

Review

Biocontrol Methods in Avoidance and Downsizing of Mycotoxin Contamination of Food Crops

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Abstract: By increasing the resistance of seeds against abiotic and biotic stress, the possibility of cereal mold contamination and hence the occurrence of secondary mold metabolites mycotoxins decreases. The use of biological methods of seed treatment represents a complementary strategy, which can be implemented as an environmental-friendlier approach to increase the agricultural sustainability. Whereas the use of resistant cultivars helps to reduce mold growth and mycotoxin contamination at the very beginning of the production chain, biological detoxification of cereals provides additional weapons against fungal pathogens in the later stage. Most efficient techniques can be selected and combined on an industrial scale to reduce losses and boost crop yields and agriculture sustainability, increasing at the same time food and feed safety. This paper strives to emphasize the possibility of implementation of biocontrol methods in the production of resistant seeds and the prevention and reduction in cereal mycotoxin contamination.

Keywords: biocontrol; molds; mycotoxins; environmentally friendly; seeds; cereals



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1. Introduction

Inefficient agricultural practices, population growth, the replacement of food crops with animal feed and biofuel crops, and the impact of global climate change impose the need for sustainable agriculture. Data show that global food production has to be doubled by 2050 to meet the increasing population demands, the challenge being made even more daunting by changing climate and competition for natural resources [1]. According to the FAO [1], farming systems aiming at the sustainable intensification of crop production must be based on conservation agricultural practices, such as the employment of fruitful seeds, with an inbuilt pest control, allowing for rich soils, watering control and fitting into other arable facilities and woodlands and farm animals' appropriateness. This will in turn require carefully targeted research focusing on sustainable agricultural practices to rise the nutritional richness of food while reducing losses caused by abiotic stresses, such as drought and salinity, which are becoming more prevalent due to the climate change responsible for up to 50% of crop losses worldwide [2].

Policies supporting agricultural intensification should also build capacity through education and the development of specialized local agricultural practices to avoid contamination of seeds with microbes, fungi, and their toxins, which can occur during cultivation, harvesting, processing, packaging, storage, and transportation. Within this context, mycotoxins are viewed as one of the most dangerous crop contaminants. Mycotoxins are

secondary metabolites of mostly fungal genera, such as the *Aspergillus*, the *Fusarium*, and the *Penicillium* genus. From the economic standpoint, food/feed mycotoxins are of great significance and include aflatoxins (AFs), ochratoxin A (OTA), patulin (PAT), and *Fusarium* toxins, such as zearalenone (ZEA), trichothecenes (T-2/HT-2 toxins, deoxynivalenol (DON)) and fumonisins (FUM) [3,4]. During the last decades, additional importance has been given to ergot alkaloids and *Alternaria* mycotoxins [5,6]. Factors involved in mycotoxin formation enhancement are numerous, and include plant susceptibility to fungi, the appropriateness of the fungal substance on which an enzyme acts, the weather, water vaporizing or condensation, and insect- and pest-inflicted physical seed damage [7,8].

Toxins chiefly arise from fungi closely linked to the accumulation of toxic substances. Based on the grain infestation site, toxicogenic fungi can be separated into three groups, i.e., open meadow fungi, storage fungi, and later stages fungi. The first category embraces plant-pathogenic fungi, i.e., the *Fusarium* genus (e.g., *F. moniliforme*, *F. poae*, *F. graminearum* and *F. culmorum*). Storage fungi are mostly of the *Aspergillus* and the *Penicillium* genus (e.g., *A. flavus*, *A. parasiticus*, and *P. nordicum*). Latter stages fungi, e.g., *A. clavatus*, *A. fumigatus*, *Chaetomium*, *Scopulariopsis*, *Rhizopus*, *Mucor*, *Alternaria*) do not usually infest whole grains, but will affect any damaged kernels, provided that the water vapor or condensation is sufficiently high [9]. Environmental conditions favoring seed germination are also ideal for the nascence of seedborne fungi, i.e., those of the *Aspergillus*, the *Fusarium*, the *Alternaria*, and the *Penicillium* genus.

Seedborne diseases are the greatest challenge for a successful crop production, since they affect the germinability and cause the seedlings to wither and shrivel resulting in low yields [10,11]. The control of pathogens occurring in/on seeds is of extreme importance, particularly when organic production using less potent plant disease protection is allowed. Despite many good agricultural and manufacturing practices, it is currently more than clear that mycotoxin occurrence represents an ever-increasing worldwide problem, which has an enormous effect on the welfare of all living creatures, not to mention the incurred costs [12].

To wipe out or at least minimize the existence of mycotoxins, their origin must be pinpointed. Various procedures employing fungicides, herbicides and/or insecticides before planting are used to stamp them out [13,14]. Nowadays, the use of non-synthetic tools is growing in popularity. These special scientific methods are vital to minimize mold growth and subsequent mycotoxin biosynthesis. Both pre- and post-harvest procedures and checkups are continuously being improved for a number of crops [15,16]. These procedures employ good agricultural practices (GAP) and are focused on the first line of defense against mycotoxin pollution of both growing and harvested food crops. Thereafter, good manufacturing practices (GMP) during food handling, storage, and distribution are used. Hand in hand with this management system is the Hazard Analysis and Critical Control Point (HACCP), a preventive system based on systematic identification of hazards, their controls, and monitoring of the achievements [8,17].

Moreover, the economic aspects of measures taken against molds and mycotoxins are not negligible. As a result of climatic changes, these measures also change to improve efficiency and lower costs [18,19]. Given that biocontrol methods use natural sources and do not require additional care, they are considered economically promising and environmentally safe.

This paper strives to emphasize the possibility of implementing biocontrol methods in the production of resistant seeds and the avoidance and downsizing of cereal contamination with mycotoxins, so as to increase the sustainability of agricultural chain in food and feed production.

2. The Main Mycotoxins, Their Occurrence, and the Producers

Many factors cumulate to affect fungal growth and mycotoxin production along the food chain. Their impact may be witnessed as early as in the field, and increase during harvesting, drying, and storage [20]. However, mold colonization does not necessarily

result in mycotoxin contamination, since the latter calls for specific and independent prerequisites [21,22]. On the other hand, the removal of molds from food and feed does not vouch for their absence because of their resistant chemical composition [23]. Table 1 brings some of the major mycotoxins, commodities in which they most commonly reside, their main producers, and their toxic effects in humans and animals.

Table 1. Important mycotoxins, their occurrence, main producers, and toxic effects.

