 33–100% | Adsorption, degradation: All tested strains adsorbed 19 to 61% AFM1 in milk | Martínez *et al.* (2019) |
| *Aspergillus and Fusarium species* | *L. plantarum spp.* | Corn kernels and corn ears | Incubated on MRS Broth for 12 h at 37 °C; anaerobic conditions for 72 h at 37 °C to allow for MRS fermentation. | LC-MS/MS | 39–63.1% | Antifungal activity of LAB metabolites | Nazareth *et al.* (2021) |
| Not known | *L. acidophilus*, *bulgaricus*, and *L. casei* | Salt fermented fish product | Individually inoculated in 100 mL of MRS broth, cultured to the log phase at 37°C | LC-MS/MS | ≈ 8–35% | Physical adsorption; high-salt stress promoted synthesis of detoxification factor in LAB. | Ye *et al.* (2020) |
| *Aspergillus flavus and Aspergillus parasiticus* | *Pediococcus pentosaceus*, *L. plantarum*, *L. mesenteroides*, *L. mesenteroides*, *L. coryniformis ssp. coryniformis* | Brewer's grains | Grown in MRS broth at 37°C in microaerobiosis for 24 h MRS | HPLC-FLD | 37.6–70.7% | Adsorption: bacterial peptidoglycans and polysaccharides act as mycotoxin binders | Asurmendi *et al.* (2020) |
| *Aspergillus flavus* | *L. rhamnosus*, *L. mesenteroides*, *L. lactis ssp.*, *L. casei*, *Streptococcus thermophilus*, *Bifidobacterium longum*, *Bifidobacterium animalis ssp.* | – | Incubated at 37°C for 24 hr in MRS broth | TLC | 27.1–56.8% | Adsorption: mycotoxin binding to bacterial cell walls | Danial *et al.* (2020) |
| **Patulin** | | | | | | | |
| *Aspergillus*, *Penicillium*, and *Byssochlamys* species | *L. casei*, *L. plantarum*, *L. fermentum*, *L. paracasei* and *L. rhamnosus* | Fruit juice | LAB strains were activated by growing on MRS liquid media at 37°C for 24 h | HPLC | 95% by *Lactobacillus casei* | Absorption and irreversible biotransformation | Zheng *et al.* (2020) |

