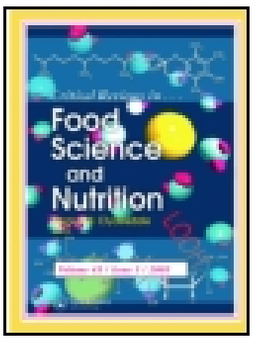

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REVIEW

Microbial detoxification of mycotoxins in food and feed

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ABSTRACT

Mycotoxins are metabolites produced by fungi growing in food or feed, which can produce toxic effects and seriously threaten the health of humans and animals. Mycotoxins are commonly found in food and feed, and are of significant concern due to their hepatotoxicity, nephrotoxicity, carcinogenicity, mutagenicity, and ability to damage the immune and reproductive systems. Traditional physical and chemical detoxification methods to treat mycotoxins in food and feed products have limitations, such as loss of nutrients, reagent residues, and secondary pollution to the environment. Thus, there is an urgent need for new detoxification methods to effectively control mycotoxins and treat mycotoxin pollution. In recent years, microbial detoxification technology has been widely used for the degradation of mycotoxins in food and feed because this approach offers the potential for treatment with high efficiency, low toxicity, and strong specificity, without damage to nutrients. This article reviews the application of microbial detoxification technology for removal of common mycotoxins such as Aflatoxin, Ochratoxin, Zearalenone, Deoxynivalenol, and Fumonisins, and discusses the development trend of this important technology.

KEYWORDS

Microbial detoxification; aflatoxin; ochratoxin; zearalenone; deoxynivalenol; fumonisins

Introduction

Mycotoxins are secondary metabolites synthesized and released by toxigenic fungi that can produce toxic effects (Juan, Ritieni, and Mañes 2012; Zhao et al. 2014). There are 300–400 types of known mycotoxins, including Aflatoxins (AFs), Ochratoxins (OTs), Zearalenone (ZEN), Trichothecene toxoids, and Fumonisins (FUMs). After ingestion exceeding a certain limit, mycotoxins can cause varying degrees of damage to the kidneys, liver, and reproductive organs, endangering the health of humans and animals (Chauhan et al. 2016; Mu, Deng, and Wen 2016; Streit et al. 2012). Mycotoxin contamination can occur in the storage, preparation, and production of various food crops, plants, and their products (Marin et al. 2013; Selvaraj et al. 2015). The contamination of food and feed by mycotoxins is widely reported worldwide, especially in developing countries, posing a serious threat to human and animal health (Chen et al. 2014; Lei et al. 2016; Lv et al., 2016), thus causing significant economic losses (Belhassen et al. 2015; Ben et al. 2019). Humans and animals are exposed to mycotoxins by the consumption of plant-derived food contaminated with toxins or the consumption of animal products that carry mycotoxins and their metabolites, such as animal tissues, milk, and eggs. Overall, detoxification of mycotoxins is critical in food, feed, and related industries (Ji, Fan, and Zhao 2016; Oluwafemi et al. 2010).

Commonly used methods for the removal of mycotoxins can be roughly classified into physical removal, chemical removal, and microbial degradation methods according to the mechanism of action (Shanakhat et al. 2018). These methods reduce or eliminate mycotoxins by destroying, modifying, or adsorbing mycotoxins. Physical removal methods include physical adsorption, microwave, radiation, high-pressure pulse, and extrusion. Chemical removal methods include ammonia fumigation and treatment with ozone, chlorine dioxide, and other strong oxidants (Hassan and Zhou 2018). Traditional physical and chemical detoxification methods have limitations, for example, the use of chemical reagents can introduce uncertain hazards, and incomplete degradation after adsorption can result in secondary environmental pollution (Moretti et al. 2018; Wang et al. 2014). Physical adsorption is limited to use in liquid food systems, for treatment of products such as water, beer, milk and peanut oil, (Diaz et al. 2004; Var, Kabak, and Erginkaya 2008). Thus, application of current methods for actual production remains limited. For this reason, there is significant interest in developing safe and effective methods to remove mycotoxins in food and feed using biological resources to degrade mycotoxins (Shi et al. 2018; Wochner et al. 2018).

Biological methods include the use of microorganisms to produce secondary metabolites or secreted enzymes to effectively degrade mycotoxins and microbial adsorption toxins to remove mycotoxins. Although the microbial degradation of mycotoxin technology is still in its infancy, microorganisms on the degradation of mycotoxin efficiency has yet to reach people's expectations, the mechanism of

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microbial degradation and enzyme degradation of mycotoxin didn't fully understand, degradation enzyme and mycotoxins degradation products of safety evaluation is not clear enough, and other problems. However compared with physical and chemical degradation technologies, microbial degradation does not lead to secondary pollution, requires only mild degradation conditions, does not cause nutrient damage, and can be done rapidly with high efficiency, low toxicity, and strong specificity (Diao et al. 2018; Yan et al. 2017). Partial microbial fermentation can even increase the nutritional value or improve the flavor of a product. Therefore, there is widespread interest in the development and application of biological methods for the removal of mycotoxins. This article reviews recent research on the removal of mycotoxins from contaminated food and feed and describes advances in the degradation of toxins such as AFB_1, ZEN, DON, OTA, and FB_1 by different kinds of bacteria, soil bacteria, yeasts, and enzymes. We have also studied the toxicity of toxin degradation products and the trend of future research on mycotoxin degradation (Figure 1).

Opportunity and challenge of mycotoxin microbial detoxification

Most approaches to the microbial degradation of mycotoxins in food and feed have included five steps. First, microorganisms or key enzymes that degrade mycotoxins must be obtained and selected from environmental resources. Second, the efficacy and influencing factors of the selected microbial degradation activities must be studied. Third, the safety of degrading strains and degradation products should be evaluated, because degradation products may not necessarily be less toxic. Fourth, the degrading strains or degrading enzymes must be isolated, identified/cloned, and expressed. Finally, the ability to use microorganisms to degrade mycotoxins in food and feed should be verified. The complete workflow is shown in Figure 2.

Microbial degradation can convert toxins into low-toxic or nontoxic products, and this approach has become the most promising mycotoxin degradation approach. However, mycotoxin microbial degradation technology remains in early stages. Although some progress has been made in the screening and isolation of mycotoxin-degrading strains, the identification of the chemical structure of the degradation products and the study of metabolic pathways are not incomplete, and some strains are also animal pathogens so are not suitable for practical production applications. Several factors have restricted the progress of mycotoxin microbial degradation research, including the requirement of mycotoxin degrading enzymes for complex processes of separation and purification, low production levels of enzymes, unstable enzyme activity, or the requirement for harsh enzyme conditions. There have been relatively few studies on the separation, purification, and acquisition of degradation products and related gene sequences of degradation products and their toxicology, genomics, proteomics and metabolomics. Therefore, how to identify and purify degrading enzymes and make the microorganisms produce high-yield target enzymes to be used in actual production is the main direction of current research, with good market prospect. Screening nonpathogenic mycotoxin-degrading strains, in-depth study of the characteristics of produced mycotoxin-degrading enzymes, applying modern molecular biology methods and genetic engineering techniques, to clone and efficiently express mycotoxin-degrading enzyme and degrading strain genes efficiently in heterologous hosts, increase enzyme production and strain detoxification activity, realize large-scale production, and application of degradation methods for the processing and production of grains, food, or feed are important development directions in the field of mycotoxin microbial degradation.

Mycotoxin microbial detoxification methods

Microbial detoxification is to use the metabolites or secreted enzymes produced by microorganisms during the growth process or the characteristics of the microorganisms themselves to degrade or inhibit the production of mycotoxins

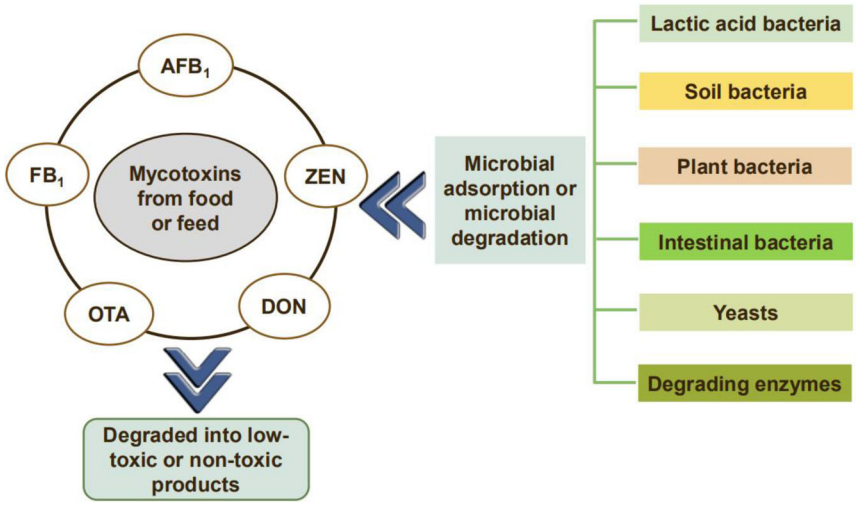

Figure 1. Framework of the review.

