Mycotoxin Biodegradation and Bioadsorption

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Mycotoxins are secondary metabolites produced by fungi. Food/feed contamination by mycotoxins is a great threat to food safety. The contamination can occur along the food chain and can cause many diseases in humans and animals, and it also can cause economic losses. Many detoxification methods, including physical, chemical, and biological techniques, have been established to eliminate mycotoxins in food/feed. The biological method, with mycotoxin detoxification by microorganisms, is reliable, efficient, less costly, and easy to use compared with physical and chemical ones. However, it is important to discover the metabolite's toxicity resulting from mycotoxin biodegradation. These compounds can be less or more toxic than the parent. On the other hand, mechanisms involved in a mycotoxin's biological control remain still unclear. Mostly, there is little information about the method used by microorganisms to control mycotoxins.

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1. Microorganism Degradation

1.1. Toxin Detoxification by Bacteria

Many species of bacteria have the ability to degrade mycotoxins, including lactic acid bacteria [1] and other species [2]. *Tetragenococcus halophilus* [3], *Rhodococcus erythropolis*, and *Mycobacterium fluoranthenivorans* [4] were proven to degrade AFB1; *Pediococcus parvulus* [5] and *Lactobacillus acidophilus* [6][7] are effective for OTA, AFB1, and AFM1 biocontrol; *Bifidobacterium animalis* [8] is useful for patulin control; *Pseudomonas otitidis* [9] and *Bacillus velezensis* Strain ANSB01E [10] are able to detoxify ZEN. The degradation process depends on many factors, such as the incubation time, the medium, the microorganism species, the concentration of the bacteria cells, and the pH.

The degradation time changes according to the bacteria strain; the microbiota from the thermophilic compost of agricultural waste have degraded AFB1 in 5 days, with a degradation yield of more than 95% after cultivation in a PCS medium at 55 °C [11], and *Rhodococcus pyridinivorans* K408 took 12 days to detoxify AFB1 in bioethanol [12]; the *Lacticaseibacillus rhamnosus* (previously *Lactobacillus rhamnosus)* strains LBGG and LC705, however, removed AFB1 very rapidly [13].

The detoxification rate can depend on the medium; *Bacillus subtilis* UTBSP1 is able to detoxify AFB1 in a higher yield in pistachio nuts than in a medium culture [14], and *Pseudomonas fluorescens* strain 3JW1 can degrade AFB1 in potato dextrose broth and peanut medium by 97.8% and 99.4%, respectively [15].

Many bacteria have been reported to be able to degrade more than one mycotoxin [16]. AFB1 and ZEN have been degraded simultaneously by a microbial consortium, TADC7 [17]; *Rhodococcus pyridinivorans* strains (K408 and AK37) are able to degrade AFB1, T-2, and ZEN simultaneously [18], but also, some *lactic acid bacteria* strains can degrade multi-mycotoxins [19][20]. On the other hand, *Pseudomonas fluorescens* strain 3JW1 is able not only to degrade AFB1 but also to inhibit the AFB1 production of *Aspergillus flavus*. It reduces the amount of AFB1 produced by Aspergillus by 97.8%, 99.4%, and 55.8%, respectively, in the medium culture, peanut medium, and peanut kernels [15].

pH also plays an important role in mycotoxin biodegradation. An *Alcaligenes faecalis* strain called ANSA176 is able to detoxify OTA at a rate of 97.43% per 1 mg/mL OTA into OTα within 12 h at 37 °C. The optimal pH is between 6.0–9.0. The bacterial species subjected to the tested pH, ranging from 2.5 to 5.0, were unable to grow [21].

Therefore, mycotoxin biodegradation is an effective method, but it depends on multiple factors. Strict studies are needed for each biocontrol strain to determine the optimal conditions for its use.

1.2. Mycotoxin Detoxification by Yeast

Yeasts are able to detoxify mycotoxins in different ways: biodegradation, bioadsorption, or the inhibition of mycotoxin production [22].

The biodegradation method can happen with an enzyme isolated from the yeast or the use of the yeast itself. Hong Cao et al. [23] demonstrated the aflatoxin B1 degradation activity of an oxidase enzyme from the fungus *Armillariella tabescens*. The degradation ability of aflatoxin oxidase has been shown by high-performance thin-layer chromatography (HPTLC). The main mechanism was thought to be the cleavage of the bis-furan ring of the aflatoxin molecule. *Meyerozyma guilliermondii* has been shown to be able to control patulin in pear. The patulin degradation ability of *Meyerozyma guilliermondii* in pear wounds increases with a higher concentration of yeast cells. The optimal temperatures are 20 °C and 4 °C in wounds, as well as in whole fruits [24].