**Continued**

**Table 2. Continued**

| Fungal species | LAB species for myco-toxin removal | Substrate | Culture conditions | Detection and quantification technique | Percent mycotoxin reduction | Proposed mechanism | References |
|---|---|---|---|---|---|---|---|
| Not known | *L. rhamnosus* | Apple juice | PBS | – | 72.73 and 70.51% for HCL-treated and heat-treated LAB | Adsorption: binding rates increased in the presence of acid (21.37%) and heat treatments (19.15%) | Li *et al.* (2020) |
| *Penicillium expansum* | *L. plantarum, L. fermentum* | Kefir grains | Water kefir grains (10% w/v) inoculated and kept at room temperature for 2 days; ground, suspended in sterile saline; inoculated on MRS agar for 3 days at 37°C | HPLC | ≈ 93% | Adsorption: smoother the bacterial cell wall exterior, and the bigger the cell wall volume and the surface area is, the higher the adsorption ability. | Bahati *et al.* (2021) |
| *Penicillium expansum* | *L. plantarum and L. acidophilus* | Synbiotic apple juice | Strain was inoculated into 10 mL MRS broth (pH 6.2) and incubated at 37°C for 48 h. | HPLC-UV | 52.36 and 59.7%, respectively | Adsorption: noncovalent interaction between patulin and carbohydrates and surface layer proteins of the bacterial cell walls | Zoghi *et al.* (2021) |
| **ZEA** | | | | | | | |
| *Aspergillus parasiticus* | *L. plantarum, L. brevis,* and *Levilactobacillus* spp. | Brazilian artisanal cheeses | Inoculation into MRS broth and incubation at 30°C for 24 h. Grown culture was centrifuged, and the cell pellet was resuspended in 10 mL 0.9% NaCl and centrifuged. The washed, resuspended culture was adjusted to 0.5 MCFarland (~ $10^8$ CFU/mL) and diluted in 0.9% NaCl in order to obtain a final cell density of 5.0 $\log_{10}$ CFU $g^{-1}$. | HPLC-FLD | ≈ 50–90% | Adsorption: exposure of binding sites and production of exopolysachharides by LAB. | Møller *et al.* (2021) |
| *Fusarium spp.* | *L. acidophilusand L. delbrueckii subsp. bulgaricus* | Animal liquid feed | Strains were grown overnight on MRS at 37°C under microaerophilic conditions and shaken with 125 strokes/min | UHPLC-FLD/DAD | 57% | Adsorption and biodegradation | Ragoubi *et al.* (2021) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Fusarium spp.* | *L. buchneri*, *L. lactis*, *L. plantarum*, *L. lactis* | Corn silage | LAB strains were grown at 37°C in MRS broth; cultures were then centrifuged for 5 min at 4600 × g at room temperature; supernatant was discarded. The pellet was washed three times with a saline solution (0.89 g/100 mL NaCl), diluted in the same solution. | HPLC-MS/MS | 40–60% | Adsorption: LAB inoculation interacted with the fungal population to change the mycotoxin profile relative to untreated silage. | Gallo *et al.* (2021) |
| *Fusarium* genus such as *F. cerealis*, *F. graminearum* | *L. paracasei* | Dairy products | Bacteria were cultured in MRS broth sterile medium 24 h at 37°C; culture at 3.83 McFarland (1.149 ´ $10^9$ CFU/mL) was transferred to a sterile conical flask with ZEA in DMSO was added; Incubation at 37°C. | HPLC-ESI-MS/MS | 84.93% | Biotransformation and biosorption: physical binding of ZEA to surface components of the cell, transport of ZEA inside the cell and its accumulation, metabolization of ZEA to a less toxic form | Zloch *et al.* (2020) |
| **Fumonisins** | | | | | | | |
| *F. verticillioides* | *Enterococcus casseliflavus* *Enterococcus faecium* | Maize grains | For LAB isolation, 25 g of maize grain were placed in MRS broth and incubated at 37°C for 24 h. | HPLC | 88.75% | – | Diaz *et al.* (2021) |
| *Fusarium species* | Not known | Ogi (fermented maize-based food) | Maize grains were soaked in water and allowed to ferment (steeping) for 2–4 days (48–96 h). The softened grains were then washed, wet-milled, and sieved using a muslin cloth. The sieved paste was diluted with water in a container and left to ferment (souring) for 1–2 days (24–48 h). | LC-MS/MS | 47.45–84.88% | Lactic acid fermentation reduces the levels of toxins. | Ademola *et al.* (2021) |
| *F. verticillioides and F. proliferatum* | *L. paracasei* | Artisanal butter of Tunisia | The inoculated cultures were incubated for 3 h at 37°C in MRS in a chamber with 95% air: 5% $CO_2$ | – | Not known | Degradation; mitigation of $FB_1$ toxicities by reduction of its bioavailability in the gastrointestinal tract | Ezdini *et al.* (2020) |
| Not known | *L. plantarum*, *L. delbrueckii subsp. Delbrueckii*, *Pediococcus pentosaceus* | Maize based fermented cereals | LAB strains were cultivated and stored on MRS agar slants at 4°C for 3 months and for long-term conservation, cryopreserved at −80°C in 12.5% glycerol | HPLC-FLD | ≈80% | Adsorption; deactivation of the mycotoxins by LAB was due to binding rather than metabolism | Dawlal *et al.* (2019) |

ESI, Electrospray ionization; FB1, fumonisin B1; FLD, Fluorescence detector; HPLC, High performance liquid chromatography; LC, Liquid chromatography; MS, Mass spectroscopy; MRS, de Man, Rogosa, and Sharpe agar; PBS, Phosphate-buffered saline buffer solution; TLC, Thin layer chromatography; UV, Ultraviolet detection; ZEA, Zearalenone.