Mycotoxin		Commodity	Main Producers	Toxic Effects	Reference
Aflatoxins (AFs)	B1, B2	Wheat Maize	<i>A. flavus</i> ,	Carcinogenic, liver cancer, immune suppressive	[24]
	G1, G2 M1, M2		<i>A. parasiticus</i> , <i>A. nominus</i> , <i>A. pseudotamarii</i>		
Ochratoxins	A, B	Wheat Barley Maize	<i>A. ochraceus</i> , <i>A. carbonarius</i> , <i>P. verrucosum</i>	Neurotoxic, nephrotoxic, kidney damage, and cancer; immune suppressive	[25,26]
			<i>F. graminearum</i> , <i>F. culmorum</i> , <i>F. acuminatum</i> , <i>F. crookwellense</i> , <i>F. avenaceum</i> , <i>F. equiseti</i>		
Type B Trichothecenes	DON (Vomitoxin) ADON, NIV, ANIV	Wheat Barley Maize		ATA (alimentary toxic leukopenia), immunotoxic, acute toxicity	[27]
Type A Trichothecenes	T-2 HT-2	Wheat Barley Oats Maize Ray	<i>F. poae</i> , <i>F. sporotrichioides</i>	Acute toxicity, linked to ATA, immunotoxic, immune system and hematological disorders	[28]
Zearalenone (ZEA)		Wheat Maize	<i>F. graminearum</i> , <i>F. culmorum</i> , <i>F. cerealis</i> , <i>F. avenaceum</i> , <i>F. equiseti</i>	Estrogenic effects, reproductive disorders, affects endocrine system	[29]
Fumonisin (FUM)	FB1 FB2	Wheat Barley Oat Maize	<i>F. verticillioides</i> , <i>F. proliferatum</i>	Esophageal cancer, sphingolipid metabolism disruption, immune suppression	[30]
Ergot alkaloids	Ergotamine, ergometrine, ergosine, ergocristine, ergocryptine, ergocornine	Wheat Ray Barley Maize	<i>Claviceps purpurea</i> , <i>Claviceps fusiformis</i>	Necrosis of limbs—St Anthony’s fire, vasoconstrictive properties, gangrenous and convulsive ergotism	[5]
Alternaria mycotoxins	ALT, AS, ALN, TeA, ALS, ATXs, alterperyleneol or alteichin, ALTCH, STE	Wheat Oat Barley Maize	<i>A. alternata</i> , <i>A. tenuissima</i> , <i>A. arborescens</i> , <i>A. radicina</i> , <i>A. brassicae</i> , <i>A. brassicicola</i> , and <i>A. infectoria</i> .	cytotoxicity, fetotoxicity, and teratogenicity, hematological disorders, esophageal cancer, mutagenic, clastogenic, and estrogenic in microbial and mammalian cell systems and tumorigenic in rats	[6]

The prevention of mycotoxin contamination is most important since it does not call for the application of any chemical or physical measure whatsoever. It can be achieved through resistant seeds of a modified genome, as well as by virtue of good agricultural practices (Figure 1).

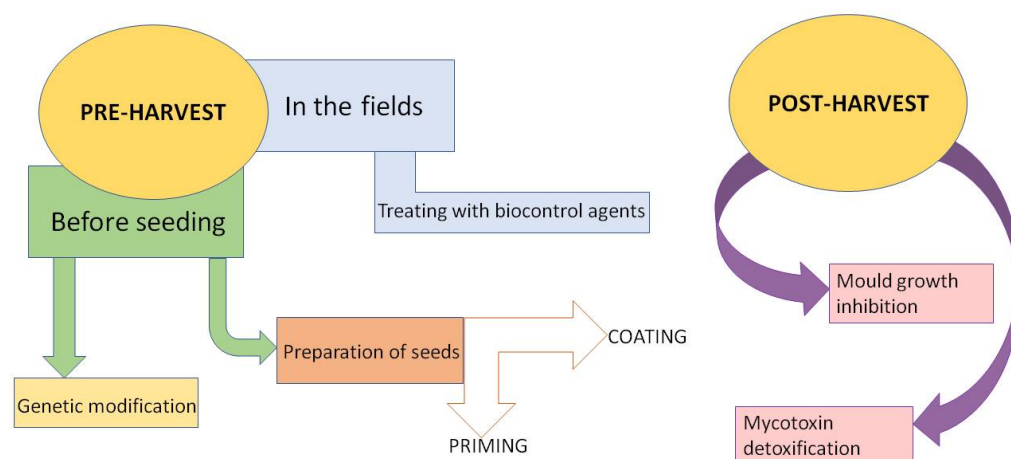


Figure 1. Pre-harvest and post-harvest methods of biocontrol of cereals -populating mycotoxins.

3. Pre-Harvesting Biocontrol Methods

The most reasonable approach to the avoidance of mycotoxin contamination is the cultivation of crops resistant to molds that do not accumulate mycotoxins. Genetic diversity gives a species the ability to adapt to changing environments, including new pests and diseases and new climatic conditions, such as global warming [31,32]. On top of that, high-quality coated and primed seed provides a resistant plant able to cope with biotic and abiotic stress [33].

3.1. Before Seeding

3.1.1. Genetic Base of Natural Resistance

Innovations introduced in the pre-harvest stage are to be attributed to plant genetic engineering as a biotechnological advancement in mold-produced mycotoxin control. Plant genetic engineering aimed at the development of mycotoxin-resistant varieties and crop detoxification places emphasis on fungi and mycotoxins most relevant from the economic standpoint [34].

Several studies have identified genes and proteins whose abundance correlates with dormancy or seed germination; they are often involved in desiccation tolerance, damage protection, or storage endurance [35–37]. Biochemical and genetic crop resistance markers are used as selection tools in breeding varieties resistant to mycotoxin accumulation. Resistant cultivars can be developed by profiling genetic diversity using a marker-assisted selection (MAS) [38] based on comparative proteomics accelerated by a nucleotide-binding site (NBS) profiling [39,40] or Diversity Arrays Technology (DArT) [41]. The above has already been achieved to a certain extent in wheat and corn. Identification of genes encoding enzymes that degrade mycotoxins allows for the transfer of these genes into the plants and the production of the above enzymes in transgenic crops.

In their review, Collinge and Sarracco [42] listed possible applications of plant engineering. The studies by Majumdar et al. [43] and Machado et al. [44] looked into the reduction in FUM, trichothecenes, and ZEA levels in the *Fusarium* spp. and the levels of AFs produced by the *Aspergillus* spp. Other genetic engineering methods increasing the production of mycotoxin-degrading enzymes such as chitinase are also being pursued [45]. Efforts to engineer plants that produce compounds able to disrupt mycotoxin synthesis have also been made. For instance, an enhanced expression of amylase inhibitor in *Aspergillus* spp. can substantially reduce AF levels [46]. Examples of enhanced disease resistance using transgenic strategies are given in Table 2.

Table 2. Examples of enhanced disease resistance using transgenetic strategies.