On the other hand, yeast biocontrol can involve bioadsorption mechanisms. Some *Saccharomyces* strains are able to remove OTA contamination via adsorption; the mechanism of removal can be enhanced from 45% to 90% by heat treatment of the microorganism and with a lower pH in the medium [25]. In another case, during OTA reduction caused by *Saccharomyces cerevisiae*, the addition of sugar at a temperature of 30 °C enhanced the OTA reduction rate in a semi-synthetic medium [26]. The binding capacity of AFB1, ZEN, OTA, and DON with respect to the *Saccharomyces cerevisiae* contained in beer fermentation residue was studied by Campagnollo et al. [27]. The results showed that beer fermentation residue has a higher binding capacity for ZEN at levels of 75.1% and 77.5% at pH 3.0 and 6.5, respectively. The volatiles of non-fermenting yeasts have shown significant binding activity against mycotoxins. The highest mycotoxin binding activities of these strains were noted against ochratoxin A (92%), AFB2 (66%), AFG2 (59%), and AFB1 (31%) [28]. One issue concerning mycotoxin biocontrol by yeast is that it can sometimes be a reversible mechanism, as has been noted with *S. cerevisiae* CECT 1891 and *L. acidophilus* 24, which were able to remove FB1 from a liquid medium. The removal was a fast and reversible process [29].

Yeasts' complicated interactions with mycotoxins indicate that cell wall structural integrity, physical structure and morphology, and chemical components all play important roles in the adsorption process. On this basis, future approaches may rely on combinations of different microorganisms to provide complementary advantages in mycotoxin adsorption by yeast [30].

Finally, mycotoxin biocontrol by yeast can concern the inhibition of mycotoxin production. Ponsone et al. studied the activity of some yeast strains isolated from Argentinean vineyards against the growth of the ochratoxigenic *Aspergillus* strain Nigri and also evaluated their effects on OTA. This entry demonstrated the natural occurrence of biocontrol agents in the environment to reduce fungi and mycotoxin problems. The results showed that these yeast strains have the ability, under different water activity (aw) and temperature conditions, to control *Aspergillus carbonarius* and *A. niger* aggregate growth and OTA accumulation with a reduction of at least 50% [31]. The same results were obtained when non-fermenting and low-fermenting yeasts were used by Fiori et al. to reduce OTA contamination in grape juice [32]. Nonetheless, some yeast strains are just able to inhibit growth parameters but not mycotoxin production.

1.3. Toxin Detoxification by Enzymes

Some enzymes isolated from microorganisms or mushrooms are able to degrade one or multiple mycotoxins. This is the case for the Ery4 laccase from *Pleurotus eryngii*, which can degrade AFB1, FB1, OTA, ZEN, and T-2 at the same time [33]. Other enzymes can detoxify only one mycotoxin; this is the case for *Armillariella tabescens*, which has been demonstrated to have an AFB1 degradation ability [23]. The degradation mechanism depends on the enzyme type and the type of mycotoxins. Enzymes can transform the parent into a new compound [23][34][35] or digest it completely [36]. Zeinvand-Lorestani et al. studied the action of a laccase enzyme against AFB1. Under optimal conditions, 67% of the total amount of AFB1 was degraded by the laccase after two days. The degraded product's prooxidative properties and mutagenicity were lower than the AFB1 one [37]. *Bacillus amyloliquefaciens* ASAG1 can detoxify OTA by 98.5% after 24 h of incubation and 100% after 72 h. On the other hand, the carboxypeptidase cloned from the bacterium is also able to degrade OTA at a level of 41% and 72%, respectively, when cultivated with the supernatant and the purified protein of the carboxypeptidase [38]. Another study showed the effect of carboxypeptidases against OTA. Commercial protease A, commercial pancreatin, and an enzyme extract isolated from *Aspergillus niger* MUM have been proven to degrade OTA to Otα, respectively, by 87.3%, 43.4%, and 99.8% under the optimal conditions of pH 7.5 and temperature 37 °C after 25 h [39]. Porcine pancreatic lipase degraded PAT in pear juice [40].