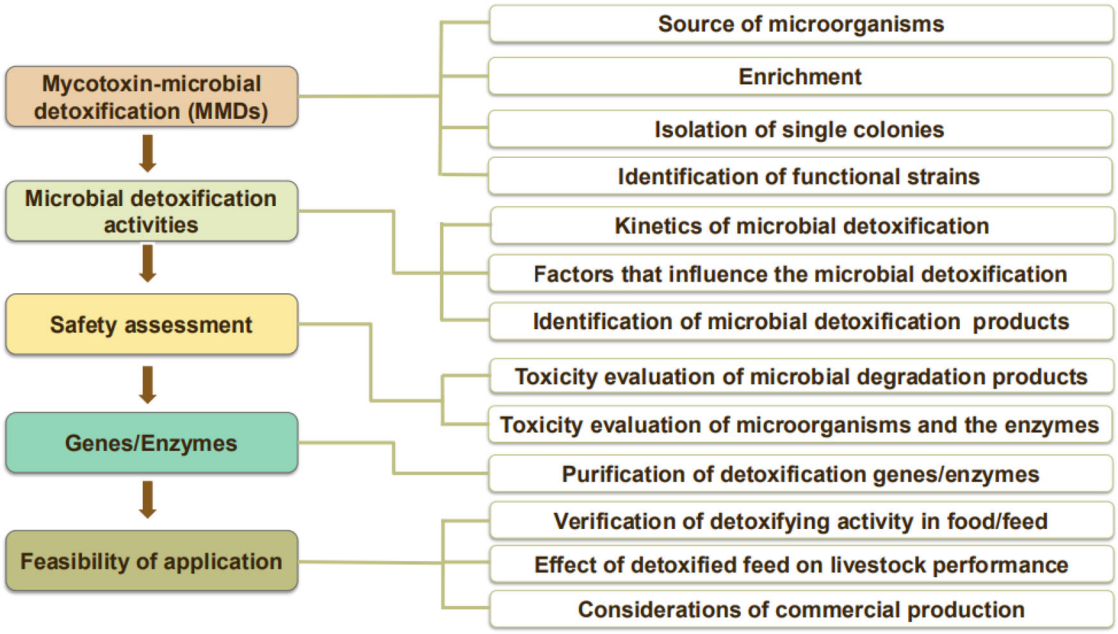

Figure 2. Research process of microbial degradation of mycotoxins.

and reduce mycotoxin pollution. Using microorganisms to directly adsorb mycotoxins in the sample can also achieve the purpose of removing or reducing mycotoxins (Gomaa, Abdelall, and El-Mahdy 2018; Ilse et al. 2017). In the first approach, it is necessary to identify enzymes and strains that can degrade mycotoxins from microorganisms, genetic technology is then applied to engineer bacteria for high-efficiency expression of these enzymes and strains, and then these enzymes and strains must be isolated and purified for use in the degradation of mycotoxins in food and feed. In the second approach, microorganisms are directly used to degrade toxins. Adsorption is inexpensive and can be used to remove toxins, but this method is not suitable for food processing. Many microorganisms, including yeast, bacteria, and fungi can degrade mycotoxins in food or feed (Ahmad and Jae-Hyuk 2017; Sheikh-Zeinoddin and Khalesi 2019).

Microbial degradation technology

In microbial degradation, toxic groups of mycotoxins are decomposed and destroyed by secondary metabolites produced by microorganisms or secreted enzymes to produce nontoxic or low-toxic degradation products. Microbial degradation avoids many of the adverse consequences of physical and chemical treatments on food or feed, and has advantages of high efficiency and strong specificity (Ji, Fan, and Zhao 2016). Microbial degradation is considered the most promising mycotoxin detoxification method, as it can theoretically degrade toxins to completion without any remaining toxic substances. Microbial degradation is carried out by enzyme catalysis, so this approach offers high specificity, and works only against mycotoxins without destroying other nutrients in food or feed, so the nutritional value of food or feed will be retained (Gallo et al. 2015). Microbial degradation technology can achieve a good detoxification effect for toxins such as ZEN, Deoxynivalenol (DON), and OTs. Microorganisms can change the molecular structure of target toxins during metabolism, and possible pathways for microbial degradation of mycotoxins mainly involve the reduction of ketone carbonyl groups, the modification of phenolic hydroxyl groups, the hydrolysis and acetylation of lactone rings, and the glycosylation of glucose. Microbial degradation can include reactions such as ring cleavage, hydrolysis, deamination, and decarboxylation. Some bacteria, fungi, and yeast can degrade mycotoxins. However, the direct use of live bacteria preparations as feed or food additives may cause biosafety issues or lead to animal refusal to eat. Therefore, the use of mycotoxin detoxification enzyme produced by bacteria or fungi can not only improve the detoxification efficiency, but also avoid the problems caused by the direct use of live bacteria preparations.

With the rapid development of methods to genetically engineer microorganisms, many researchers have made initial progress in studying degradation of mycotoxins by key enzymes and heterologously expressed degrading enzymes. The key enzymes overexpressed in engineered strains by genetic engineering techniques, were isolated, purified and added to food and feed to degrade toxins. The principle of degradation has been preliminarily studied (Figure 3A). On the other hand, based on the one of the most important branches of genetic engineering is the expression of recombinant proteins using biological expression systems. Nowadays, preliminary progress has also been made in using different expression systems to express recombinant proteins to degrade mycotoxins, including bacteria, yeast, molds, mammals and plants. Yeast heterologous proteins expression systems used to study the degradation of mycotoxins such as *Saccharomyces cerevisiae* (*S. cerevisiae*) and *Pichia pastoris* (*P. pastoris*) are more popular (Figure 3B). At the same time, there have been studies on degradation OTA with the addition of halogenase through exogenous expression using

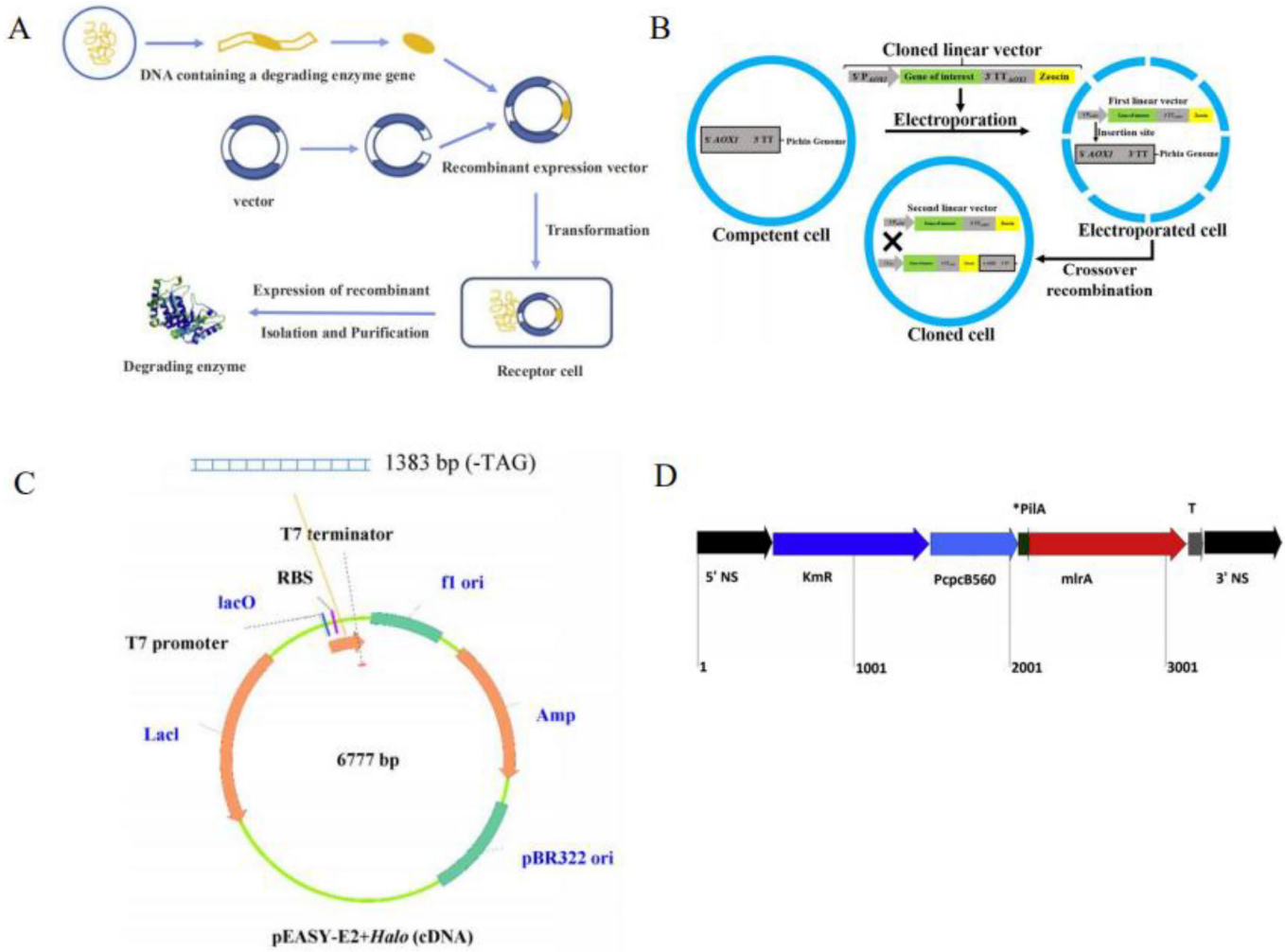

Figure 3. (A) The mechanism of heterologous expressed degrading enzyme (adapted from Wang and Xie 2020); (B) Crossover recombination phenomenon in the *Pichia pastoris* genome (adapted from Karbalaei et al. 2020). (C) Expression of halogenase in *E. coli* BL21. Recombinant pEASY vector with halogenase cDNA transformed into *E. coli* (adapted from Yan et al. 2018). (D) USTB-05 mlrA Gene, Codon optimized for expression in Synechocystis PCC 6803 was optimized for the study of microcystin degradation (adapted from Dexter et al. 2018).

genetic engineering technology (Figure 3C) (Yan et al. 2018). In addition, scholars establish proof-of-principle demonstrating for the first time genetic engineering of heterologous expression of Mara in a photoautotrophic host-engineering cyanobacteria to degrade microcystins (Figure 3D) (Dexter et al. 2018). The acquisition and cloning of mycotoxin-degrading enzyme genes and the safe expression of genes in microorganisms have become new development directions. Applications of microbial degradation technology for the removal of mycotoxins from food and feed are listed in Table 1.