Strategy	Gene/Construct	Cereal	Pathogen	Phenotype	Reference
Host-induced gene silencing (HIGS)	<i>aflC</i> aflatoxin biosynthetic gene	Maize (<i>Zea Mays</i>)	<i>A. flavus</i>	Reduced aflatoxin levels	[47]
	<i>aflR</i> aflatoxin biosynthetic gene	Maize (<i>Zea Mays</i>)	<i>A. flavus</i>	Reduced aflatoxin levels	[48]
	Cytochrome P450 lanosterol C-14 α -demethylases using a double and inverted CaMV 35S promoter	Barley (<i>Hordeum vulgare</i>)	<i>F. graminearum</i>	Strong resistance	[49]
	Chitin synthase(<i>Chs</i>)3b	Spring wheat (<i>Triticum aestivum</i> L.)	<i>F. graminearum</i>	Reduction in DON accumulation	[50]
Nonspecific lipid transfer protein (nsLTP)	<i>AtLTP4.4</i> using maize ubiquitin promoter	Spring wheat (<i>T. aestivum</i>)	<i>F. graminearum</i> (FHB)	Reduction in DON accumulation	[51]
Antimicrobial protein (chitinase)	Class II chitinase using maize ubiquitin promoter	Spring wheat (<i>T. aestivum</i>) cv. Bobwhite	<i>Fusarium graminearum</i> (FHB)	Reduced infection and deoxynivalenol (DON) levels	[52]
	Class I chitinase (McCHIT1) using maize ubiquitin promoter	Rice (<i>Oryza. sativa</i> var. <i>indica</i>)	<i>Magnaporthe grisea</i> and <i>Rhizoctonia solani</i>	Reduced infection and DON levels	[53]

Another way of lessening mycotoxin presence is to minimize insect-inflicted harm to plant kernels. Insects are held responsible for the spread of molds out in the fields and during storage. At the beginning of the last century, plant resistance to insects was achieved through the use of several Bt (*Bacillus thuringiensis*) genes in corn, wheat, and other cereal grains, so that today insect damage due to the *Fusarium* (*F. verticillioides* and *F. proliferatum*) ear rot is far lesser [54]. However, in 2018 Gassmann [55] reported that pest species have repeatedly demonstrated the resistance to maize that produces the Bt toxin Cry3Bb1. Abbas's review [56] summarizes global doubts about the safety of Bt crops for the environment and mammals. Nowadays, plant-mediated RNAi that targets essential pest genes is becoming an encouraging approach to crop protection [57].

These efforts will hopefully be successful, although molds have always had the advantage over selective breeding because time is needed to generate resistant cultivars. Genetic engineering would accelerate the development of resistant crops, but genetically modified agriculture in the EU remains controversial. Novel strategies to protect seeds of the existing cultivars from fungi are therefore required in the interim.

3.1.2. Preparation of Seeds before Sowing

Seed quality is affected by the maternal environment, maturity at harvest, collection procedures, and storage conditions [58,59]. One of the safe, cheap, and widely applicable approaches is to coat seeds and seedlings with plant-derived antifungal peptides or metabolites [60,61]. Plant-beneficial microbes (PBMs), such as plant growth-promoting bacteria, rhizobia, arbuscular mycorrhizal fungi (AM), and *Trichoderma*, can minimize the use of agrochemicals and increase the plant yield, nutrition, and tolerance to biotic/abiotic stresses.

Seed coating (Figure 2), a process that implies the coverage of seeds with small quantities of exogenous materials, is gaining attention as an efficient PBM system. Microbial seed coating comprises the use of a binder, in some cases a filler, mixed with inocula, and can use a simple mixing machine (e.g., a cement mixer) or a more specialized/sophisticated apparatus (e.g., a fluidized bed). Microbial survival can be ensured using binders/fillers [62]. The most common types of seed coating are seed dressing, film coating, and pelleting. The main-

tenance of plants and an increase in productivity can be helped with the use of PBS while reducing the input of agrochemicals, restoring soil fertility, and/or overcoming problems caused by abiotic and biotic stresses [63,64]. In the last few decades, the interest in PBM use for increasing yields and resilience of agricultural crops has been steadily growing [65–67]. Bacteria are the most abundant microorganisms present in the rhizosphere [68]. Different bacterial genera (e.g., *Azospirillum*, *Azotobacter*, *Pseudomonas*, *Bacillus*, and *Burkholderia*) contain species that enhance plant growth and development. These beneficial bacteria, also designated as the PGPB, protect plants from biotic and abiotic stresses and directly and indirectly facilitate plant growth and performance [69].

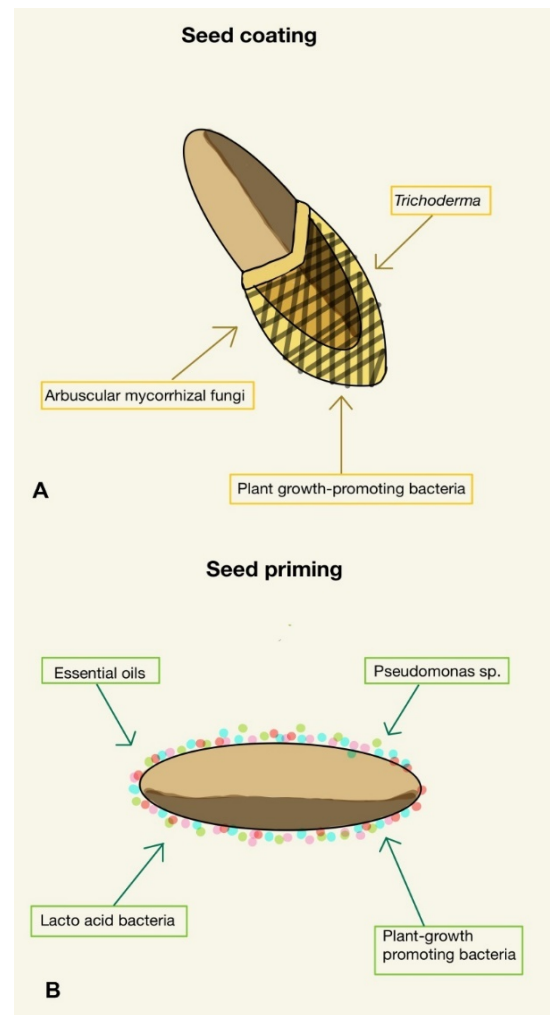


Figure 2. Microorganisms that can be used in (A) seed coating and (B) seed priming.

An increase in grain yield and stability has been associated with seed coating formulation with the AM fungi and *Trichoderma* consortium with reduced or withheld fertilizer application in winter wheat, wheat, and maize [70–72]. Various studies on biocontrol agents (BCA) and inducers of systemic acquired resistance (SAR) were carried out to the end of reducing the fungicide administration. Perelló and Dal Bello [73] validated the effects of *T. harzianum* strains and synthetic compounds (acibenzolar-S-methyl and thiamethoxam) on wheat growth and the suppression of tan spot caused by *Pyrenophora tritici-repentis*. Biological and chemical agents are both used as SAR inducers. The study showed that both biological and chemical agents can reduce the severity of tan spots and increase the plant height and weight. Activation of SAR in plants can maintain crops as healthy and vigorous. The correct combination of SAR inducers applied via seed coating and lower-concentration fungicides is a promising option for sustainable agriculture.