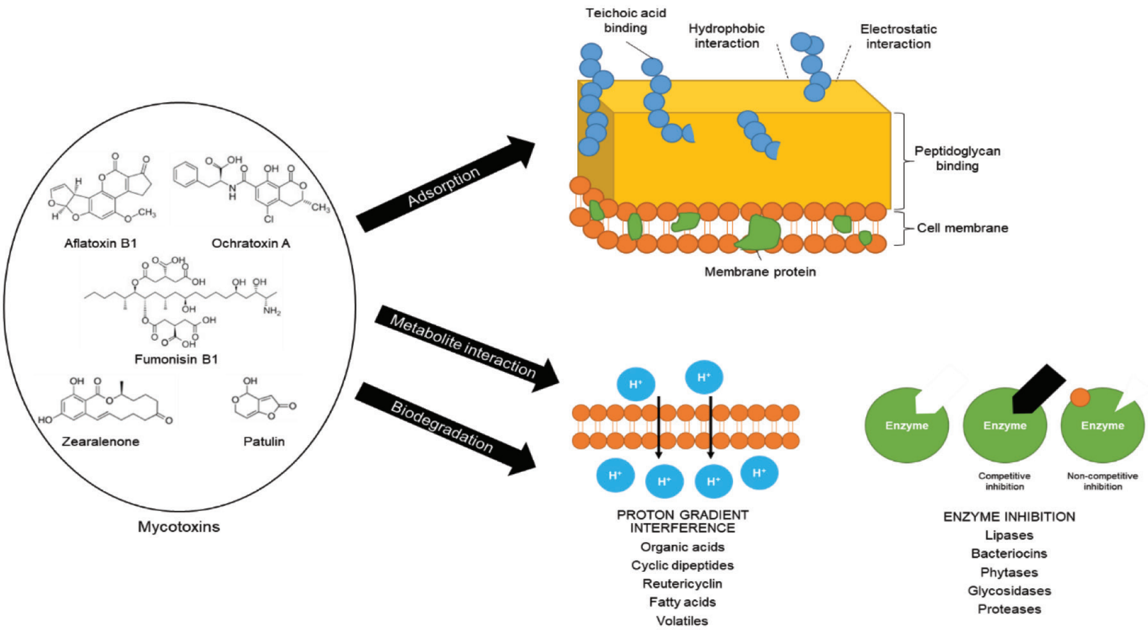


**Figure 1. Possible binding mechanisms of mycotoxins to LAB cell wall components.**

through a reversible noncovalent interaction, independent of the cell activity (Liu *et al.*, 2020). Peptidoglycans, carbohydrates, teichoic acids or proteins, form an inherent part of the LAB cell wall that interact with functional groups and bind to the toxin through physical adsorption, ion exchange, and complexation (Asurmendi *et al.*, 2020; Chlebicz and Śliżewska, 2020). Many authors have studied and validated the involvement of adsorption and degradation of aflatoxins under the influence of LAB strains as decontaminating agents (Kademi *et al.*, 2019). Martínez *et al.* (2019) reported adsorption of AFM1 by *Lacticaseibacillus rhamnosus* in *Artemia salina*.

Similar adsorption and degradation phenomena to reduce aflatoxin $AFB_1$ were observed by Taheur *et al.* (2020) in black tea. The authors revealed that the binding was attributed to the adsorption of the toxin. At the same time, the degradation was carried out by processes like hydroxylation, epoxidation, reduction, and dehydrogenation based on the degrading agent. Asurmendi *et al.* (2020) stated that aflatoxin detoxification is more of a bonding process and less of a metabolic degradation process (Asurmendi *et al.*, 2020). The binding, however, is dependent on existing environmental conditions (Mosallaie *et al.*, 2019). As evidence to this statement, a recent study found that the production ability of aflatoxins ($AFB_1$, $AFB_2$, $AFG_1$, and $AFG_2$) by *A. parasiticus* was significantly affected by the applied conditions like pH (YES agar, YES broth, and MRS agar), time of treatment, heat-killed LAB strains (four strains of *L. plantarum*, two strains of *L. brevis,* four strains of *Lactobacillus* spp.), and the matrix used (milk or buffer) (Møller *et al.*, 2021). Danial *et al.* (2020) also stated that $AFG_1$ adsorption distinctions by different LAB strains are mainly due to varying cell divider components (comprising a peptidoglycan framework and a proteinaceous layer; polysaccharides) and cell envelope structures.

Another effect of environmental conditions was depicted by Ye *et al.* (2020), where they emphasized the presence of high salt stress in the environment that promoted the synthesis of detoxification factors in LAB strains *Lactobacillus acidophilus*, *Lactobacillus bulgaricus*, and *Lacticaseibacillus casei* by increasing their metabolism against aflatoxin $B_1$ and causing physical absorption. Interestingly, heat-killed and acid-killed cells have been shown to have the highest binding capacity with aflatoxins. For example, heat-killed and acid-killed LAB cells from *L. rhamnosus, Lactococcus lactis* ssp. *lactis*, and *L. lactis* ssp. *cremoris* in contaminated skim milk have shown exceptionally high binding ability with $AFM_1$ (Muaz *et al.*, 2021). This was attributed to the denaturation of membrane proteins, peptidoglycans, and degradation of polysaccharides components of the cell wall, thereby changing their hydrophobicity and respective binding capacities. Muaz *et al.* (2021) also found that the addition of an additive, sorbitan monostearate (SM), further increased the binding capacity of heat-killed LAB strains as the hydrophobic end of SM gets attached to the hydrophobic sites of LAB cells, such as peptidoglycan and teichoic acids, thus leaving the other hydrophilic end of SM to bind to hydroxy groups of $AFM_1$. Similar trends have been observed for detoxifying yogurt that evidenced enhanced binding of AFM1 to viable LAB strains by adding inulin as an additive (Sevim *et al.*, 2019). Inulin supplementation promoted the growth and viability of mixed

LAB inoculations (*B. bifidum-Bifidobacterium animalis, L. plantarum-B. bifidum, L. plantarum-Bifidobacterium animalis*) at extended storage periods.