Microbial adsorption

Efforts to utilize adsorption of microorganisms to mycotoxins have mainly focused on adsorption by yeast and yeast cell walls, lactic acid bacteria, and other probiotics (Wang et al. 2019). The adsorption of yeast to mycotoxins may be related to the glucomannan on the surface of yeast cell walls. Yeast or yeast cell wall components can be used as adsorbents of mycotoxins in food and feed. With polysaccharides, proteins, lipids, and other substances on the yeast cell wall, the adsorption of toxins can be achieved through hydrogen bonds, ionic bonds, and hydrophobic forces. The special structure of the yeast cell wall allows strong adsorption to mycotoxins. The most commonly used method for adsorption of mycotoxins is to reduce the bioavailability of mycotoxins by adding yeast strains and using the yeast cell wall components as adsorbents, thereby reducing the content of mycotoxins. In addition, many lactic acid bacteria can bind to mycotoxins and reduce their biological activity in food and feed. At the same time, it can also produce some bacteriocins with antibacterial function and inhibit the growth of pathogenic bacteria. Therefore, detoxification using lactic acid bacteria's adsorption effect on mycotoxins is recognized as a safe and ideal detoxification method. It is necessary to determine the effectiveness of adsorbents of mycotoxins at different pH values (acidic or neutral) to comprehensively characterize potential mycotoxin adsorbents. Mycotoxin adsorbent complexes must remain stable to prevent the desorption of toxins during digestion. Fungi and lactic acid bacteria can adsorb mycotoxins (Garda-Buffon, Kupski, and Badiale-Furlong 2011). Applications of microbial adsorption for the removal of mycotoxins from food and feed are listed in Table 2.

Table 1. Application of bacteria, yeast and fungal microbial degradation and removal of mycotoxins.

Mycotoxins	Degrading strain/degrading enzyme	Degradation rate/degradation products	References
AflatoxinB_1	Catalase	Nontoxic product	Taylor et al. (2010)
	Kombucha	97%	Ben Taheur et al. (2020)
	Bacillus licheniformis (BL010)	89.1%∼97.3%	Wang et al. (2018)
	Fusarium oxysporum PG41	66%∼78%	Shcherbakova et al. (2015)
	Lactobacillus brevis	90.43%∼96.31%	Gomaa et al. (2018)
	Lactobacillus paracasei		
	A. *niger*	98.6% (AFB_{2a})	Wu et al. (2009)
Zearalenone	*Bacillus pumlius* ANSB01G	66.34%∼88.65%	Lei et al. (2014)
	Lactobacillus plantarum	45%	Zhao et al. (2015)
	Bacillus subtilis	65%∼100%	Ju et al. (2019)
	Bacillus natto		
	Lactose hydrolase ZHD101	Nontoxic product	Takahashi-Ando et al. (2002)
	Bacillus amyloliquefaciens	92%	Je-Ruei and Petr (2017)
Deoxynivalenol	3-O-acetyltransferase	/	Khatibi et al. (2011)
	13 aerobic degrading bacteria	3-epi-DON	Ikuo et al. (2012)
	bacterial	deepoxy-DON/ DOM-13-epi-DON	Pierron et al. (2016)
	Microbial enrichment bacteria	3-epi-DON/3-epi-DOM-1	Ilse et al. (2017)
Ochratoxin A	*Aspergillus oryzae* strain M30011	94%	Xiong et al. (2020)
	Bacillus licheniformis	92.5%	Petchkongkaew et al. (2008)
	Pediococcus parvulus strains	OTα	Abrunhosa et al. (2014)
	bacillus amyloliquefaciens ASAG1	98.5%	Chang et al. (2015)
	Saccharomyces cerevisiae W13	57%	Leonardo et al. (2014)
Fumonisin B_1	*Sphingomonas* MTA144	2-ketone- HFB_1	Heinl et al. (2010)
	Sphingomonas sp. ATCC55552	2-keto- HFB_1	Heinl et al. (2011)
	Mixed bacteria SAAS79	90%	Zhao et al. (2019)

Table 2. Bacteria, yeast and fungus adsorption methods to remove mycotoxins.

Mycotoxins	Adsorbed strains	Adsorption body	Adsorption effect/%	References
Aflatoxin B_1	*Lactobacillu srhamnosus* GG	Peptidoglycan	80	El-Nezami et al. (1998)
	Lactobacillu srhamnosus GG-ATCC 53103	Peptidoglycan	36.6	Rania et al. (2005)
	Streptomyces cacaoi subsp. asoensis (K234) strain	Peptidoglycan	88	Harkai et al. (2016)
Aflatoxin M_1	*Lactobacillus bulgaricus Streptococcus thermophilus*	Peptidoglycan	/	El Khoury, Atoui, and Yaghi (2011)
Zearalenone	Yeast cell	Glucomannan	0.4 mg/L 100	Shang et al. (2015)
	Bacillus strains	β-D-glucan	5 mg/kg 56	Chen et al. (2019)
	Saccharomyces cerevisiae	Yeast cell wall	/	Armando et al. (2012)
	Lactobacillus rhamnosus	Glucomannan	38 ∼ 46	El-Nezami, Chrevatidis, et al. (2002)
	Bacillus licheniformis CK1	Glucomannan	>30	Tsui-Chun et al. (2018)
Deoxynivalenol	*Aspergillus oryzae* *Rhizopus oryzae*	Glucomannan	/	Garda-Buffon, Kupski, and Badiale-Furlong (2011)
	Lactobacillus rhamnosus *Propionibacterium fischeri*	Glucomannan	64 ∼ 93	El-Nezami, Chrevatidis, et al. (2002)
	Lactic acid bacteria *Propionibacterium*	Glucomannan	/	Niderkorn et al. (2006)
Ochratoxin	*Saccharomyces cerevisiae*	Yeast cell wall	/	Farbo et al. (2016)
	Lactobacillus Cocci *Enterococcus*	Yeast cell wall	8.23 ∼ 28.09	Prete et al. (2007)
	Saccharomyces cerevisiae	Yeast cell wall	/	Andrea et al. (2012)
	L.kefiri KFLM3 *K.servazzii* KFGY7	Polymer adsorption	82 ∼ 100	Taheur et al. (2017)
Fumonisin B_1	*Propionibacterium*	Yeast cell wall	/	Niderkorn et al. (2006)
	Fermentation bacteria	Peptidoglycan	/	Niderkorn et al. (2007)

Microbial detoxification technology for the removal of mycotoxins

Microbial detoxification of AFs

Food crops are often contaminated by *Aspergillus flavus* and *Aspergillus parasiticus,* leading to the production of AFs, with Aflatoxin B_1 (AFB_1) as the most common of the AFs (Hruska et al. 2014). Many studies have investigated the removal of AFB_1 in food or feed. The most widely used and most effective method in production is the addition of non-nutritive chelating agents to food or feed for detoxification by physical combination, but this method achieves only incomplete detoxification, can reduce nutrients in food or feed, and can cause environmental pollution and other problems (Adebo et al. 2017; Samuel, Sivaramakrishna, and Mehta 2014). Studies have found that many different microorganisms can remove or degrade AFs in food and other materials, including bacteria, yeasts, molds, actinomycetes, and algae.

Microbial degradation of AFs

Microbial degradation of AFs mainly occurs through the action of secondary metabolites produced by microorganisms or secreted enzymes that change the lactone ring structure of AFB_1 and the double-bond structure of the bifuran ring. These molecules can cause the decrease or loss of toxicity. The process of a chemical reaction is completely different from adsorption and binding (Lee et al. 1981) Studies have shown that the use of *Pseudomonas putida*,

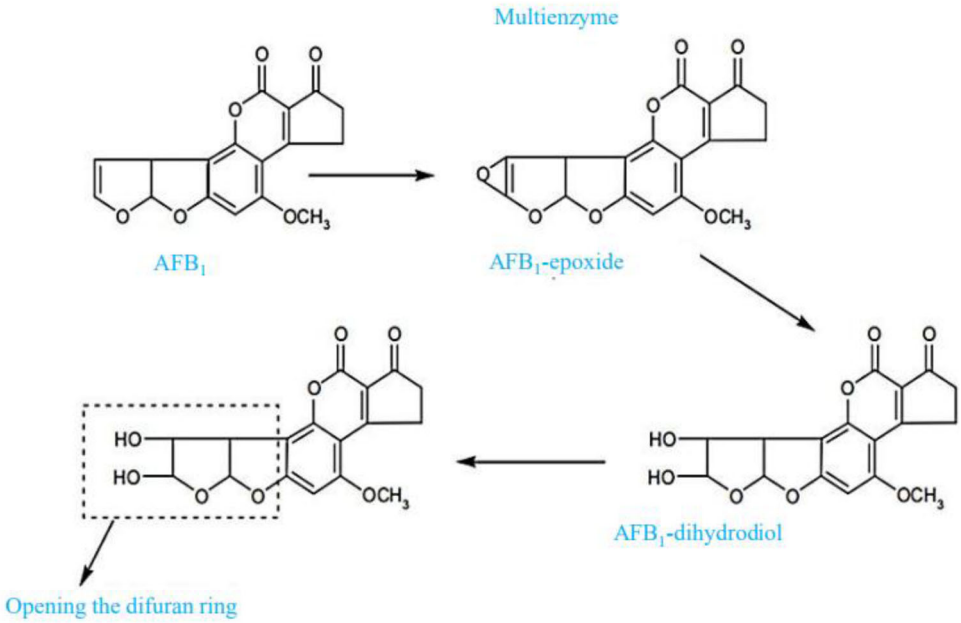

Figure 4. Pathway of degradation of AFB_1 by *Armillariella tabescens* (adapted from Wu et al. 2009).