Mahmood et al. [74] found that both fungicides and BCA are almost equal against the chickpea wilt pathogen *F. oxysporum*. Shahzad et al. [75] showed that seed coating with *Bacillus* spp. improved wheat physiology, nutritive values, growth, and yield in saline soils. The experiment that made use of chickpea seeds coated with *Paenibacillus lentimorbus* B-30488 in combination with sodium alginate and calcium chloride (CaCl_2) increased the germination percentage and the number of colony-forming units of B-30488 in the rhizosphere, resulting in the amelioration of drought stress by virtue of reinforcing the dehydration-induced physiological responses [76]. Such environmentally friendly plant protection strategies developed through the molecular analysis of cereal grains could easily be integrated into sustainable agricultural practices to increase yields, safety, and quality without damaging the environment.

Other important PBMs are AM fungi (e.g., *Glomus intraradices*, *Rhizophagus irregularis*, *Glomus mosseae* (renamed to *Funneliformis mosseae*), and *Rhizophagus fasciculatus*) and *Trichoderma*. AM fungi associate with roots of almost 80% of terrestrial plants to form arbuscular mycorrhizas [77]. AM fungi can improve soil aggregation, hinder pathogens, and increase water acquisition [64,78–80]. On top of structural and nutritional benefits, AM fungi help crops cope with salinity and drought stresses [81–85]. *Trichoderma* spp., a common free-living fungus in the rhizosphere and soil, is known to produce a wide range of antibiotics and parasitize other fungi. Metabolites released during plant–*Trichoderma* interaction can affect plant growth, root morphology, and nutritional status and even trigger an induced systemic resistance, biocontrol of pathogens, and inactivation of toxic compounds in the root zone [86].

Seed priming (Figure 2), as another approach, is a pre-sowing treatment that enables the seed to germinate more efficiently, especially when applied to poor-quality seeds and young seedlings, which often become more vigorous and resistant to abiotic stresses than seedlings obtained from unprimed seeds [87]. Biopriming involves seed imbibition and bacterial inoculation [88]. Hydration of seeds infected with pathogens resulted in stronger microbial growth and consequent plant health impairment. An ecological solution to this problem is the application of antagonistic microorganisms during priming [89]. Moreover, some bacteria used as biocontrol agents can colonize the rhizosphere and support the plant both directly and indirectly after germination [57].

Nowadays, there seems to be much promise in the use of biopriming with plant growth-promoting bacteria (PGPB) as an integral component of agricultural practices [90,91]. In pearl millet, biopriming with *Pseudomonas fluorescens* isolates enhanced plant growth and resistance against downy mildew disease [92]. In addition, lactic acid bacteria (LAB) produce bacteriocin-like inhibitory substances (BLIS-phenomenological analogs of paramecium-killing factors produced by yeast) that not only reduce contamination with pathogenic fungi but also increase the germination capacity by 25–30%. The seedlings were also found to be more vigorous and less prone to stress, although controlled experiments are needed to confirm this. Genetic engineering can be used to increase the efficiency of bacteriocin production, allowing for LAB use in seed preparation. The use of antifungal LAB to degrade mycotoxins in seeds and growing plants will, together with molecular genetics, lead to the ultimate increase in cereal productivity and their sustainable resistance [93,94].

To alleviate problems associated with the use of synthetic fungicides, such as pollution, phytotoxicity, and resistance, much research has been undertaken to evaluate the effectiveness and reliability of essential oils as biological agents with a low environmental impact [95]. Essential oils have been studied for their bactericidal and fungicidal properties arising from their active compounds [96–98]. Confirmatory studies of the effects of rosemary, oregano, thyme, and rose essential oils in terms of improving the resistance to pathogens, water and nutrition status, and drought resistance of cultured grains have been carried out [99–101]. Velluti et al. [102] showed that essential oils obtained from oregano, cloves, cinnamon, lemon grass, and palmarosa alleviate *Fusarium verticillioides* infection in maize seeds. Simic et al. [103] reported that rosewood, bay, saffron, and cinnamon essential oils inhibit the growth of *Aspergillus* spp., *Fusarium* spp., and *Penicillium* spp.

in vitro. The study of Chatterjee [104] showed that cassia, cloves and star anise, geranium, and basil, prevent an in vitro infection of maize seeds with *A. flavus*, *A. glaucus*, *A. niger*, and *A. sydowi*.

3.2. In the Fields

The use of bio-fungicides involves different microorganisms, microbial antagonists, or competitors that can suppress toxic fungi. Selected microbes are used during the flowering phase to limit the growth of toxigenic fungi or wipe them out [105]. A major success in applying this method was achieved by Dorner [106] and Pitt et al. [107] with maize and rice. Microorganisms that can be used in the fields are shown in Figure 3.

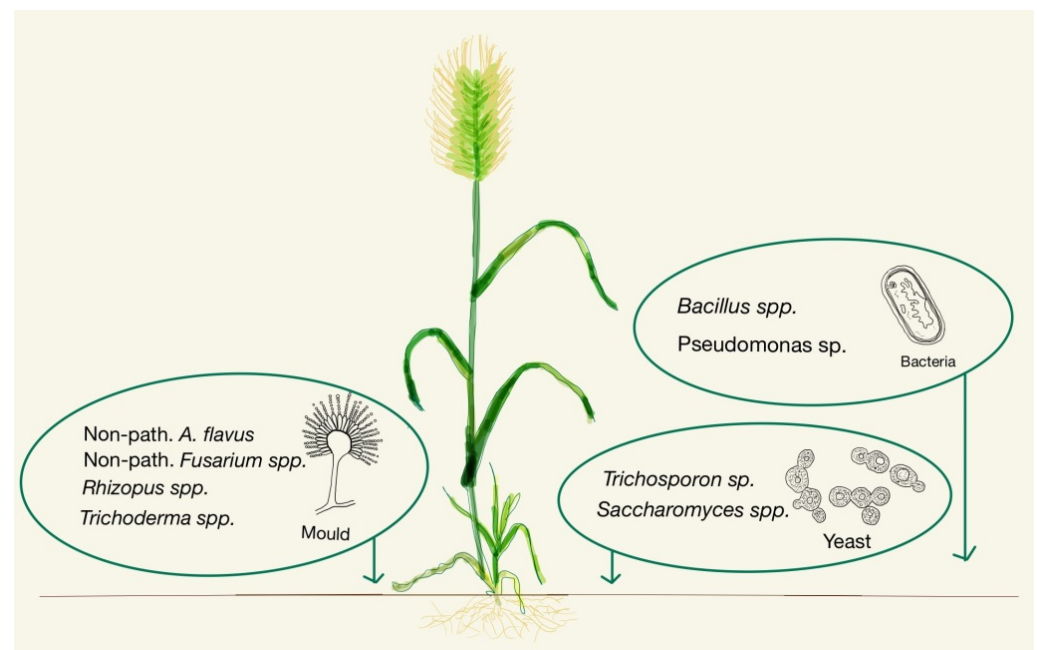


Figure 3. Bio-controlling microorganisms of use in the fields.