***(3) Fuminosins:*** Among various fumonisins, fumonisin $B_1$ ($FB_1$), and fumonisin $B_2$ ($FB_2$) are the major feed contaminants that adversely affect livestock and human health. The interaction and adsorption of $FB_1$ and $FB_2$ depend on the cell wall components and functional groups, specifically peptidoglycan and similar compounds (Sadiq *et al.*, 2019). The decrease in fumonisin is mainly due to its quick binding ability to the peptidoglycan layer, which is considered to be the most credible binding site (Chlebicz and Śliżewska, 2020). Apart from this, reduction in pH with lactic acid production also leads to the transformation of fumonisin, leading to less toxicity (Ademola *et al.*, 2021). Diaz *et al.* (2021) characteristically found that $FB_1$ produced from a phytopathogenic fungus responsible for maize gain contamination in the silo storage structure, *Fusarium verticillioides*, could be inhibited with a heterogeneous mixture of volatile organic compounds (diacetyl, acetoin, acetic acid, etc.) produced from LAB strain *E. casseliflavus* as a result of its metabolic activity. The authors also revealed that acetoin has potential in mycotoxin biosynthesis.

Dawlal *et al.* (2019) visualized and quantified the interaction between fumonisins and LAB strains and found that LAB metabolism was not required for interaction and binding with fumonisins without biodegradation, as both viable and nonviable LAB cells showed binding capacity, nonviable cells having the higher binding ratio. This was reasoned as the heat treatment promoted denaturation or disintegration of LABs, which opened up the available sites for higher fumonisin binding. Similarly, in viable cells, electrostatic potential favored the binding interaction between fumonisins and LABs. Apart from varying cell structure and components of LAB strains, the variance in fumonisin molecules' structural conformation and charge also contributed to the binding and interaction. $FB_1$ and $FB_2$ carry different surface electrostatic potentials, chemical structure ($FB_1$ has an additional hydroxyl group in C10), and physical structure, making them preferential binding. The authors reviewed that LAB cells and fumonisin binding interaction were mainly mediated by long-range (steric and electrostatic interactions) and short-range (Van der Waals, Lewis acid–base, hydrogen bonding, and biospecific interactions) forces. However, the study failed to visualize this discrepancy as both fumonisins had the same fluorescing.

***(4) Patulin:*** Like other mycotoxins, patulin reduction using LABs is also based on its adsorption in the cell wall and degradation by intracellular or extracellular enzymes (Zheng *et al.*, 2020). Patulin adsorption is mainly observed as binding with the LAB cell wall protein, including thiol, esters, and alkaline amino acids. The main functional groups involved are C–O, OH, C– – O, COO–, C–N, and/or N–H (Wei *et al.*, 2020). Ngea *et al.* (2021) critiqued the ability of LAB cells to reduce patulin in apple juice to be affected by critical environmental factors, including cell density, cell viability, patulin initial concentration, pH, and incubation time. The extent of patulin reduction is closely related to LAB cell surface area's physical and chemical properties, cell wall volume, nitrogen–carbon (N/C) ratio, hydrophobicity, and functional groups. Large surface area, adsorptive selectivity, and large functional groups make nonviable cells more efficient in patulin reduction than viable cells (Bahati *et al.*, 2021; Sajid *et al.*, 2019). Exposure of LAB cells to conditions such as high temperature, acidic environments, etc., brings about structural changes to the cell walls that reduce the glycan layer crosslinking and increase cell wall permeability. Interestingly, Li *et al.* (2020) revealed that hydrochloric acid-treated LAB strains had significantly higher patulin detoxification ability and stability than heat-treated (121°C) LAB cells, owing to the disruption of hydrophobic interaction. This was speculated due to changes in cell wall structures that attain different degrees of cross-linking, thereby obstructing the toxin release. Additionally, additives like fructooligosaccharides, ascorbic acid, and citric acid to the apple juice demonstrated enhanced patulin binding by *L. plantarum* by reducing pH that stimulated S-layer proteins synthesis in the LAB cell wall (Zoghi *et al.*, 2019).