2. Detoxification Mechanism

2.1. Biodegradation Mechanism

The toxin biodegradation mechanism depends on the microorganism and toxin nature. In their study of AFB1 biodegradation, J. Li et al. demonstrated that aflatoxin B1 degradation by *Tetragenococcus halophilus* is first caused by adsorption and then by the enzymatical pathway. The amount of AFB1 binding caused by adsorption

was smaller than the one degraded by the enzymatical pathway. Two mechanisms have been offered as possible pathways for enzymatical action, and six degradation products have been identified: $C_{14}H_{10}O_4$, $C_{18}H_{16}O_8$, $C_{14}H_{12}O_3$, $C_{16}H_{20}O_4$, $C_{14}H_{16}O_2$, and $C_{14}H_{20}O_2$. The first pathway involves the lactone ring, and the second one involves the double bond of the furan ring. Both mechanisms result in the same compound: $C_{14}H_{20}O_2$ [3]. The same results were obtained with another salt-tolerant *Candida versatilis*, CGMCC 3790 [41]. In that case, four resulting compounds were identified by LC/TOF-MS: $C_{14}H_{10}O_4$, $C_{14}H_{12}O_3$, $C_{13}H_{12}O_2$, and $C_{11}H_{10}O_4$. Elsewhere, Hong Cao et al. suggested that the aflatoxin oxidase (AFO) extracted from *Armillariella tabescens* detoxifies the AFB1 by cleaving the bis-furan ring [23]. Adebo et al. found that the pathway of AFB1 degradation by the culture and lysate of a *Pontibacter* species is enzymatical and suggested that when the AFB1 is hydrolyzed, it has probably been transformed into new compounds, which were not identified in that paper [42]. AFB1 has been partially bio-transformed into aflatoxin D1 (AFD1) by deleting a mutant of the bacC gene in *Baccilus subtilis* UTB1. The mechanism was a reduction in the double bond of the lactone ring in the coumarin moiety, followed by the hydrolysis of the ester bond and, finally, the des-carboxylation of the yield to aflatoxin D1 (AFD1); all the processes were catalyzed by the BacC [43]. AFD1, AFD2, and AFD3 have been shown to be degradation compounds of AFB1 detoxification by *Pseudomonas putida*. The mechanism might be lactone [44]. *Phanerochaetesordida YK-624* is able to transform AFB1 into AFB1-8,9-epoxide by, firstly, the oxidation of the manganese protease; thereafter, hydrolysis obtains the final product, AFB1-8,9-dihydrodiol [35]

A yeast enzyme, orotate phosphoribosyltransferase, from *Rhodotorula mucilaginosa* was tested against patulin in apple juice samples and under optimum degradation conditions, which are 0.15 g/L of orotate phosphoribosyltransferase for every 1 mg/L patulin at 25 °C for 18 h; the degradation rate of patulin reached over 80% [45]. During a study of patulin degradation by the yeast *Rhodosporidium paludigenum*, the authors of [46] made the statement that the enzyme(s) responsible for patulin degradation synthesis was enhanced by the presence of patulin. In fact, an assay with protein extracted from cells contaminated by patulin was more active than those with proteins from cells grown without patulin. This difference was attributed to the synthesis of the enzyme. Patulin degradation screening of *Saccharomyces cerevisiae*, tested by M. Li et al., showed that the mechanism was enzymatical and that the PAT-metabolizing enzyme production by the yeast cells is not induced by PAT preincubation [47]. These results were not in accordance with those of Ianiri et al., who concluded in their study that the patulin degradation mechanism by the yeast *Sporobolomyces* sp. IAM 13481 can be induced via pretreatment with the mycotoxin; the pre-incubation with patulin can induce the earlier activation of the gene-encoding proteins of the antioxidant system and the proteins involved in the patulin efflux and patulin degradation [48].

Young et al., in their study, showed that microbial isolate microbiota and pure cultures from chicken intestines have the ability to degrade twelve trichothecenes. The degradation compound identification by MS has suggested that the mechanism includes de-epoxidation and or a diacylation, with the route depending on the presence and position of acyl functionalities [49]. In addition, Gao et al. isolated a bacterium, *Eggerthella* sp. DII-9, which has the ability to degrade some types of trichothecenes, including DON, HT-2, T-2 triol, and T-2 tetraol, into other compounds. T-2 triol was degraded into de-epoxy T-2triol (88.0%), de-epoxy HT-2 (8.6%), and de-epoxy T-2tetraol (2.3%). T-2 tetraol was converted into de-epoxy T-2 tetraol (85.9%), and about 2.3% de-epoxy T-2 triol. HT-2 was transformed into de-epoxy HT-2 (81.4%) and 4.7% de-epoxy T-2 triol. To identify the molecular mechanism, the

complete genome of DII-9 was sequenced, but the location of the responsible genes was not found. After the enzymatical study, de-epoxidation was found to be a complex phenomenon [50].