Qualities expected of a bio-controlling agent include genetic stability, low concentration efficacy against a wide range of pathogens, simple nutritional requirements, survival in adverse environmental conditions, growth on cheaper substrates in fermenters, a lack of pathogenicity for the host plant, inability to generate metabolites potentially toxic to humans, resistance to the most frequently used pesticides, and compatibility with other chemical and physical treatments [108]. Fungus-based bio-pesticides are criticized for their slow action and limited crop protection. Pathogen virulence determinants should be identified and used in strain selection and quality control [109].

When it comes to the application of biocontrol agents, timing is of the essence. Applications of fungal bio-controlling agents are usually timed to coincide with frequent rainfall and high soil moisture. When drought conditions prevail, the fungi remain alive on the carrier grains and will in all probability sporulate when the conditions are conducive. Drought-induced sporulation has also been observed with low soil moisture on carrier grains situated under the plant canopy, with the canopy both protecting the carrier and providing humidity for night sporulation [109]. Screening and natural selection are essential to biocontrol. They ensure that biocontrol agents have the features requisite to gain the most effective result out of the screened lot. Whenever estimating the efficacy of biocontrol agents, timing and environmental conditions must be taken into account.

Garber and Cotty [110] reported a reduced spore production of non-toxicogenic *A. flavus* strains exposed to herbicides, indicating that non-toxicogenic strains should be applied in the field after a herbicide. In the same year, Pitt et al. [107] recommended a delayed application of non-toxicogenic strains once the soil temperature reaches 20 °C, at the very least, so as

to ensure high population levels when the threat of crop infection is at its greatest [111]. Nevertheless, unanswered questions about the ability of atoxigenic fungi to produce other mycotoxins or to potentially exchange genetic material and become aflatoxigenic still pend. Despite their high laboratory potential, the low field efficacy of many antagonists is an additional concern. Therefore, integrated management approaches should be considered, involving a combination of multiple BCAs, reduced fungicide application, good agricultural practices, and good post-harvest management [112].

Weaver and Abbas [113] reported that the leading self-sustaining, commercially effective, and environmentally friendly technology of AFs downsizing is the use of atoxigenic *A. flavus* isolates capable of displacing aflatoxigenic fungi. As aflatoxin contamination represents a huge problem in Africa, the application of the method across Nigerian fields provided exceptional results in terms of consistent reduction in maize and groundnut contamination by 80–90% [114]. The success encouraged researchers to develop, adapt, and improve maize and groundnuts biocontrol [115–117]. Other microorganisms, such as *Bacillus*, *Pseudomonas*, and *Bulkholderia* strains, can fully inhibit *A. flavus* growth [118].

FUM biocontrol involves extensive use of bacteria and fungi. For example, maize seed treatment with *Bacillus amyloliquefaciens* and *Enterobacter hormaechei* may improve the quality of harvested maize grains by reducing their toxin content [119]. The use of *Bacillus amyloliquefaciens* and *Microbacterium oleavarans* to reduce FUM in maize has also been reported [120]. Additionally, the inhibitory effect of *Trichoderma* species on FUM-producing *Fusarium* has been traced to antibiosis attained through volatile compounds, extracellular enzymes, and antibiotics [121]. Many *Trichoderma* species are also known to produce microbe-associated molecular patterns (MAMPs), which respond by reflex to the presence of a foreign body by expressing anti-microbials.

Out of many wild yeasts tested for OTA reduction, *Pichia anomala* and *Saccharomyces cerevisiae* proved superior in inhibiting toxin-producing strains [122]. Ponsone et al. [123] investigated two epiphytic strains of the *Lanchancea thermotolerans* yeast able to control ochratoxigenic fungi and OTA accumulation both in vitro and in vivo. Nowadays, several yeast species are considered as biocontrol candidates to be employed to the above goal [123]. OTA is also known to be controlled by the *Trichosporon mycotoxinivorans*, the yeast that can also detoxify zearalenone [124]. A substantial ZEN biotransformation provided by two fungal genera (*Aspergillus* and *Rhizopus*) was reported by Brodehl et al. [125]. Biotransformation can result in less toxic derivatives, which was the case with the lactonohydrolase enzyme present in the *Clonostachys rosea* fungus, which converts ZEN to a less estrogenic compound [126].

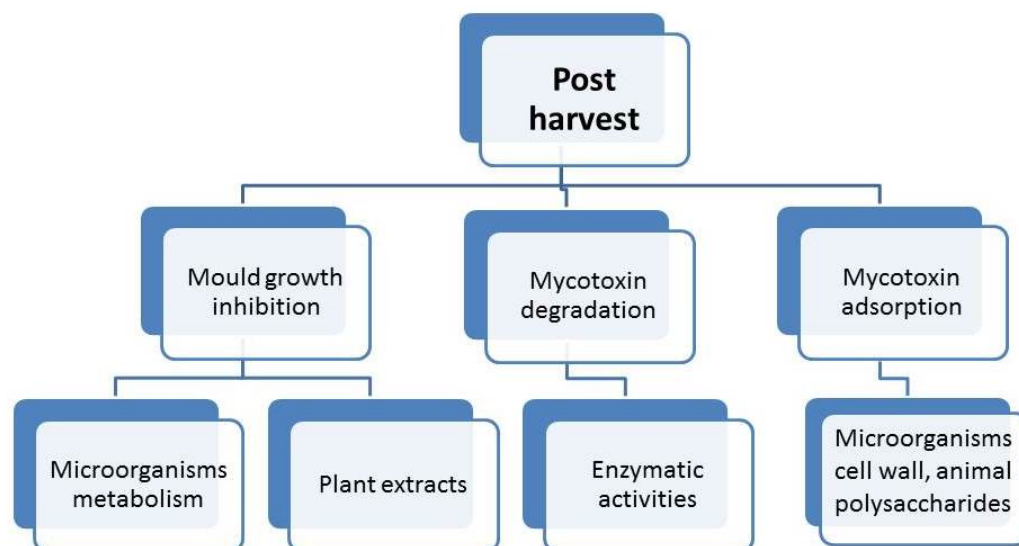
According to Rose et al. [127], soil treatment with non-toxicogenic *F. verticillioides* was useful in eliminating FUM-producing strains, inhibiting toxin synthesis, and lowering the presence and activity of toxigenic *F. proliferatum* and *F. verticillioides* in corn residues. Sarrocco and Vannacci [128] described the gain from the pre-harvest application of beneficial fungi in the field, which prevented the accumulation of mycotoxins during storage. Sarrocco et al. [129] examined the history of implementation of non-aflatoxigenic isolates of *A. flavus* in corn and the prospective usage of competitive filamentous fungi in counteracting *Fusarium* head blight in wheat and alleviating *Fusaria* toxin synthesis. Their analysis focused on both competitive and intervening exploitation of the above. According to the authors, field application of such isolates could be a true approach to the prevention of mycotoxin pollution of fundamental crops [130].