***(5) Zearalenone (ZEA):*** Last but not least, LAB-assisted ZEA removal involves either interaction with LAB cell wall components like peptidoglycans and surface proteins or interaction with intracellular proteins followed by absorption into the LAB cell wall (Sadiq *et al.*, 2019). According to Złoch *et al.* (2020), ZEA neutralization by *Lactobacillus paracasei* cells is a nonlinear two-step process involving biosorption/binding techniques of ZEA by *L. paracasei* cells, as well as metabolization and biotransformation of ZEA to less toxic α-ZOL, β-ZOL forms. ZEA removal depends on cell wall protein type and structure, thus making it a strain-specific process. Out of the 17 strains of plant-derived LAB, *L. plantarum* isolated from wild spider flower pickle possessed the highest ZEA removal capability (Adunphatcharaphon *et al.*, 2021). As per the results obtained by the authors, LAB cell wall polysaccharides did not affect ZEA removal stating non-involvement of hydrogen bonds in the interaction between LAB strain and ZEA. As far as lipids were concerned, lipase-treated LAB cells showed a significant reduction in ZEA as lipase hydrolyzed the ester bond lipid, causing a change in lipid structure. In addition, the presence of hydrophobic interactions was confirmed with a dominance of C–OH, C–C, and C–O–C functional groups of polysaccharides and single form bending functional groups of bonds in $CH_2$ and $CH_3$ present in teichoic acids, peptidoglycan, lipopolysaccharides, and phospholipids (Adunphatcharaphon *et al.*, 2021). An adsorption–desorption study by Ragoubi *et al.* (2021) exposed that the viable cells of LAB caused ZEA biodegradation in PBS medium, with ZEA being the only carbon source. However, no related metabolites like, α and β-zearalenol, zearalenone, and its reduced metabolites were detected in inoculated PBS at the end of the incubation period, stating the absence of biodegradation. On the contrary, Adunphatcharaphon *et al.* (2021) showed that heat-treated nonviable *Lactobacillus plantarum* cells had a higher capacity to reduce ZEA. Still, since no ZEA degradation products were detected, the authors suggested the properties of heat-inactivated LAB cells for ZEA reduction and not biotransformation.

## Mycotoxin Reduction in Foods Using LABs

LABs have been used for bio-preservation as an innovative approach to foods, including dairy products, bakery products, juices, meat, fruits and vegetables, and feeds (Table 3), for thousands of years due to their inhibitory properties. The contamination can occur at various stages during the manufacturing process. In cereal grains, mycotoxins can be formed by several spoilage-indicating molds, including, above all, *Aspergillus* spp. and *Penicillium* spp. Even in dry grains, mycotoxins can also be formed if either moisture migration due to temperature changes creates condensation points with a higher water content (hot spot theory) or moisture is formed through the respiratory activity of grains weevils or other grain pests (mites, larvae of flour moths) and then secondary mold growth occurs, and often not noticed. The stability of the silage (animal feed) cannot be estimated in advance, and therefore can be contaminated in similar proportions as grains (Liu *et al.*, 2018).

For the food and feed industry, the production of compounds derived from LAB metabolic activity is of high importance; their antimicrobial spectrum has inhibitory potential against spoilage organisms such as fungi (especially by mycotoxigenic fungi), yeasts, Gram-negative and Gram-positive bacteria, protozoa, retarding microbial growth y extending considerably shelf-life as shown in Table 3 (Strack *et al.*, 2020). LABs inhibit microbial decay by generating antagonist metabolic products or establishing antimicrobial compounds. Organic acids, mainly lactic acid followed by acetic acid, are the main metabolites of LAB, but depend on the LAB strains, their mechanism of action, and carbohydrates as substrate, other kinds of antimicrobial substances, namely low molecular weight metabolites (reuterin, reutericyclin, diacetyl, fatty acids), hydrogen peroxide, antifungal compounds (propionate, phenyl-lactate, hydroxyphenyl-lactate, and 3-hydroxy fatty acids) can be produced (compounds metabolized by different LAB strains listed in Table 3) (Wang *et al.*, 2021). They have been used for food bio-preservation as an innovative approach for dairy products, bakery products,