The zearalenone degradation of Bacillus pumilus ES-21 was studied by G. Wang et al. The degradation rate was more than 95.7%, and the degradation compound was identified as 1-(3,5-dihydroxyphenyl)-60-hydroxy-l0-undecen-l00-one. Nonetheless, the compound was not very stable and degraded very rapidly. The mechanism was found to be enzymatical and was thought to be due to esterase activity [34]. on the other hand, during the process of ZEN degradation by Bacillus amyloliquefaciens [36], no resulting compounds were detected. It was concluded that during the biodegradation of Zen by the bacteria's extracellular enzyme, no ZEN derivatives were produced; in fact, a study of ZEN derivative biodegradation by Bacillus amyloliquefaciens, including α-zearalenol, β-zearalenol, α-zearalanol, and β-Zearalanol, resulted in no metabolites. Koch et al. (2014) studied the ZEN detoxification ability of nine different fungal strains of the genera Rhizopus and Aspergillus, which are known to produce and transform steroids. The results showed that all the strains were able to detoxify ZEN. Biodegradation and adsorption happen simultaneously. Five resulting compounds were identified: ZEN-14-sulfate, ZEN-O-14, ZEN- O-16-glucoside, α-zearalenol, and α- zearalenol-sulfate. The nine biocontrol agents were divided into three groups: (1) *Rhizhopus oryzae* DSM 907 and *Rhizhopus stolonifera* DSM 855, which can catalyze ZEN glycosylation; (2) *Rhizhopus oryzae* DSM 906 and *Rhizhopus oligosporus* DSM 1964 and *Aspergillus oryzae* DSM 1864 and *Aspergillus oryzae* NBRC 100959, which are involved in the formation of sulfated ZEN metabolites; (3) Rhizopus DSM 908, DSM 1834, and Rhizopus oligosporus LMH 1133 T, which have shown the ability to produce the metabolite of both patterns [51]. The bacterial gut flora of pigs are able to transform ZEN into α-zearalenol and an unidentified compound via hydrolysis and DON into de-epoxy-DON via a de-epoxydation reaction [52].

OTA biodegradation by *Pediococcus parvulus* UTAD depended on the inoculum size and the incubation temperature coupled with a latency phase before biodegradation initiation. This later effect is due to the biodegradation enzyme synthesis of the bacteria [5]. OTA has been biodegraded into Otα by OTA amide group hydrolysis. On the other hand, OTA reduction by *Debaryomyces hansenii* involves neither absorption nor detoxification. It is a repression of the expression of the non-ribosomal peptide synthetase (otanpsPN) gene linked to the OTA biosynthetic pathway, which was observed in [53].

Generally, mechanisms of mycotoxin degradation by microorganisms include different types of enzymes (protease, esterase, intracellular enzymes, etc.). The degradation process can include one or two types of reactions. The mechanisms elucidated by now include oxidation, hydrolysis, the cleavage of the lactone ring, des-carboxylation, de-epoxidation, glycosylation, and sulfate-conjugation reactions.

Many studies have focused on the mycotoxin detoxification abilities of microorganisms, but a better understanding of responsible enzymes and the mechanisms involved is still needed. In some specific cases, no resulting metabolites were detected after mycotoxin biodegradation caused by microorganisms, but mostly, one or multiple compounds are usually detected.

2.2. Decontamination by Removal Mechanism

The use of microorganisms as agents for toxin sequestration in order to remove them from food and feed is an approach that has shown many good results.

Taheur et al. showed that strains isolated from a kefir culture are efficient in binding mycotoxins. The binding ability was dependent on the strain and the mycotoxin type [54]. From the same perspective, *Saccharomyces cerevisiae CECT 1891* and *Lactobacillus acidophilus 24* FB1 were shown to have a binding ability by Pizzolitto et al. The binding process needed a little time (1 min), and the mechanism involved was demonstrated to be a toxin molecule via the physical adsorption of the microorganism's cell wall components. Cell viability was not necessary for FB1 binding, but the microorganism's cell wall structural integrity was required, and the process did not involve FB1 chemical modification [29]. From the same perspective, two strains of *Enterococcus faecium*, which are present in dairy products, particularly in cheese, are efficient in AFB1 and PAT removal [16]. The same results were obtained by Elsanhoty et al. when they studied the AFM1 removal ability of some strains of *Lactobacillus* in milk samples [55].