4. Post-Harvest Biocontrol Methods

Biological methods of fungal growth and mycotoxin production control, which can be implemented in the post-harvesting period, are environmentally friendly and chemical-free. The most essential requirement for pipeline decontamination technologies is to leave physicochemical cereal traits intact and no toxic residues behind [112,131]. In addition, decontamination costs should not exceed the product value. Fragmentary mycotoxin removal may be accomplished by dry grain cleaning and milling because during fractionation, more

mycotoxin co-separates with the bran than with the flour [132,133]. Most mycotoxins are thermostable, so heat treatment can hardly be effective [134,135].

The best way to reduce mycotoxins in the food chain is not to allow any mold growth; if not possible, one has to prevent mycotoxin production. The possibilities of post-harvest biocontrol of mold growth and mycotoxin elimination are presented in Scheme 1.



Scheme 1. The possibilities of post-harvest biocontrol of mold growth and mycotoxin elimination.

4.1. The Inhibition of Mold Growth

4.1.1. Microorganisms and Their Metabolites

Metabolites produced by other microorganisms may inhibit fungal growth and toxin production. Some proteins and peptides inhibit the growth of microorganisms and are therefore termed antifungal proteins (AFPs) and antimicrobial peptides (AMPs). Mold AFPs are highly stable at different pH values, not prone to proteolysis, and exhibit a broad inhibition spectrum against filamentous fungi [114]. Delgado et al. [136] demonstrated that an AFP isolated from *Penicillium chrysogenum* (PgAFP) reduced the growth of *A. flavus* by more than 50%. The same authors [137] showed that a compilation of 16 antifungal peptides produced by molds of the *Aspergillus*, the *Penicillium*, the *Fusarium*, the *Monascus*, and the *Neosartorya* spp., isolated from B-TL2 *Bacillus* strain, strongly inhibited the mycelial growth of *A. niger*, *Bipolaris maydis*, *Alternaria brassicae*, and *Cercospora personata*. Moreover, these peptides were proven thermostable, meaning that they are fully active at 100 °C [138].

Devi and Sashidhar [139] demonstrated that four AMPs, namely, PD1 (FRLHF), 66-10 (FRLKFH), 77-3 (FRLKFHF), and D4E1 (FKLRAKIKVRLRAKIKL), applied in concentrations ranging from 1 to 40 µg/mL, can reduce the aflatoxin production of *A. flavus* and *A. parasiticus* in a dose-dependent manner. At near minimum inhibitory concentrations (MIC), AMPs inhibited aflatoxins with almost 99% efficiency, but were unable to prevent the growth of *A. parasiticus*. According to Devi and Sashidhar [139], these peptides also affected the fungi conidia-producing ability. After a 48 h incubation, a peptide purified from *Lactobacillus plantarum* reduced the growth of *A. parasiticus* in a liquid medium by 73% [140]. Chen et al. [141] reported that three newly identified peptides isolated from *Bacillus megaterium* (L-Asp-L-Orn (D1O), L-Asp-L-Asn (D1N), and L-Asp-L-Asp-L-Asn (D2N)) significantly inhibited the growth of *A. flavus*, but had no effect on spore germination. Microscopical evidence and quantitative reverse transcription polymerase chain reaction (RT-PCR) results indicate that three peptides from *B. megaterium* (D1O, 1N, and D2N) spontaneously entered the hyphae of *A. flavus* and inhibited conidiation and aflatoxin production but did not stop vegetative hyphal growth and spore germination. This shows that, depending on the target cell type, a single peptide is often capable of more than one

action, so that antifungal activities of peptides cannot be judged solely based on the studies of their antibacterial activities [112].

AMPs usually resort to membrane permeability, whereas their antifungal activity is generally more intricate. A more detailed mode of their action has been described by Devi and Sashidhar [139], who showed that at concentrations near MIC, AMPs induce membrane permeabilization. AMPs also show antioxidant properties that interact with oxidative stress and impair aflatoxin production. At the molecular level, AMPs are responsible for the downregulation of the aflatoxin gene cluster “*aflR*” (regulating aflatoxin biosynthesis) and the expression of downstream genes. Some non-peptidic metabolites occurring during food fermentation have been shown to have antifungal properties. These metabolites are produced by lactic acid bacteria and include organic acids, phenolic compounds, hydroxy fatty acids, hydrogen peroxide, and reuterin [142]. For instance, acetic and phenyl lactic acids produced by *L. plantarum* CRL 778, *L. uteri* CRL 1100, and *L. brevis* CRL 772 and CRL 796 displayed antifungal activity against *A. niger* (<40%), *Penicillium* spp. (40% to 70%), and *F. graminearum* (>70%), isolated from a contaminated bread.

The effect of organic acids depends on the type of acid, its concentration, the type of matrix, and matrix pH [143]. Selected *Lactobacillus* spp. (*L. fermentum* M107 and *L. fermentum* 223) and yeasts (*Hanseniaspora opuntiae* H17 and *Saccharomyces cerevisiae* H290) were used to inhibit the growth of *A. flavus*, *P. citrinum*, and *Gibberella moniliformis* during cocoa bean fermentation. When cultured individually, *Lactobacillus* spp. achieved a stronger inhibition than yeasts (75% and 63%, respectively). Romanens et al. [144] demonstrated that in a co-culture of *Lactobacillus* and yeasts, *A. flavus* became completely inhibited after 10 to 14 days. Hassan et al. [145], and Bourdichon et al. [146], reported the antifungal action of lactic acid bacteria or yeasts that affected mold growth and mycotoxin production. Application of AMPs and AFPs, as well as fermentation metabolites, seems to be an optimistic strategy for fungal and mycotoxin control. Further research is needed to elucidate the mechanism of action and potential negative effects of microbes or microbial metabolites.

4.1.2. Plant Extracts

Some higher plants produce secondary metabolites known as essential oils (EOs), which have numerous biochemical and physiological functions [147]. The major EO ingredients are phenylpropanoids, phenolics, terpenoids, steroids, aromatics, and alkaloids [148]. In their review, Prakash et al. [147] reported that EOs are currently used as food preservatives and are generally accepted as safe (GRAS). Being volatile in nature, EOs may be used as plant-based fumigants of stored food and play a significant role in storage losses' reduction and shelf-life extension. The benefits of *Lavandula multifida* EOs in terms of *A. niger*, *A. fumigates*, and *A. flavus* inhibition were reported by Zuzarte et al. [149]. Prakash et al. [150] reported that clove basil (*Ocimum gratissimum*) EO has antifungal effects that reduce aflatoxin contamination. The food preservative potential of plant EOs extracted from marjoram (*Origanum majorana*), coriander (*Coriandrum sativum*), spiked ginger lily (*Hedychium spicatum*), myrrh (*Commiphora myrrha*), and ylang-ylang (*Cananga odorata*) is based on their antifungal, anti-aflatoxin, and antioxidant efficacy claimed by Prakash et al. [151]. Perczak et al. [152,153] indicated that the EOs of cinnamon (*Cinnamomum zeylanicum*), palmarosa (*Cymbopogon martini*), orange (*Citrus aurantium dulcis*), and spearmint (*Mentha viridis*) stop the growth of *Fusarium* fungi and reduce the concentration of mycotoxins in wheat and maize seed, even down to zero.