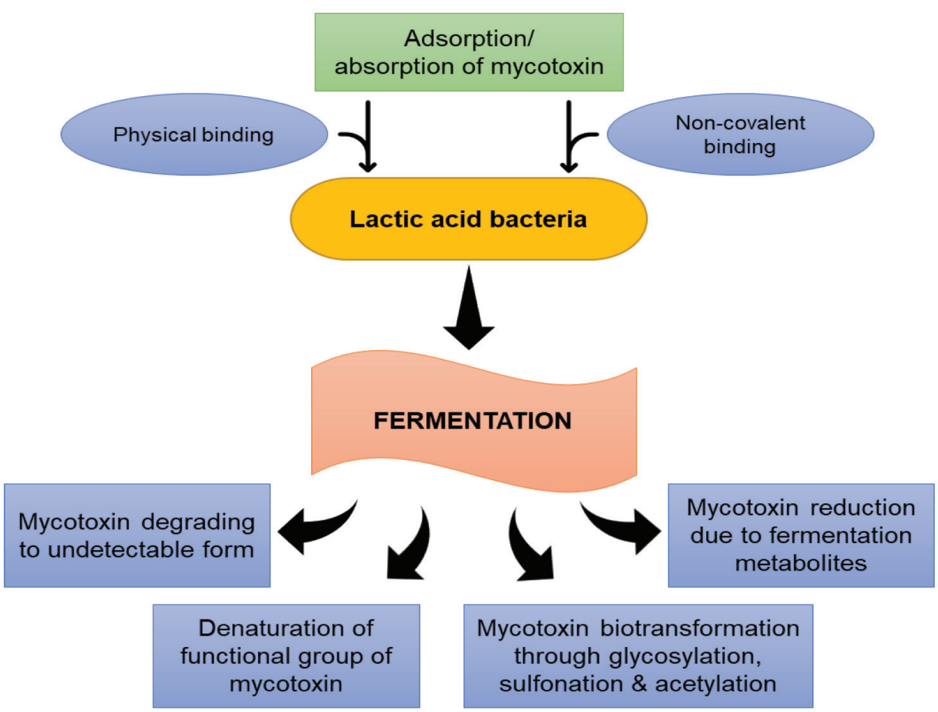


**Figure 2. Anti-mycotoxin effect of LAB fermentation in foods.**

**Table 3. Practical food applications of LABs to the extended shelf life of food products.**

| Lactic acid bacteria | Strain | Possible compounds derived from metabolic activity | Food/Feed product | Targeted fungi/mycotoxins | Extended shelf-life/Inhibition percentage | References |
|---|---|---|---|---|---|---|
| *Limosilactobacillus reuteri* | – | p-Coumaric acid<br>Azelaic acid<br>Reuterin/Acrolein<br>Reutericyclin<br>Hydrogen peroxide | Bread | *Fusarium culmorum* | Compared to control < 4 days extra | Schmidt *et al.* (2018) |
| | | | Whole wheat sourdough | *Aspergillus niger* | <7 days | Sadeghi *et al.* (2019) |
| *Limosilactobacillus reuteri* and*Levilactobacillus brevis* | R29R2Δ | (mentioned above)<br>4-Hydroxyphenyllactic acid<br>Hydrogen peroxide | Quinoa and rice bread | Mold growth | 2–4 days | Axel *et al.* (2016) |
| *Lactobacillus hammesii* | R29 | – | Bread | Mold growth | 2–6 days | Black *et al.* (2013) |
| | – | – | Flaxseed sourdough bread | *Aspergillus niger* and *Penicillium roqueforti* | Compared to control < 2 days extra | Quattrini *et al.* (2018) |
| *Lactiplantibacillus plantarum* | UFG 121 | Benzoic acid<br>p-Coumaric acid<br>Cyclic dipeptides<br>3-Phenyllactic acid<br>2-Hydroxy-4-methypentanoic acid<br>Methylhydantoin<br>Mevalonolactone<br>∂-Dodecalactone<br>Hydrogen peroxide | Bread | *Fusarium culmorum* | No growth of the targeted fungus up to 7 days | Russo *et al.* (2017) |
| | – | | | *Aspergillus parasiticus* | <3–4 days extra | Saladino *et al.* (2016) |
| | CCFM259 | | Chinese steamed bread | *Penicillium roqueforti* | Up to 7 days no growth | Yan *et al.* (2017) |
| | CRL 778 | | Quinoa flour-based bread | Mold growth | Significant increased compared to control | Dallagnol *et al.* (2015) |
| | C10 | | Muskmelon fruit | *Trichothecium roseum* | Inhibited pink rot | Lv *et al.* (2018) |
| | – | | Grape berries | *Aspergillus carbonarius* | – | Lappa *et al.* (2018) |
| | E3<br>E4 | | | *B. cinerea* and *A. ochraceus* | reduced the growth | Dopazo *et al.* (2021) |
| | – | | Cottage cheese | *Penicillium commune* | ≥ 25 days | Cheong *et al.* (2014) |
| | 5BG | | Spanish-style table olives | Fungal growth | ≥ 5 months | Lavermicocca *et al.* (2018) |
| | TK9 | | Citrus and apple juice | Old-growth | <3–4 days extra | Zhang *et al.* (2016) |
| | UFG 121 | | Oat-based beverage | *Fusarium culmorum* | ≥ 21 days | Russo *et al.* (2017) |
| | LR/14 | | Grains | *Mucor racemosus, Rhizopus, stolonifer, Penicillium chrysogenum*, and *Aspergillus niger* | 2.5 years | Gupta and Srivastava (2014) |
| | YML007 | | Animal feed | Mold growth | 30 days | Rather *et al.* (2014) |