OTA removal by *Saccharomyces* strains was demonstrated by Bejaoui et al. to be an adsorption mechanism. This mechanism was dependent on the OTA molecule's ionic properties, the yeast membrane state, and the biomass concentration [25].

Lactococcus lactis and *Bifidobacterium* sp. Isolated from milk are able to neutralize ZEN contents via absorption. The *Lactococcus lactis* absorption is not homogeneous, and the process happens in two different steps. The first one includes a ZEN absorption of 88%, and the second one consists of ZEN diffusion into bacterial cells. This was contrary to that of *Bifidobacterium* sp., where the adsorption mechanism only had a single homogeneous step. The deprotonated carboxyl groups of the bacterial proteins and peptidoglycan play a significant role in the absorption process [56].

AFB1 binding via the *Saccharomyces cerevisiae* mannoprotein is possible because of AFB1 absorption onto mannose sites, where the new structure is maintained. Indeed, the new structure nature does not match that of a natural AFB1 molecule, so AFB1 can be removed from the media [57].

2.3. Degradation Compound Toxicity

Knowing the degraded compound's toxicity is very important because it can be more or less toxic than the parent. Therefore, many cytotoxicity studies have been conducted.

Adebo et al. studied the toxicity of the compounds resulting from AFB1 degradation caused by *Staphylococcus warneri*, *Sporosarcina* sp., and *Lysinibacillus fusiformis*. The experiment was conducted by monitoring the mortality of lymphocyte cells (from human blood) after the cells were exposed to degraded compounds. A lower mortality rate was recorded compared with aflatoxin B1. The authors concluded that there was lower toxicity [58]. On the other hand, *Escherichia coli* DH5a, *Arabidopsis thaliana*, and human hepatocyte LO2 were used by [46] to determine the degradation toxicity of the compound identified as desoxypatulinic acid (DPA) due to patulin detoxification caused by *Rhodosporidium paludigenum*. The lower toxicity of DPA compared with PAT was demonstrated.

Elsewhere, no toxicity reduction has been found after ZEN and FB1 biocontrol using lactic acid bacteria. One toxicity study was conducted using human esophageal carcinoma cell lines [59]. Some ZEN degradation products are known to be more toxic than ZEN. In the case of α-ZOL, it shows higher estrogenicity than ZEN [56]. The compounds derived from ZEN biocontrol toxicity can be ranked as follows: α-zearalenol > α-zearalanol > zearalenone > β-zearalenol [60].

3. Functional Enzymes Extraction from Bacteria

Nowadays, enzymes, as shown in Section 3.3, play a key role in mycotoxin biodegradation. Therefore, it is important to have a general method of enzyme extraction from microorganisms.

The process of enzyme extraction from microorganisms can be divided into three parts: extraction, purification, and characterization.

The extraction step's main idea is to extract the enzyme outside the host. Some procedures are performed by harvesting the mycelia pellet via centrifugation and then washing it with phosphate buffer, followed by a second centrifugation to remove cell debris [23]. More recently, the homogenization of cells with protein extraction buffer followed by ultrasonication and centrifugation has been performed [45].

The purification step's aim is, after the extraction step, to obtain an enzyme that is as pure as possible. Ammonium sulfate is the most used compound to precipitate enzymes [61]. This step is generally followed by centrifugation. In some cases, the precipitation step can be performed by using both organic solvents, such as methanol, ethanol, or acetone, and ammonium sulfate separately [62]. After enzyme activity determination, some purification techniques are used. Chromatography purification can be performed by using hydrophobic interaction chromatography (HIC) followed by immobilized metal ion affinity chromatography (IMAC) [23] or ion-exchange chromatography on a DEAE-Sepharose GE column, followed by dialysis and lyophilization [62]; dialysis can also be performed with a DEAE-Sepharose column [63]. Further purification can be performed using a Superdex 75 column followed by dialysis and lyophilization [62].

The last step is purified enzyme characterization. This step permits us to find the characteristics of the enzyme. It can be feasible to use SDS polyacrylamide gel electrophoresis (SDS-PAGE) to determine the molecular weight [23] [62], HPTLC analysis to determine the enzymatic activity, and ESI-MS/MS to identify the enzyme [23]. Finally, the determination of the optimum pH, the optimum temperature, the ion metal effect on the enzyme activity [62], and the protein concentration (which can be determined using the method of Bradford) can be performed. Then, the enzyme can be stored at −85 °C until used.

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