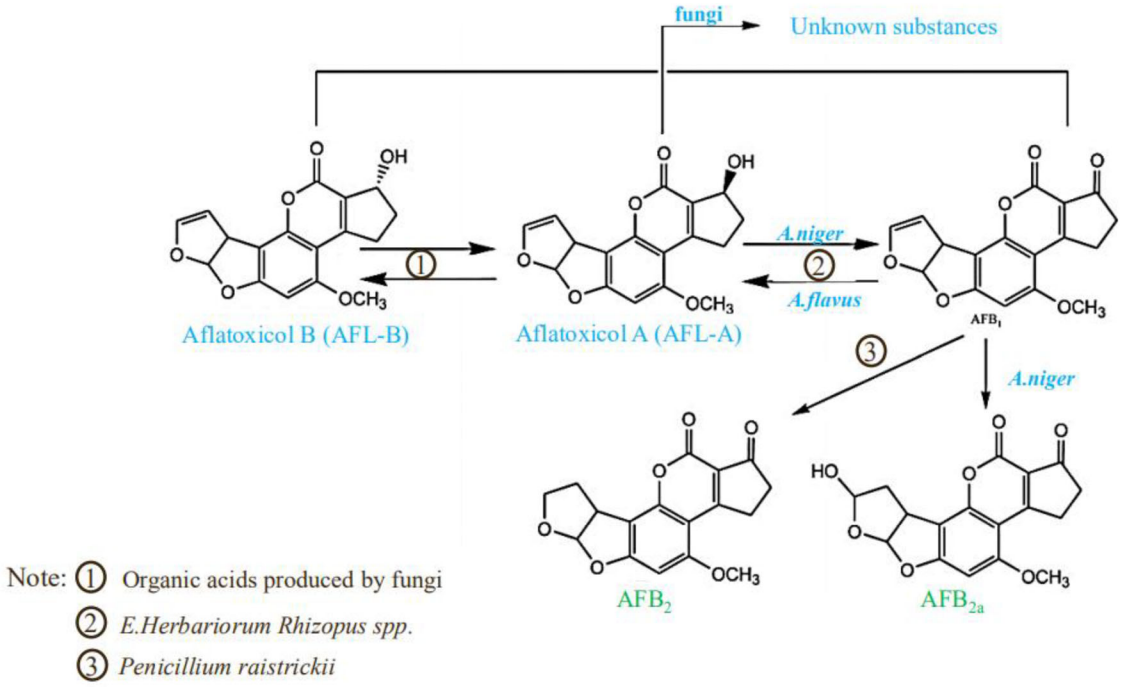

Figure 5. Degradation of AFB_1 by fungi (adapted from Wu et al. 2009).

Streptomyces sp. and *Bacillus licheniformis* can effectively degrade AFB_1 (Raksha et al. 2017; Samuel, Sivaramakrishna, and Mehta 2014). In addition, (Liu et al. 2001) isolated and purified Aflatoxin-detoxifizyme (ADTZ) from *Armillariella tabescens* (E-20), with degrading activity for AFB_1. These authors described a degradation process for AFB_1 using multiple enzymes, with conversion of AFB_1 to AFB_1-epoxide, followed by hydrolysis of the epoxide to obtain dihydrodiol and difuran ring opening (Figure 4). A. *niger* can convert Aflatoxicol (AFL) to AFB_1 and further convert AFB_1 molecules to Aflatoxin B_{2a} (AFB_{2a}). The content of AFB_1 and Aflatoxicol (AFL) will decrease with time and the final conversion rate will reach 98.6%, with both AFB_1 and AFL are metabolized into other low-toxic or nontoxic substances (Figure 5). The fungi, bacteria and detoxification enzymes mentioned above are mostly based on the destruction of the double bond of the furan ring or the detoxification effect based on the hydrolysis of the coumarin lactone ring. The double bond of the furan ring is the main functional group that induces gene mutation, cancer and malformation, and it is also the site of action for AFB_1 to form a complex with protein and DNA. The lactone ring of coumarin is the main cause of carcinogenesis of AFB_1, and this group is more active. These two ways of destroying the molecular structure of AFB_1 are the most direct ways to eliminate its toxicity. In the degradation process, microorganisms or enzymes do not

act on a single toxic site, and can produce less toxic degradation products by changing one or more of furan ring, decarbonylation, hydrolysis, and O-alkylation. Applications of microbial degradation technology for removal of AFs from food and feed are listed in Table 1.

Catalase was isolated and purified from *Mycobacterium smegmatis* by (Taylor et al. 2010) and shown to degrade the reduction of α, β-unsaturated esters of AFB_1, thereby activating the spontaneous hydrolysis of AFB_1 to form a new nontoxic degradation product. Ben Taheur et al. (2020) isolated new strains (lactic acid bacteria and yeast) from Kombucha culture, and studied the degradation performance of AFB_1 in liquid culture medium (Man Rogosa and Sharpe broth (MRS), yeast extract peptone dextrose broth and black tea). DNA sequencing was used to identify the main strains involved in the removal of AFB_1, and the toxicity of the transformed products was evaluated on Hep2 cells and brine shrimp (Artemia). The results show that Kombucha can degrade 97% of AFB_1 in black tea after 7 days of fermentation. The cytotoxicity test data on Hep2 cells and brine shrimp showed lower toxicity of biodegradation products than that of the first generation AFB_1. These findings indicate that the Kombucha isolate has AFB_1 detoxification properties and suggest potential applications in the food and feed industries. Wang, Zhang, et al. (2018) showed that *Bacillus licheniformis* (BL010) can effectively degrade AFB_1, reducing the toxin content by more than 89.1% within 120 h. After three induction periods, BL010 exhibited the highest degradation of the crude enzyme solution (97.3%). High performance liquid chromatography (HPLC) analysis results showed that the cell-free extract reduced the content of AFB_1 significantly (93.6%, $p < 0.05$), with little degradation of AFB_1 by cell culture fluid treatment. Bioinformatics methods were used to analyze the critical gene of BL010 and determine the secondary structure of two degrading enzymes (Chia010 and Lac010), providing an important basis for subsequent homology modeling and function prediction. Shcherbakova et al. (2015) studied the degradation of AFB_1 after co-culturing *Fusarium* wilt PG41 with AFB_1 at 27 °C for 72 h. The results showed a 78% degradation rate of AFB_1, and 66% of PG41 metabolites exhibited significant degradation activity, mainly related to the high molecular weight components of protein-rich extracellular metabolites. Research by Gomaa, Abdelall, and El-Mahdy (2018) explored antifungal compounds produced by *Lactobacillus brevis* and *Lactobacillus paracasei*, and tested the ability of these compounds used to inhibit AFB_1 produced by strains such as *Aspergillus flavus* and *Aspergillus parasiticus* during the growth process. *Lactobacilli* strains were isolated from traditional Egyptian dairy products, and fungal strains were isolated from infected grain seeds. *Lactobacillus brevis* and *Lactobacillus paracasei* exhibited AFB_1 inhibition of 96.31% and 90.43%, respectively. The amino acid concentration of the antifungal compound produced by *Lactobacillus brevis* was significantly higher than that produced by *Lactobacillus paracasei*. Treatment of corn seeds with antifungal compounds can efficiently control fungal infections and increase seed germination. The results confirmed that *lactic acid bacteria* can be used to control the contamination of fermented food and dairy products.

Microbial adsorption of AFs

Lactic acid bacteria and yeast cells can bind AFs and reduce their biological activity in food or feed. Yeast and lactic acid bacteria bind different molecules, including macromolecular substances and metal ions, on the cell wall and special binding sites. The peptidoglycan cell wall of lactic acid bacteria contains N-acetylmuramic acid and N-acetylglucosamine that can physically adsorb AFB_1. In addition, lactic acid bacteria are the most studied bacteria that can degrade AFs because these bacteria can be added in the food fermentation process to degrade AFs during production (Shetty and Jespersen 2006). In particular, *Lactobacillus rhamnosus* GG (LGG) exhibits strong adsorption of AFs. Therefore, probiotics such as *lactic acid bacteria* and yeast have practical application value in the food production process. Examples of microbial adsorption for the removal of AFs from food and feed are listed in Table 2.

El-Nezami et al. (1998) reported that *lactic acid bacteria* and other gram-positive bacteria have higher AFB_1 removal activity than *E. coli* (a gram-negative bacteria), and this observed difference in AFB_1 removal is closely related to the structure of the bacterial cell walls. Comparison of the AFB_1 removal activity of pre-cultured activated bacteria, heat-treated bacteria, and freeze-dried non-activated bacteria revealed that pre-culture treatment can cause changes in cell wall composition and enhance the ability of bacteria cells to remove AFB_1. Studies by Rania et al. (2005) have shown that both acid and heat treatment can significantly improve the ability of *Lactobacillus* to bind AFB_1. This may because these treatments can induce exposure of the inner surface of the bacterial membrane bilayer to reduce cross-connection or increase the pore size to facilitate the binding of toxins. In addition, the surface of the heat-treated *Lactobacillus* cell wall changes from smooth to uneven. The permeability of the cell wall is increased, with exposure of some new adsorption sites on the cell surface. Additionally, the area of contact between the cell and AFB_1 is increased, allowing improved adsorption capacity. There are also reports on the use of lactic acid bacteria to adsorb AFs. For example, El Khoury, Atoui, and Yaghi (2011) screened the lactic acid bacteria (*Lactobacillus bulgaricus* and *Streptococcus thermophilus*) used in Lebanon's traditional industries and found a strain that can degrade Aflatoxin M_1 (AFM_1) in milk and yogurt. Harkai et al. (2016) tested 10 strains for the biodegradation of 1 mg/L AFB_1. The results showed that *Streptomyces cacaoi subsp*. asoensis (K234) strain had a degradation rate of over 88% for AFB_1 and completely eliminated genetic toxicity. Unlike yeast, the ability of lactic acid bacteria to bind AFB_1 is highly species-specific, and this is mainly related to the peptidoglycan of the cell wall. The binding of this toxin by lactic acid bacteria is reversible, and repeated elution or the addition of organic solvents can release the toxins.

The use of microorganisms to degrade AFs has advantages of safety, high efficiency, environmentally safe, and

nontoxicity, making these methods attractive for the large-scale treatment of AFs. However, the detoxification mechanism and enzyme-producing properties of these strains need to be further studied. On this basis, the AFs degrading enzymes are recombinantly expressed in mature model organisms through enzyme engineering, genetic engineering and other means to achieve large-scale industrial production. The final realization of the development of high-purity and high-activity AFs degrading enzyme products used in food and feed additives is currently the main research direction.