In some plants, AFPs and AMPs have been identified, as well [154,155]. These substances include defensins, lectins, chitinases, glucanases, and other proteins obtained from seeds, bulbs, leaves, tubers, fruits, shoots, and roots [156]. Both low- and high-MW proteins can enhance the antifungal potential. For example, a highly homologous 5.4 kDa plant defensin peptide purified from *Phaseolus vulgaris* L. impeded the growth of *F. oxysporum* [157]. At 35.7 and 65 kDa, respectively, lectin from the seeds of *Archidendron jiringa* and *Pachira aquatica* effectively hindered the growth of *F. oxysporum* [158].

Plant antifungal metabolites are not limited to EOs, AFPs, and AMPs. Polyphenols and flavonoids also play an important role in antifungal defense [159]. Butanol extract and oxime derivative of fresh peppermint (*Mentha piperita*) were found to inhibit the growth of *F. moniliforme* [160]. Moreover, a high maize carotenoid content can lower the fumonisin production of the *Fusarium* spp. or aflatoxin production of the *Aspergillus* spp. [161,162]. Atanasova-Penichon et al. [163] summarized the contribution of grain antioxidant secondary metabolites, such as phenolic acid and tocopherols, to the mechanisms of plant resistance to the *Fusarium* species and mycotoxin accumulation.

It can be concluded that the diversity of plant metabolites makes plants promising sources of antifungal agents. Some secondary metabolites, which can be extracted from agricultural by-products, may also offer a possible solution to the fungi problem [164].

4.2. Biological Degradation of Mycotoxins

Biological enzymatic degradation includes acetylation, glucosylation, ring cleavage, hydrolysis, deamination, and decarboxylation, all caused by extra- or bacterial and fungal intracellular enzymes [165]. The use of living cells and bioactive metabolites, such as enzymes produced by certain microorganisms, seems highly applicable to the food and feed industries [166]. Some microorganisms are capable of degrading mycotoxins via their enzymes and use them as a carbon source [167]. Guan et al. [168] reported that *Stenotrophomona smaltophilia* displayed a reducing effect on AFB₁ (82.5%) when incubated at 37 °C for 72 h. After this treatment that has been shown to affect enzymatic activity, the reaction efficiency significantly dropped, which indicates that AFB₁ probably decreased due to enzymatic degradation. Similarly, efficient microbial species, including *Bacillus* spp., *Brevibacterium* spp., *Eubacterium* spp., *Flavobacterium aurantiacum*, *Mycobacterium fluoranthenorans*, *Myxobacteria* spp., *Pseudomonas* spp., *Rhodococcus erythropolis*, *Trichosporon mycotoxinivorans*, *Aspergillus* spp., and *Rhizopus* spp. have been listed by Hathout and Soher [169]. The degraded toxins covered AFs, OTA, *Fusarium* toxins, and PAT.

Moreover, some enzymes found in mushrooms were shown to have a detoxification ability. Manganese peroxidase purified from the mushroom *Pleurotus ostreatus* detoxified AFB₁ by 6% at 0.1 U/mL enzyme activity for 8 h and by 90% at 1.5 U/mL enzyme activity for 48 h [169]. Several fungi belonging to the *Aspergillus* genus were reported to degrade and convert aflatoxin B₁ in foodstuffs to B₂ and B₃ due to their enzymes [170]. Through the production of laccase enzymes in a liquid media, the white-rot fungi efficiently degraded aflatoxin B₁ (by 87%) [171]. The study by Zhang et al. [172] described a 58.2% degradation of aflatoxins by *A. niger* (ND-1) supernatant in ambient conditions. Sato et al. [173] reported the possibility of using certain bacteria to detoxify mycotoxins in foodstuffs. One of the first bacteria used to degrade AFB₁ in feed was *Flavobacterium aurantiacum*; its activity was found to be related to bacterial enzymes [174]. Sangare et al. [175] reported the *Pseudomonas aeruginosa* N17-1 detoxification potential, enabling it to highly degrade several aflatoxins, including AFB₁, AFB₂, and AFM₁, in a nutrient broth. Furthermore, some bacteria have been reported to be able to degrade mycotoxins. *Bacillus subtilis* can degrade AFs [176]. Schatzmayr and Streit [177], and Ahad et al. [178], reported that DON can be degraded by *Eubacterium* spp. BBSH797/soil bacterial consortium (called DX100), respectively.

In their review, Jard et al. [179] summarized the multiple degradation pathways of each major mycotoxin. Briefly, the AFB₁ lactone or difuran ring can be opened, resulting in a loss of toxicity. It should be mentioned that during the degradation process, ZEN was degraded to α -zearalenone (classified as a hydroxyl compound), which is more toxic than the original compound, while other degradation products showed no toxicity. In another study, *Devosia mutans* 17-2-E-8 bacterium degraded DON to the major metabolite 3-epi-deoxynivalenol and the minor metabolite 3-keto-deoxynivalenol, both showing toxicity lower than that of the parent mycotoxin [180]. Microorganisms capable of detoxifying mycotoxins are summarized in Table 3.

Table 3. Microorganisms capable of detoxifying mycotoxins.

Microorganisms	Mixotoxin	Reference
Bacteriae		
<i>Flavobacterium aurantiacum</i>	AFB, OTA, ZEA	[181]
<i>Phenylobacterium immobile</i>		
<i>Gliocladium roseum</i>	DON	[182]
<i>Eubacterium BBSH 797</i>		
<i>Devosia</i> genus	DON	[183]
<i>Eggerthella</i> spp. DII-9	DON, T-2, HT-2	[184]
<i>Bacillus</i>	AFB, ZEA, DON, OTA	[185]
<i>Brevibacterium</i>		
Yeasts		
<i>Candida krusei</i> AUMC 8161	AFB, OTA, ZEN, alternariol	[186]
<i>Pichia anomala</i> AUMC 2674		
<i>Pichia guilliermondii</i> AUMC 2663		
<i>Saccharomyces cerevisiae</i> AUMC 3875		
<i>Saccharomyces cerevisiae</i>	DON	[187]
<i>Candida utilis</i>	AFB, OTA, ZEA	[188]
<i>Yarrowia lipolytica</i>	OTA	[189]
Fungi		
<i>Rhizopus oryzae</i>	AFB1, AFB2, AFG1, AFG2	[122]
<i>Trichoderma reesei</i>		
<i>Clonostachys rosea</i>	ZEA	[190]
<i>Trichosporon mycotoxinivorans</i>	ZEA	[191]

Lactic Acid Bacteria

Lactic acid bacteria (LAB) are preferred over other microorganisms because of the ability of their metabolites to remove mycotoxins from foods without harming a living organism (tagged as GRAS). The fact that they are easily cultured and maintained is also to their advantage [192]. Although research on the applicability and efficiency of LABs to reduce mold and mycotoxin contamination in different food matrices is challenging and time consuming, it is worth conducting [94]. LABs have two mechanisms of detoxification of food mycotoxins; the first makes use of viable microbial cells, while the second utilizes enzymes produced by certain LAB strains. LABs produce several bioactive metabolites, such as acids, carbon dioxide, hydrogen peroxide, phenyllactic acid, and low molecular weight bioactive peptides [193] that can limit the growth of fungi and prevent the production of mycotoxins. LABs also produce numerous proteolytic enzymes that can hydrolyze proteins, such as a cell wall-bound proteinase that hydrolyzes proteins into polypeptides, peptide transporters that transfer peptides into the cell, and abundant intracellular peptidases that degrade the transferred peptides to amino acids [180]. Proteolytic LAB enzymes play an important role in the detoxification of mycotoxins in foodstuffs [194,195]. The application of LABs for mycotoxin elimination in foods has been summarized by Muhiaddin et al. [167].