**Continued**

**Table 3. Continued**

| Lactic acid bacteria | Strain | Possible compounds derived from metabolic activity | Food/Feed product | Targeted fungi/mycotoxins | Extended shelf-life/Inhibition percentage | References |
|---|---|---|---|---|---|---|
| *Lactiplantibacillus plantarum* | – | – | Fermented milk: Doogh (Iranian traditional) | AFM1 | 99% | Sokoutifar *et al.* (2018) |
| | – | – | Skim milk | AFM1 | | Panwar *et al.* (2018) |
| *Lactiplantibacillus plantarum* *Lactobacillus acidophilus* | – | – | Apple juice | PT | 90% | Zoghi *et al.* (2019) |
| *Lactiplantibacillus plantarum* in combination with *Lacticaseibacillus rhamnosus* and/or *Lactobacillus harbinensis* | L244CIRM-BIA1113<br>L172 | 3-Phenyllactic acid Hydrogen peroxide | Sour cream | *Rhodotorula mucilaginosa*, *Penicillium commune*, and *Mucor racemosus* | Inhibition of targeted fungi from 2 to 24 h | Salas *et al.* (2018) |
| *Lactiplantibacillus plantarum* in combination with other lactobacilli | – | Hydrogen peroxide Vanillic acid | Caciotta cheese | *Penicillium chrysogenum* ATCC 9179 and *Aspergillus flavus* ATCC 46283 | ≥ 30 days | Cosentino *et al.* (2018) |
| *Limosilactobacillus fermentum* | C14 | | Bread | *Mucor sp.* | Up to 25 days | Barman *et al.* (2017) |
| | GA715 | | Banana | *Fungal growth* | Increased three times | Wayah and Philip (2018) |
| | YML014 | | Tomato puree | *Aspergillus niger, Aspergillus flavus*, and *Penicillium expansum* | Increased by nine days at 25°C | Adedokun *et al.* (2016) |
| *Lactobacillus citreum* and *Levilactobacillus brevis* | L123<br>Lu35 | | Pain au lait or plain cakes | *Penicillium corylophilum* | Significant increase | Le Lay *et al.* (2016) |
| *Lactobacillus amylovorus* | DSM19280 | Cinnamic acid derivatives Salicylic acid | Gluten-free quinoa sourdough bread | Mold growth | compared to control < 2 days extra | Axel *et al.* (2016)<br>Ryan *et al.* (2011) |
| *Lacticaseibacillus rhamnosus* | GG | 3-Phenyllactic acid | Whole pears | *Fungal growth* | Up to 9 days | Zudaire *et al.* (2018) |
| | – | – | Apple juice | *Mycotoxin PT* | 80% | Hatab *et al.* (2012) |
| *Lactobacillus delbrueckii* spp. *Bulgaricus* *Lacticaseibacillus rhamnosus*, and *Bifidobacterium lactis* – in combination | | | Milk | AFM1 | 12% | Corassin *et al.* (2013) |
| *Lacticaseibacillus rhamnosus* alone or in combination with *Bifidobacterium animalis* subsp. lactis | A238<br>A026 | | Cottage cheese | *Penicillium chrysogenum* | Up to 21 days | Fernandez *et al.* (2017) |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lacticaseibacillus casei* | AST18 | 2-hydroxy-4-methypentanoic acid | Yogurt | *Penicillium* sp. | compared to control < 4 days extra | Li *et al.* (2013) |
| *Lactobacillus harbinensis* | K.V9.3.1Np | | | *Mold growth* | Up to 6 weeks | Delavenne *et al.* (2013) |
| *Lactobacillus parafarraginis* | – | | Silage | *Yeast* | Stability up to 144 h | Liu *et al.* (2018)<br>Broberg *et al.* (2007) |
| *Lactobacillus helveticus* | KLDS 1.8701 | | Soybean milk | *Penicillium* sp. | Up to 21 days | Bian *et al.* (2016) |
| *Lactococcus piscium* | | | Food matrixes | *Brochothrix thermosfacta* | | Fall *et al.* (2012); Saraoui *et al.* (2016); Leroi *et al.* (2015) |
| | CNCM1-4031 | | Shrimps | L. monocytogenes | | Saraoui *et al.* (2016) |
| | All strains | – | Salmon and cod juices | *Photobacterium phosphoreum, B. thermosphacta, S. baltica*, and *L. monocytogenes* | Strongly inhibited | Wiernasz *et al.* (2017) |
| | | | | *Shewanella baltica, Serratia proteamaculans, H. Alvei*, and *L. sakei* | Broadly inhibited | |
| *Leuconostoc gelidum* | All strains | | Salmon juice | *Shewanella baltica* | Strongly inhibited | |
| | | | Fish juices | *L. monocytogenes* | Highly inhibited | |
| | | | Fish juice | *P. phosphoreum* | Slightly inhibited | |
| | | | Cooked peeled shrimps | *P. phosphoreum*, *B. thermosphacta*, *S. proteamaculans* | Slightly inhibited | Leroi *et al.* (2015) |
| genus *Lactobacillus* | | | Ready-to-eat (RTE) seafood | pathogenic bacteria commonly reported in RTE | High antimicrobial activity | Sahnouni *et al.* (2016) |
| *L. sakei* | cocktail (3 strains/ genomic diversity) | | Ground beef | *E. coli/Salmonella* | | Chaillou *et al.* (2014) |
| *Lactococcus garviae* | | $H2O_2$ | Milk<br>Cheese | *S. aureus* | Higher inhibition | Delbes Paus *et al.* (2010); Delpech *et al.* (2015); Delpech *et al.* (2017) |
| *Lacticaseibacillus paracasei* subsp. *paracasei* | KU517839 | Bacteriocin | Cheese<br>Cheese made from pasteurized milk | S. aureus | | Heredia-Castro *et al.* (2015); Yoon *et al.* (2016); Madi and Boushaba (2017) |
| *Carnobacterium divergens* | V41 | Bacteriocin: divercin | Smoked salmon | *L. monocytogenes* | | Richard *et al.* (2003) |