Microbial detoxification of ZEN

Zearalenone is a type of dihydroxybenzoic acid lactone mycotoxin produced by *Fusarium gramin-earum* and *Fusarium culmorum*. Its acute toxicity is relatively low, and its chronic toxicity is mainly manifested in reproductive toxicity and its impact on the endocrine system. These compounds are widely present in corn, barley, wheat, and sorghum and other grain feeds and their by-products, and can seriously endanger the health of livestock and humans. Therefore, there is an urgent need for improved strategies to detoxify ZEN (Dong-Ho et al. 2017; Eckard et al. 2011; Rai et al. 2018). In recent years, the use of microbial detoxification to remove ZEN has become more common, and screening has allowed identification of strains that can degrade ZEN to low or nontoxic substances (Cynthia et al. 2017). In order to ensure the safety of feed, the most promising ZEN removal methods use microorganisms such as yeast and *Bacillus* sp. because they play a role in feed production, so much, the current research focuses on these two microorganisms (Wang and Xie 2020).

Microbial degradation of ZEN

The mechanism for fungi to remove ZEN mainly includes reduction of hydroxy ketones, double bond cleavage, hydroxylation, methylation, vulcanization, glycosylation, ring rupture, etc. There have been many studies on the degradation of ZEN using probiotics, including by yeast, *Bacillus*, and lactic acid bacteria. Some microorganisms can degrade ZEA to obtain a variety of different products with different degrees of toxicity. Applications of microbial degradation technology for the removal of ZEN from food and feed are listed in Table 1.

Lei et al. (2014) screened a strain of *Bacillus pumlius* ANSB01G that can efficiently degrade ZEN. The ZEN degradation rates of this strain in liquid culture medium, natural moldy corn, distiller's grains, and pig feed were 88.65%, 84.58%, 66.34% and 84.04%, respectively. This strain degrades ZEN is using an extracellular enzyme produced by the bacteria. Zhao et al. (2015) reported selection of three strains of *Lactobacillus* able to degrade ZEN from 27 traditional fermented foods, with a 45% clearance rate of ZEN in solution within 48 h. Several studies have found that microorganisms can produce enzymes that can degrade ZEN, including lactone hydrolases, proteases, and peroxidases. Ju et al. (2019) studied the ability of *Bacillus subtilis* and *Bacillus natto* to degrade ZEN, analyzed the content of ZEN in cell residues, and investigated the effect of different processing conditions on the ability of bacteria to degrade ZEN. Finally, *Bacillus subtilis* and *Bacillus natto* were used for the removal of ZEN in food. The results showed that within 48 h, the degradation rates of *Bacillus subtilis* and *Bacillus natto* were 100% and 87%, respectively, with 2.3% of ZEN in the cell residue and 1.6% in the supernatant of *Bacillus subtilis*. *Bacillus subtilis* and *Bacillus natto* exhibit good degradation of ZEN beer, with degradation rates of 65% and 73% respectively. In solid state fermentation (SSF), *Bacillus subtilis* and *Bacillus natto* have the strongest degradation effects in corn flour and soybean meal, with degradation activities of 75% and 70%, respectively. *Bacillus natto* and *Bacillus subtilis* have obvious degradation effects on ZEN in food, and also show degradation effects in liquid food and SSF, it is found that they also have good degradation effects on ZEN. This finding has important implications for the degradation of ZEN in food. Studies have pointed out that a strain of *Clonostachys rosea* can produce a lactose hydrolase ZHD101, which specifically binds to ZEN and hydrolyzes ZEN into less toxic 1-(3,5-dihydroxyphenyl)-10-hydroxy-1-Undecene-1 (Takahashi-Ando et al. 2002) (Figure 6). Kakeya et al. (2002) determined that a protease secreted by *Gliocladium roseum* is responsible for the ability of this fungus to degrade ZEN, α-zearalenol (α-ZEL), and *β*-zearalenol (*β*-ZEL) into nontoxic products. This group cloned the gene (ZHD101) encoding the protease,

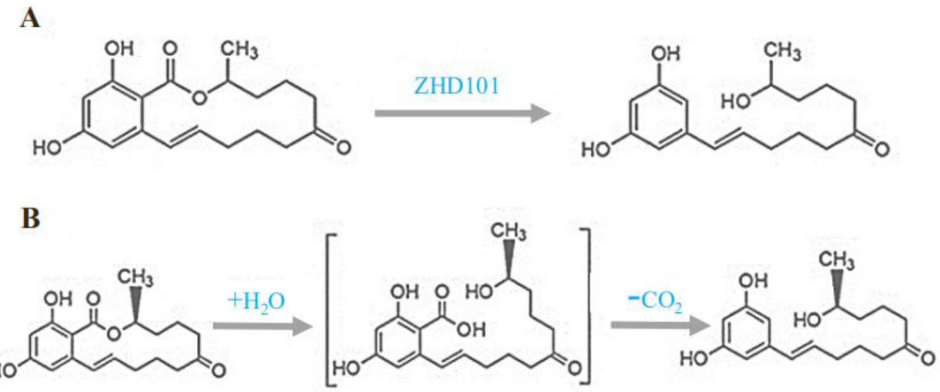

Figure 6. The mechanism of ZHD101 degrading ZEN (adapted from Xu et al. 2016). (A) The hydrolytic process of ZEN by ZHD101. (B) The structures of the substrate (left), intermediate (middle), and product (right).

and found that expression of this gene in *Escherichia coli* provided the ability to degrade ZEN into nontoxic products. Xu et al. (2016) showed that ZEN degradation by ZHD101 proceeds in two steps: cracking the polylactone bond of ZEN and generating nontoxic alkyl resorcinol products. Kuan et al. (2017) isolated a *Bacillus amyloliquefaciens* toxin with ZEN removal ability from moldy corn samples. After cultivating *Bacillus amyloliquefaciens* in Luria-Bertani (LB) medium containing 3.5 ppm ZEN, the ZEN concentration was below the detection limit within 24 h. After 36 h of cultivation, in the ZEN contaminated corn meal medium, *Bacillus amyloliquefaciens* reduced the ZEN concentration by 92%. The amount of ZEN adsorbed by *Bacillus amyloliquefaciens* cells did not increase with the extension of the culture time, which indicates that *Bacillus amyloliquefaciens* both adsorbs, and degrade ZEN. *Bacillus amyloliquefaciens* can be used as a feed additive to reduce the concentration of ZEN in feed.

Microbial adsorption of ZEN

ZEN biosorption uses strains or culture media and has good specificity. However, due to the general adsorption effect, this method is rarely used today. Yeast cell walls can adsorb ZEN, and β-D-glucan and other polysaccharides on yeast cell walls can adsorb ZEN in samples through hydrophobic effects. The cell walls of certain probiotics contain carbohydrates (such as peptidoglycan, mannose, dextran), proteins and lipids. With multiple potential sites of adsorption, there may be multiple adsorption mechanisms involved, including hydrogen bonds, ionic interactions, or hydrophobic interactions (HAGgblom and Nordkvist 2015). Applications of microbial adsorption for ZEN removal from food and feed are listed in Table 2.

Work from Shang et al. (2015) showed that yeast is a relatively stable adsorbent for mycotoxins including ZEN, mainly by adsorption by functional carbohydrates (glucomannan polymer) in the cell wall. Addition of 0.2% yeast cell wall extract can effectively decrease the reproductive toxicity of ZEA in piglets. Chen et al. (2019) screened a *Bacillus* strain with the ability to detoxify ZEN, and used a fermentation process to verify its potential application in the feed industry. In the fermentation test of high ZEN-contaminated corn (5 mg/kg), the degradation rate of strain B2 was the highest at 56%. Compared with corn without ZEN, corn contaminated with ZEN fermented by B2 strain exhibited better fermentation characteristics (lactic acid $>$ 110 mmol/L; acetic acid $<$ 20 mmol/L; pH $<$ 4.5). In addition, B2 can detoxify AFB_1, DON, fumonisin B_1 (FB_1) and T2 toxins. For the feed industry, choosing the right microbe is an important factor to consider for the removal of ZEN contaminated corn. The use of fermentation technology is a reliable choice to solve the problem of ZEN contamination in animal feed. In recent years, *Saccharomyces cerevisiae* has been developed as a nutritional additive and added to food or feed in production practice to inhibit ZEN toxicity. Armando et al. (2012) mixed different concentrations of *Saccharomyces cerevisiae* with ZEN and found that the *Saccharomyces cerevisiae* concentration was related to the ZEN adsorption capacity. The material basis for the adsorption of ZEN by *Saccharomyces cerevisiae* is β-D-glucan. *Saccharomyces cerevisiae* can remove ZEN by adsorption, but the specific degradation mechanism needs to be further studied. *Saccharomyces cerevisiae* strains can reduce the level of AFB_1 in contaminated food (Gonçalves et al. 2015; Shetty, Hald, and Jespersen 2007). LGG is a food additive that can effectively remove mycotoxins in food or feed and reduce the toxin content in samples. For example, when ZEN (2.0 g/mL) is added to LGG culture, the adsorption rate of LGG on ZEN reaches 38%∼46% (El-Nezami, Polychronaki, et al. 2002). Tsui-Chun et al. (2018) reported greater than 30% adsorption efficiency of *Bacillus licheniformis* CK1 on ZEN. Despite the effects described above, for almost all *Bacillus* strains, most degradation is caused by secretase, with little contribution of adsorption to mycotoxin detoxification. The microorganisms that have been reported to have the ability to adsorb ZEN toxins in food and feed are mainly lactic acid bacteria and yeasts, and with variation in adsorption types and abilities of different strains.

Although there have been many studies of ZEN microbial degradation, further work is required for practical application. There are recognized safe strains of yeast and *Bacillus* that can be used to detoxify ZEN in feed. The use of this process to improve the safety of feed and food will be facilitated by identification of strains or enzymes that degrade ZEN more efficiently and the development of improved technologies for the microbial degradation of ZEN. Additionlly, more efforts should be devoted to the study of the harmful effects of degradation products.