The adsorption of mycotoxins onto the cell wall of LAB strains is another mechanism of mycotoxin removal from foods. This ability is linked to the presence of polysaccharides, proteins, and peptidoglycans in the LAB cell wall [196]. The binding of mycotoxins onto LAB cells was proposed dependent on certain factors, such as the initial concentration of mycotoxins, the LAB cell number, the LAB strain, and its complexity, food pH, and the incubation temperature [197]. According to Dalié et al. [142], cell viability is not essential because aflatoxin B₁ is bound to the specific monoclonal antibody found in the cell wall. Another mechanism of mycotoxin downsizing is the interaction between mycotoxins and metabolites generated by LAB strains, including acids, phenolic compounds, fatty acids, reuterin, and low molecular weight bioactive peptides [198]. These metabolites can bind mycotoxins and reduce their toxicity.

4.3. Adsorption by Microorganisms

Microorganisms not only cause mycotoxins to decompose into other molecules but also remove them totally through the adsorption onto their cell walls. The latter adsorption ability is a characteristic feature of the most Gram-positive bacteria and yeasts, such as lactic acid bacteria. It was observed that microorganisms can adsorb 20% to 90% of mycotoxins present in different fluid food systems [199]. It has been suggested that heat-treated (inactive) microorganisms show similar or even higher mycotoxin adsorption capacity than living microorganisms when it comes to aqueous solutions [200–202]. It has also been suggested that the adsorption in question is of a physical rather than a biological nature, meaning that during their adsorption, mycotoxins do not enter into a chemical reaction with the binder. This interaction usually occurs with the peptidoglycans present in the cell walls of different microorganisms. Peptidoglycans (purified from the cell walls) were isolated from LABs [202–204] and were found to bind more toxins than the cell pellets left behind after the cell wall removal. They play an important role in adsorption, while the number of adsorption sites and the adsorption efficiency can be increased using chemical methods (e.g., acid and heat treatment) [205–207].

Haskard et al. [208] suggested that the addition of urea (an anti-hydrophobic agent) or organic solvent destroys the cell wall–toxin complex, proving a hydrophobic effect between adsorptions. Yeasts have a two-layer cell wall; the inner layer is composed of β -1,3-glucan and chitin, while the outer layer consists of β -1,6-glucan with heavily glycosylated mannoproteins [209]. At the pH range of 2.9–4.2, mannoproteins have negative charges, while the OTA amine function (NH_3^+) has a positive charge so that the cell wall and the toxin can establish partial electrostatic and ionic interactions. Moreover, as a less polar mycotoxin, OTA can adhere to the hydrophobic surfaces of yeast cell walls through the phenol group and via interactions of the two- π -electron orbital [210]. However, the adsorption becomes relatively weak after washing with a PBS buffer because toxin–microbe complexes release approximately 25% to 40% of toxins [204,211]. This might be the reason why adsorption hardly occurs under non-polar circumstances.

Most adsorbing microorganisms belong to the fermenting microorganisms; therefore, in real-life production, biological adsorption usually occurs during fermentation. Food fermentation is a process of microbial decomposition of carbohydrates to alcohol or organic acids in aerobic or anaerobic environments, used in the production of fermented dairy products, wine, vinegar, and bread. Raw materials commonly used for fermentation cover dairy, meat, fish, vegetables, fruits, legumes, and cereals [146], which can be contaminated by mycotoxigenic fungi or metabolic mycotoxins. Therefore, mycotoxins are generally present when the fermentation process is in progress. Adsorption of mycotoxins by microorganisms during fermentation is summarized in the review by Liu et al. [112].

In recent years, more attention has been focused on animal mycotoxin-adsorbing polysaccharides. Assaf et al. [212] investigated chitin from shrimp shells for its ability to bind AFM₁. The authors demonstrated that chitin bound up to 54% of AFM₁ in the PBS buffer, depending on the concentration of both chitin and the toxin and the incubation time. It is worth mentioning that, applied in the same concentration and during the same incubation time, ground and intact shrimps demonstrated lower adsorption rates than the extracted chitin, but after a triple buffer washing, the AFM₁ adsorption rate decreased by approximately 15% to 45%, suggesting the contribution of electrostatic bonds (e.g., hydrogen bonds and van der Waals interactions) to the adsorption process. Due to the presumed environmental and health acceptability of natural products (e.g., enzyme and microorganism cell wall), these approaches have attracted more attention. In addition, the reduction in mycotoxins during the production of fermented products justifies the use of slightly contaminated raw materials.

In general, biological detoxification is a promising method that can be further improved by focusing on the production of detoxification enzymes. Hence, isolation of suitable microorganisms, identification of their most favorable growth and production conditions, preparation of low-cost production media, and the establishment of down-

stream techniques are key to the successful use of these enzymes in the food and feed industries. The advantages of biological mycotoxin degradation are low costs, applicability to a broad spectrum of target mycotoxins, minimal side effects on nutrients, minimal training requirements, and suitability for a wide range of liquid and solid foods [167].

5. Conclusions and Perspective

These days, when the use of cereals and cereal-based products is ever-growing, it is very important to ensure their safety and cost-effectiveness. Biocontrol methods in terms of production of resistant seeds and avoidance and downsizing of cereal mycotoxin contamination seem promising, primarily because of the perceived harmlessness to humans and animals. Biocontrol of cereal molds and mycotoxins implies pre- and post-harvest activities. The efficacy of these methods might be reinforced by the selection of orderly microbial strains, gene manipulations, and combinations of various agents and methods. Biocontrol of cereal mycotoxins has shown encouraging results but should be combined with good agricultural practices, starting from quality seed preparation down to the effective post-harvest management in all production stages and, ultimately, controlled storage. In view of the above, the use of industrial by-products has the greatest perspective in the biodegradation of mycotoxins due to the acceptable costs and vast sustainability contribution. However, the main goal should be the avoidance of mold infestation and accumulation through proper seed preparation because any decontamination procedure affects the nutritional value and incurs expenses. It should be noted that most of the mycotoxin biocontrol studies were either laboratory or simple system studies. Therefore, a complete evaluation of practical uses of bio-controlling organisms or their enzymes in the field and industrial settings and storage environments should be performed.

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