Aflatoxin M1: AFM1; Aflatoxin B1: AFB1; Ochratoxin A: OTA; Patulin.Conclusion and Future Perspectives juices, meat, fruits, and vegetables. Various mechanisms that impart the anti-mycotoxin effect in foods by LAB fermentation are presented in Figure 2. Table 3 shows a consolidated overview of the selected recent applications of LABs in various food products.

### Conclusion and Future Perspectives

Bio-preservation, including the use of LABs and their active metabolites, is a natural tool to prevent fungal growth, prolong shelf-life, and increase the safety of foods. LABs are GRAS and possess a large potential for bio-preservation due to their production of antimicrobial compounds. LABs effectively reduce mycotoxin production by fungi via adsorption of mycotoxin with LABs cell surface components, degradation of fungal mycotoxins, and inhibition of mycotoxin production. However, the antifungal and anti-mycotoxin potential of LABs depends on pH, initial viable count, growth medium and condition, and incubation temperature and time. Due to antifungal and anti-mycotoxin agents, LABs could be an ideal bio-preservative candidate for sustainable food systems, including dairy products, fruits and vegetables, cereal grains, bakery goods, nuts and seeds, and meat and meat products.

Mycotoxin detoxification capacity of LABs through cell wall bindings is an effective way for the removal of mycotoxins from food and feed. However, possible *in vivo* release of bound toxins during the detoxification process can be a matter of human health concern. Thus regulating the environmental conditions that can lead to this release is an important aspect. Further studies on the effect of several factors, like pH, growth medium, initial bacterial count, incubation time and temperature, growth condition (single or mixed), bacterial state (viable or nonviable), on the detoxifcation mechanism can help better understand the anti-mycotoxin activity of LAB. Additionally, understanding the LAB's detoxification capacity and potential interaction of compounds obtained with mycotoxin degradation for particular food products may also serve as an important source of data, that can be further industrialized for the food sector.

## Conflict of Interest

There are no conflicts of interest to declare.

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## Ethical Approval

Ethics approval was not required for this research.

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