Microbial detoxification of DON

DON is the most common mycotoxin in cereals, and is produced by *Fusarium culmorum* and *Fusarium graminearum* (Hope, Aldred, and Magan 2005; Magan et al. 2002). DON is a sesquiterpene triphenyl containing 12,13-epoxy groups, and causes toxicity by inhibiting protein synthesis (Repeckiene˙ et al., 2013; Ehrlich and Daigle 1987; Sobrova et al. 2010). Acute exposure can cause vomiting, nausea and diarrhea; chronic low-dose exposure can cause weight gain, anorexia, reduced nutritional efficiency and changes in immune function (Pestka 2007; Pestka 2010). DON can also reduce production of livestock and poultry, weaken animal immune systems, and alter cell signal transduction and gene expression. The degree of DON pollution is showing an increasing trend, making the control of DON pollution urgent. The structure of DON is very stable and although chemical detoxification may be more effective, this may introduce other toxic substances and affect the nutritional quality of grains. Physical detoxification methods for DON have mainly relied on physical adsorption, but poor adsorption to DON results in little change in toxin toxicity. Biological detoxification methods may be better than chemical and physical methods, but require screening microorganisms to identify ones that release extracellular enzymes under mild conditions. Some recent results are described below.

Microbial degradation of DON

The method of biodegradation and detoxification of DON is mainly to use microorganisms or strains to change the structure of DON. The key point is to change the epoxy groups at positions C12 and C13, remove them or open their rings to achieve detoxification. DON degradation to products of low or no toxicity can occur through hydroxylation, hydrolysis, de-epoxidation, deacetylation, and glycosylation (Awad et al. 2010). The epoxy structure at C12 and C13 in the DON structure and C3-OH group is the main toxic group of DON, and these groups exert toxicity by binding to ribosomes and causing ribosomal toxic stress effects. Protein kinases that regulate gene expression are activated, effecting protein synthesis and cytotoxicity, and this is a main research focus of DON biodegradation studies (Wu et al. 2007) (Figure 7). Microorganisms reported to degrade DON include *Devosella*, *Nocardia*, anaerobic bacteria, *Bacillus spp.*, and fungi in animal intestines. The application of microbial degradation technology for the removal of DON from food and feed is described in Table 1.

Khatibi et al. (2011), compared the characteristics of 3-O-acetyltransferases from seven species of *Fusarium*, expressed two optimal gene fragments, *FgTRI101* and *FfTRRI201* in *Saccharomyces cerevisiae*, and found that the expressed products effectively degraded DON. Ikuo et al. (2012) isolated 13 degrading bacteria from samples from various environments including soil and wheat leaves, and find nine Gram-positive bacteria and four Gram-negative bacteria with ability to degrade. Pierron et al. (2016) studied that bacteria can deepoxidize or epimerize DON into deepoxy-DON or DOM-13-epi-DON. Using different methods, the intestinal toxicity of 3 molecules were compared, and the molecular basis of reducing toxicity was studied. In human intestinal epithelial cells, deepoxy-DON and 3-epi-DON are not cytotoxic, and do not change oxygen consumption or impair barrier function. Bacterial deepoxidation or epimerization of DON changes the interaction of DON with ribosomes, resulting in a lack of MAPKinase activation and reduced toxicity. Ilse et al. (2017) used bioassays to screen microbially enriched cultures produced in rumen juice, soil, digestive juice and activated sludge, and investigated their biotransformation and detoxification capabilities for DON. Samples of enriched bacteria extracted from soil and activated sludge can detoxify and degrade 5 and 50 mg/L DON, and, the metabolites 3-epi-DON and 3-epi-DOM-1 were found to be the main conversion products of DON. This research provides a new valuable tool for screening the detoxification ability of microbial cultures.

Microbial adsorption of DON

DON biosorption is similar to the AFB_1 biosorption process. Adsorbents and toxins are combined to form a complex in the animal body that is discharged with the adsorbent, thereby reducing the biological effects of toxins, reducing the concentration of toxins in the blood and the intestine, other target organs. Among the traditional detoxification methods, ozone detoxification is a relatively effective method, but the residual ozone will contaminate the sample, which limits the use of ozone. Both fungi and *lactic acid bacteria* have been reported to adsorb DON (Wan et al. 2016). Four types of yeast, *Maggi Meschia*, *Saccharomyces cerevisiae*, *Kluyveromyces marxianus*, and *Geotrichum fermentum* exhibit good adsorption effects on DON (Repečkienė et al. 2013). Applications of microbial adsorption for the removal of DON from food and feed are listed in Table 2.

Garda-Buffon, Kupski, and Badiale-Furlong (2011) found that filamentous fungi *Aspergillus oryzae* and *Rhizopus oryzae* can absorb DON into the mycelium and degrade DON through submerged fermentation, with maximum degradation rate after 48 h. El-Nezami, Polychronaki, et al. (2002) found that addition of 20 μg/mL DON to cultures of LGG, LC-705, and *P. freudenreichii* strains for 1 h resulted in 64–93% of DON in the supernatant adsorbed and eliminated. Further investigation revealed that there was no significant difference in the DON adsorption capacity of inactivated cells and living cells (>0.05). Niderkorn, Boudra, and Morgavi (2006) tested 29 kinds of lactic acid bacteria and *propionic acid bacteria* for DON removal and found that six showed good effect. The removal effect is related to the bacterial concentration and the type of bacteria, but at

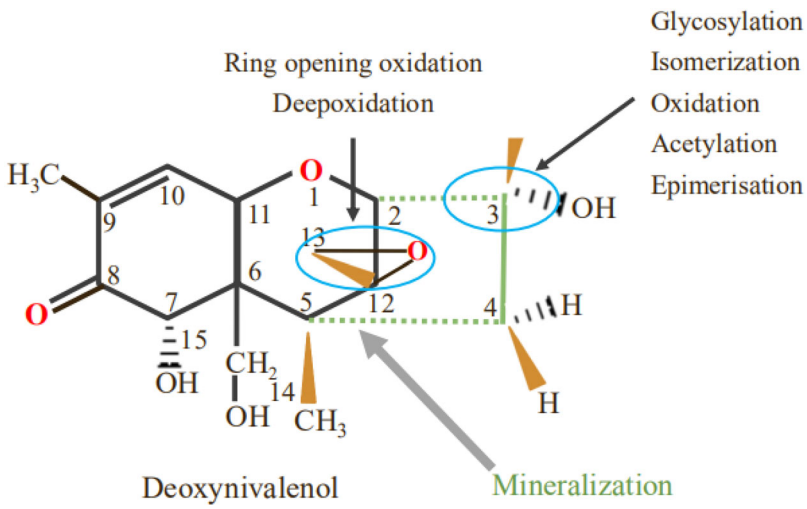

Figure 7. The main sites of DON biodegradation research (adapted from Wu et al. 2007).

the same bacterial concentration, propionic acid bacteria were less effective than lactic acid bacteria for DON removal. Live or dead lactic acid bacteria showed no significant difference in the ability to eliminate DON. Adsorption of DON by microorganisms mainly occurs through the glucomannan on the microbial cell wall, and this material has been extracted and used in the food and feed industries. The adsorption of DON on the microbial cell wall is reversible, and this adsorption is related to the type and concentration of bacteria. To improve adsorption for DON removal, the quality and stability of the adsorbent should be improved (Girgis et al. 2010).

The use of microorganisms or microbially-produced detoxification enzymes to eliminate or reduce the damage of DON is an effective strategy for treatment of this toxin. Current research is mainly aimed at the screening of detoxification conditions and the identification of strains that degrade DON, but there have been relatively few studies of the separation and purification of detoxified substances or the determination and toxicity characterization of degradation products. Future research should try to isolate and purify intracellular or extracellular enzymes that degrade DON, obtain the gene sequences of key enzymes, and apply genetic engineering methods to modify genes to increase enzyme activity.

Microbial detoxification of OTA

Ochratoxin A (OTA) is a secondary metabolite of fungi that can contaminate agricultural products and cause serious global health risks (Müller et al. 2003; Markowiak et al. 2019; Péteri et al. 2007). OTA is the most toxic Ochratoxin and a kind of isocoumarin, composed of Ochratoxin α (OTα) and L-β-phenylpropane linked by an amide bond. OTA can induce the production of reactive oxygen species, changes in mitochondrial structure and function, cell signal transduction, cell apoptosis, and affect the interaction with other substances. These are the causes of OTA toxicity. OTA has nephrotoxicity, liver toxicity, genotoxicity, mutagenicity, teratogenicity, and embryotoxicity to humans and animals, but degradation products OTα and phenylalanine have no negative effects. There are several physical and chemical methods available for OTA detoxification (Akiyama et al. 1997; Bhat and Reddy 2017; Poór et al. 2015; Zhang and Sang 2015; Purnell 2012; Zhang et al. 2016). Microbiological degradation does not reduce the nutritional value of food, and has high efficiency and specificity for OTA detoxification (Abrunhosa et al. 2014; Braun et al. 2018; Fuchs et al. 2008). Studies have shown that, except for fungal genera *Aspergillus*, *Penicillium*, and *Rhizopus*, most of the strains that show strong degrading ability to OTA are genera *Rhizobium*, *Bacillus*, and *Acinetobacter* (Qu et al. 2013). Microbes remove OTA by both adsorption and metabolic activity. Adsorption of OTA occurs by microbial cell walls in yeast and lactic acid bacteria, and microbial enzymes can convert OTA into other substances.

Microbial degradation of OTA

OTA biodegradation is to degrade OTA into nontoxic compounds, thereby eliminating the toxicity of OTA. The biodegradation of OTA is mainly the use of microbial metabolic enzymes to break the amide of L-β-phenylalanine and 7-carboxy-5-chloro-8-hydroxy-3,4-dihydro-R-methylisocoumarin Key to hydrolyze OTA into basically nontoxic L-β-phenylalanine and OTα (ochratoxin α). Therefore, the selection of appropriate microbial strains capable of reducing OTA is the basic work, and clarifying the detoxification mechanism and extracting and purifying detoxified substances that can degrade OTA are the main scientific issues that scholars explore. There have been many recent studies showing the detoxification of OTA by microorganisms in animal intestines. The structures of OTA and degradation products are shown in Figure 8, and applications of

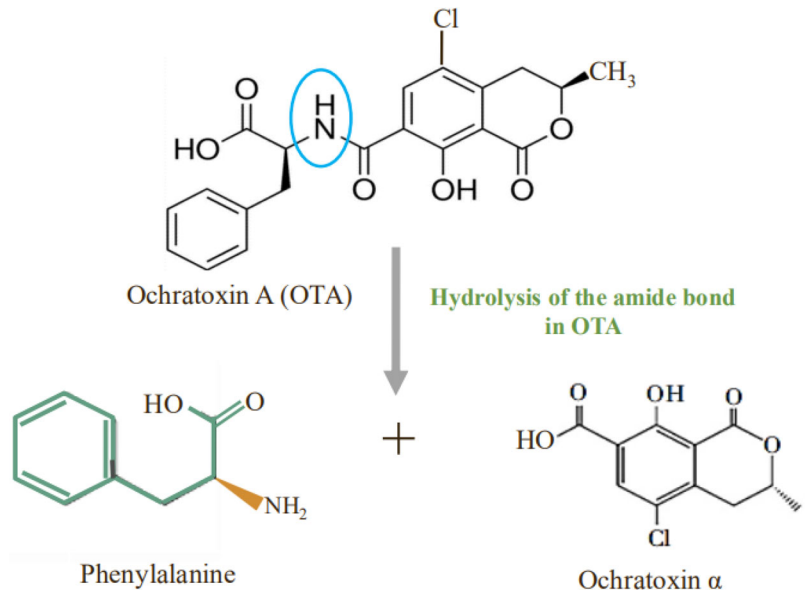

Figure 8. Hydrolysis of the amide bond in OTA to yield OTα and phenylalanine as considered the primary degradation/detoxification pathway for Ochratoxins (adapted from Haq et al. 2016).

microbial degradation technology for OTA removal from food and feed are listed in Table 1.

Petchkongkaew et al. (2008) studied the detoxification performance of *Bacillus licheniformis* in soybeans and found 92.5% degradation of OTA after culturing at 37 °C for 48 h. The high degradation of OTA is due to the destruction of its structure during the microbial degradation process. In addition, this strain may also be a source of effective enzymes for OTA degradation in other foods or feeds. Abrunhosa et al. (2014) isolated *Pediococcus parvulus* strains from Douro wines and found they reduced OTA toxicity in food through spontaneous malolactic fermentation. After culturing on MRS medium supplemented with OTA, OTA was biodegraded into OTα by some *P. parvulus* strains. Using LC-MS/MS to confirm the presence of OTα, the conversion of OTA to OTα derivatives indicated that the OTA amide bond was hydrolyzed by the putative peptidase. The biodegradation rate of OTA depends on the size of the inoculum and the incubation temperature. Under optimal conditions, OTA was degraded by 50% and 90% in 6 h and 19 h, respectively. The biodegradation effect of *P. parvulus* UTAD 473 on grape plant OTA was also studied. As some *P. parvulus* strains have related probiotic properties, the identified strains may be particularly suitable for treatment of food and feed to offset the toxic effects of OTA. Chang et al. (2015) grew *Bacillus amyloliquefaciens* ASAG1 cells with OTA and observed 98.5% OTA degradation after 24 h. Similarly, work from Leonardo et al. (2014) showed that the wild strain *Saccharomyces cerevisiae* W13 removed more than 57% of OTA after being cultured at 30 °C for 72 h. Xiong et al. (2020) isolated the *Aspergillus oryzae* strain M30011 and studied its OTA degradation ability. An OTA degradation product was obtained by processing the ears of rice, and was identified as Ochratoxin (C11H9O5Cl). Toxicity experiments showed that *Aspergillus oryzae* had a significant detoxification effect on OTA, with a maximum degradation rate was 94% after 72 h. The results suggest the *Aspergillus oryzae* strain M30011 can be used for OTA detoxification in the food industry to improve food safety and quality.

Microbial adsorption of OTA

Some detoxification effects of microbial strains on OTA are due to adsorption rather than degradation. In addition, different OTA degradation strains have different degradation efficiencies (Csutorás et al. 2013; Ji, Fan, and Zhao 2016; Luo, Liu, and Li 2018; Luz et al. 2018). OTA biosorption by microbes results in a bacterial-OTA toxin complex, which reduces the amount of free OTA toxin. The applications of microbial adsorption for removal of OTA from food and feed are listed in Table 2.

Farbo et al. (2016) studied the adsorption of OTA in grape juice by yeast cells immobilized on calcium alginate beads, and found that heat-treated *Saccharomyces cerevisiae* cells had higher OTA adsorption capacity than living cells, and inactivated cells did not present a safety hazard, making use of these treated cells one of the most valuable biological detoxification methods currently available. Prete et al. (2007) studied the in vitro interaction between OTA and *Saccharomyces cerevisiae*. Several strains of *Saccharomyces cerevisiae* cultivated in liquid synthetic medium decreased the OTA concentration, with adsorption efficiencies of 8.23–28.09%. Commercial *Saccharomyces cerevisiae* strains have higher adsorption efficiency for OTA than other *Saccharomyces cerevisiae* strains, with OTA adsorption efficiencies ranging from 17.35% to 28.09%. Andrea et al. (2012) studied the OTA adsorption phenotype of two variants of *Saccharomyces cerevisiae*, finding that OTA adsorption is genetically controlled and is a polygenic genetic characteristic. The ultrastructure analysis of the cell wall of *Saccharomyces cerevisiae* by transmission electron microscope (TEM) revealed that the cell diameter or thickness of the cell wall of Saccharomyces cerevisiae affects its ability to remove mycotoxins. Taheur et al. (2017) showed that when *Lactobacillus kefiri, Kazachstania servazzii* and *Acetobacter syzygii* strains and toxins are co-cultured in milk, the microorganisms exhibit effective adsorption of AFB_1, ZEA, and OTA of 82%∼100%. Kefir consumption may help reduce the absorption of these mycotoxins from the gastrointestinal tract, thereby reducing their toxic effects. The isolated strain may be of interest to the development of fermented dairy products for human consumption due to its new probiotic property of adsorption of mycotoxins.

There have been few studies of OTA biological detoxification and there are limitations of our current knowledge. Overall, there is a need for more efficient and stable detoxification strains, the detoxification mechanisms need to be determined, and the genes responsible for detoxification should be identified. Additionally, the safety of detoxification products needs further evaluation. Given these limitations, microbial detoxification is not yet sufficiently developed for large-scale production and application. With increased research, the theoretical basis of OTA biological detoxification will be improved to facilitate application of this technology.

Microbial detoxification of FB_1

FUMs are water-soluble secondary metabolites produced by *Fusarium moniliformis*, *Fusarium verticillium*, *Fusarium polyuria*, and other *Fusarium* species (Li et al. 2015). FUMs are mainly found in corn, wheat, beans, and other grains and their processed products. In a lower concentration range, FUMs can interfere with the normal physiological metabolism of plants, causing agricultural economic losses and presenting serious carcinogenicity for humans and animals. About 28 FUMs analogs have been described, which can be divided into four categories according to their structures (Alberts, Van, and Gelderblom 2016). Of these, FB_1 is the most widely distributed and the most toxic, causing horse brain white matter softening, pig lung edema, and the liver and immune system of poultry (Helle-Katrine et al. 2018; Voss, Smith, and Haschek 2007). FB_1 also causes hepatotoxicity and nephrotoxicity in most mammalian species (Loiseau et al. 2015). Human esophageal cancer and infant neural tube defects are also associated with high FB_1 exposure (Braun and Wink 2018). Structurally, FUMs are very stable, so physical and chemical methods are not effective

for removal of FUMs or result in production of other toxic substances. Thus, biological methods are highly promising because they can transform and metabolize FUMs into low-toxic or nontoxic products.

Microbial degradation of FB_1

FUMs are a class of diester compounds with structures composed of different polyhydric alcohols and glycerin. The structure has an aliphatic chain composed of 20 carbons and two side chains of the same ester bond connected via the 14th and 15th carbon chains. Degradation of FUMs occurs by microbes that utilize FUMs as the sole carbon source, using a two-step degradation process. In the first step, the C-15 and C-15 tricarboxylic acid groups are removed under the action of carboxylesterase to convert FB_1 into hydrolyzed fumonisins B_1 (HFB_1). In the second step, HFB_1 is converted into 2-keto-HFB_1 or another compound under the action of transaminase. Further research will identify key coding genes and clarify the enzymatic detoxification mechanism (Figure 9). Based on the above research results, the proposed degradation pathway of FB_1 is shown in Figure 10. So far, only a few strains have been identified with the ability to degrade FB_1, such as Delftia/Comamonas group (Benedetti et al. 2006), *Sphingomonas sp.* ATCC55552 (Heinl et al. 2011) and MTA144 (Heinl et al. 2010). In addition, the European Food Safety Authority (Rychen et al. 2016) and other groups have evaluated the safety and effectiveness of an enzyme-based feed additive (FUMzyme®) produced by a genetically modified yeast strain for FB_1 detoxification (Masching et al. 2016; Schwartz-Zimmermann et al. 2018). Applications of microbial degradation technology for the removal of FB_1 from food and feed are listed in Table 1.

Heinl et al. (2010) found the key genes for FB_1 biosynthesis and degradation in the bacterium *Sphingomonas* MTA144. One gene encodes a decarboxylase and one encodes a transaminase, respectively. showed detoxification of FB_1 occurs through a two-step enzymatic reaction. Overall, *Sphingomonas* MTA144 has great application potential for microbial degradation of aromatic compounds. Heinl et al. (2011) reported the sequence and HFB_1-deaminating activity of a novel aminotransferase encoded by fumonisin-degrading bacteria ATCC55552. The identified genes are expressed heterogeneously in *E. coli*, and the recombinase can deaminate HFB_1 in the presence of a-keto acid pyruvate, pyruvate, and its coenzyme pyridoxalphosphate. The determination of the genetic basis of HFB_1 deamination in ATCC55552 bacteria will help to fully understand the catabolism of FB_1 in this organism. Zhao et al. (2019) isolated a mixed bacterium SAAS79 with high FB_1 degradation activity from mushroom residue. After culturing at pH 5.7 and room temperature for 24 h, the degradation rate of 10 μg/mL FB_1 by mixed bacteria SAAS79 exceeded 90%. In addition, liquid chromatography/time of flight tandem mass spectrometry (LC-TOF/MS) analysis identified two degradation products of FB_1, that are significantly less toxic to monkey kidney cells (MARC-145) compared with the first generation of FB_1 ($p < 0.05$). Overall, the mixed bacteria SAAS79 and its crude enzymes may allow FB_1 decontamination in the feed and food industries. Moreover, mixed bacteria provide a new source of genes for the development of enzyme antidote.

Microbial adsorption of FB_1

A few studies have reported microbial adsorption of FBs, as listed in Table 2.

Niderkorn, Boudra, and Morgavi (2006) determined the ability of three *Propionibacterium* strains to remove FB_1 and Fumonisin B_2 (FB_2) in acid MRS broth samples (pH 4.0) and observed a better detoxification effect of FB_2 than that for FB_1. In addition, the efficiency of bacteria binding to toxins was affected by pH, and at pH 7, lactic acid bacteria were unable to bind FB_1 and FB_2. Niderkorn et al. (2007) also found that the degradation of FUMs by fermenting

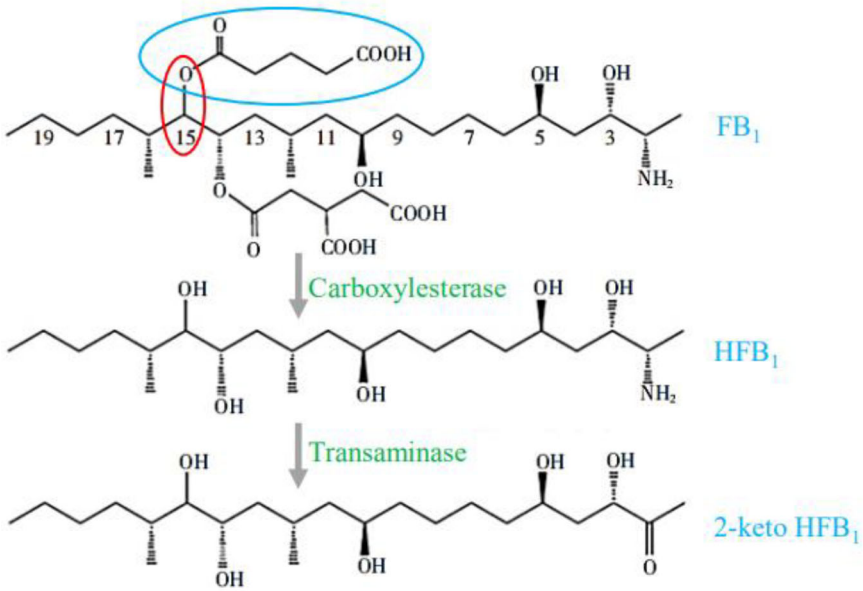

Figure 9. Transaminase catalyzes the FB_1 reaction (adapted from Wu et al. 2018).

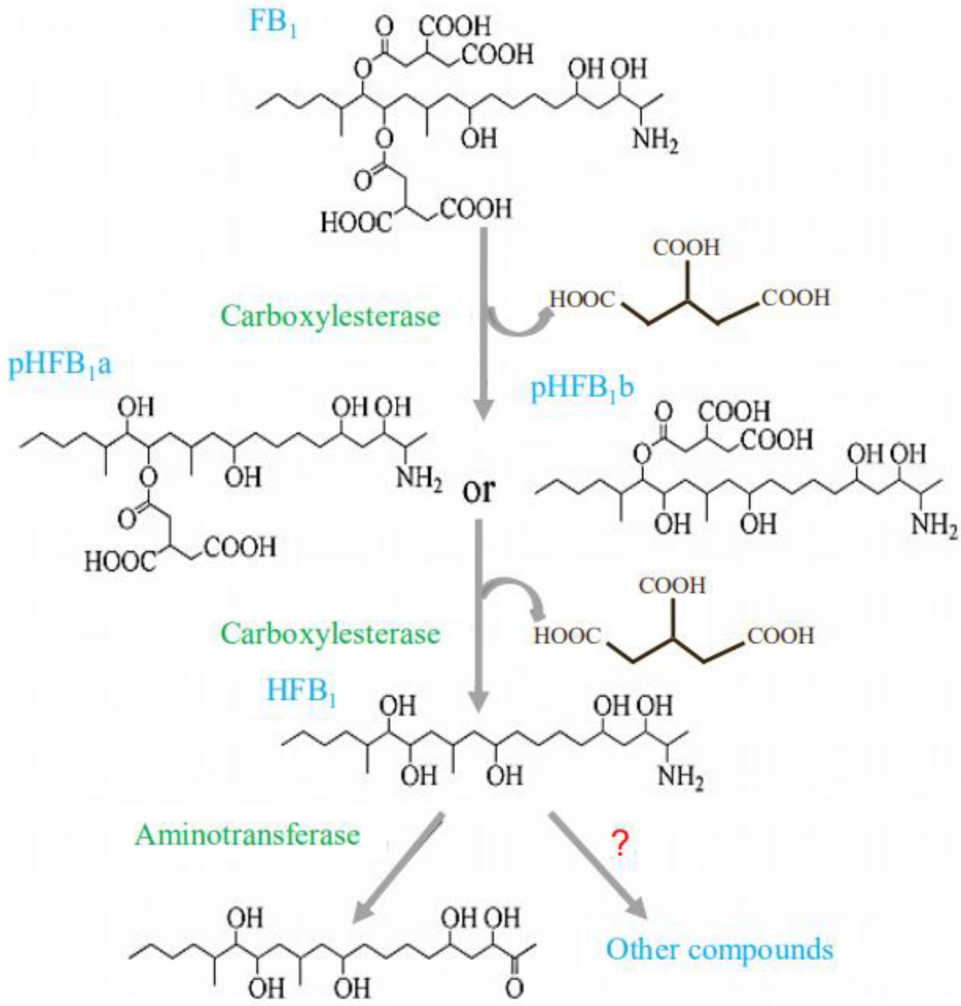

Figure 10. Degradation pathway of FB_1 by the enzymes in intracellular supernatant (adapted from Zhao et al. 2019).

bacteria is due to the high affinity of FUMs of the peptidoglycan in the bacterial cell wall.

It is theoretically and technically feasible to convert FUMs into nontoxic substances by biotransformation. Genetic transformation can be used to insert new genes into the genetic material of crops to increase their capabilities. Biological degradation approaches may be effective strategies to reduce toxin pollution by inhibiting the synthesis of toxins or by degrading toxins into nontoxic substances.

Conclusion and outlook

The detoxification of mycotoxins by microorganisms such as bacteria, yeasts, and fungi is a promising method, with high efficiency and strong specificity. Microbial degradation can decompose toxins without residual toxic substances or only a few low-toxic compounds, for improved food and feed safety.

This article reviews advances in the use of microbial degradation and microbial adsorption for the conversion of several common mycotoxins into relatively safe substances, thereby improving the safety of food and feed. Recent studies of the detoxification of microbial mycotoxins in food or feed have mainly focused on the removal of single mycotoxins and the application of strains in the laboratory, however, the detoxification mechanism, detoxification-related genes, and active ingredients of strains have not been characterized.

There are several key future directions suggested by this review. First, the practical use of detoxified strains or the degrading enzymes released in food or feed. Second, it is important to study the combination of multiple strains and the mechanism of microbial degradation of mycotoxins to improve degradation ability and reduce mycotoxin stability. Third, to determine the suitability of detoxification methods, a qualitative risk analysis is required to evaluate the toxicity of mycotoxin degradation products and degrading strains. This risk assessment should consider the safety of food and feed production before commercial application. Therefore, how to identify and purify the relevant degrading enzymes, and make the microorganisms produce high-yield target enzymes to be used in actual production, is the main research direction at present, and has a good market prospect in detoxification of mycotoxins in food and feed. Current related research focuses on screening and cloning bioactive enzyme genes that have specific degradation effects on mycotoxins, and using biotechnology to cultivate excellent crop varieties that are resistant to mycotoxins. With the completion of genome sequencing of toxin-producing fungi and the emergence of new technologies such as genomics,

proteomics, and metabolomics, the use of biotechnology to reduce, prevent and control of mycotoxins in food and feed will usher in unprecedented development opportunities.

Disclosure statement

No potential conflict of interest was reported by the authors.

Abbreviations

AFs	Aflatoxins
AFB_1	Aflatoxin B_1
AFM_1	aflatoxin M_1
AFB_{2a}.	Aflatoxins B_{2a}
AFL	Aflatoxicol
OTs	Ochratoxin
OTA	Ochratoxin A
OTα	Ochratoxin α
ZEN	Zearalenone
α-ZEL	α-zearalenol
β-ZEL	β-zearalenol
α-ZAL	α-zearalanol
β-ZAL	β-zearalanol
FUMs	Fumonisins
FB_1	Fumonisin B_1
FB_2	Fumonisin B_2
HFB_1	Hydrolyzed fumonisin B_1
DON	Deoxynivalenol
DDGS	Distillers dried drains with solubles
LGG	*Lactobacillus rhamnosus* GG
ADTZ	Aflatoxin-detoxifizyme
HPLC	High performance liquid chromatography
HPLC-MS/MS	High performance liquid chromatography-tandem mass spectrometry
ELISA	Enzyme-linked immunosorbent assay
SSF	Solid state fermentation
LB	Luria-bertani
TEM	Transmission electron microscope
MRS	Man rogosa and sharpe broth
EFSA	European Food Safety Authority
LC-TOF/MS	Liquid chromatography/time of flight tandem mass spectrometry

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