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Review

Current Strategies in Controlling *Aspergillus flavus* and Aflatoxins in Grains during Storage: A Review

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Abstract: *Aspergillus flavus* is a ubiquitous pathogen that can infect many foods and grains, and it produces large amounts of aflatoxins during their storage. Aflatoxins are considered highly toxic and carcinogenic to humans, and they cause great damage to crop production, food security, and human health. Thus, controlling *A. flavus* and aflatoxins in grains presents a great challenge to humans worldwide. Over the past decade, many strategies have been demonstrated to be useful in controlling *A. flavus* and aflatoxins during food storage. These methods involve physical agents, chemical agents, biological agents, etc. Some of these methods are currently used in actual production. In this review, we summarize the reported methods for controlling *A. flavus* and aflatoxins during food storage in the past ten years and elucidate their advantages and disadvantages. The methods discussed include irradiation technology; low oxygen atmospheres; chemical fungicides (benzalkonium chloride, iodine, ammonium bicarbonate, and phenolic and azole compounds); biological agents from plants, animals, and micro-organisms; and aflatoxin elimination methods. We expect that this review will promote the applications of current strategies and be useful for the development of novel technologies to prevent or eliminate *A. flavus* and aflatoxins in food and feed during storage.

Keywords: *Aspergillus flavus*; aflatoxin; control; in storage

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1. Introduction

Aspergillus flavus is an opportunistic pathogen that can infect many grains and foods during storage, such as maize, peanut, rice, nuts, etc. [1,2]. Once it has gained access to the food, it produces large amounts of conidia. Owing to their small volume, conidia can become suspended in the air and spread easily among grains and foods in storage facilities [3]. Moreover, *A. flavus* produces vast quantities of aflatoxins during infection, which contaminate the grains, leading to great economic losses and health damage to humans and animals [1].

Between 2006 and 2016, aflatoxins in unprocessed food-grade cereals (such as barley, maize, wheat, rice, and oats) had a prevalence of 55% across Africa, America, Asia, and Europe, ranging from 15% in the Americas to 63% in Asia [4]. The annual loss of grains due to aflatoxins was estimated to be USD 500 million in the USA [5]. The situation in developing countries is even worse [6]. In Lucknow, India, it was found that 21% of groundnut and maize samples were unfit for human consumption [7]. The export of groundnut products declined from 550 metric tons (USD 42.5 million) to 265 metric tons (USD 32.5 million) due to aflatoxin contamination in India over a decade. In China, the crop yield losses were up to 21 million tons after harvest owing to aflatoxins, which represented 4.2% of the total annual crop produced.

More than 20 types of aflatoxins produced by *Aspergillus* spp. have been identified. Of these aflatoxins, aflatoxin B1 (AFB1), with the highest toxicity, was classified as a Group 1 human carcinogen by the International Agency for Research on Cancer [1]. Optimal

humidity and temperature have remarkable effects on *A. flavus* growth and aflatoxin production during storage. Sumner and Lee reported that the optimal temperature for *A. flavus* growth and aflatoxin development is 86 °F (30 °C). The optimal relative humidity for *A. flavus* growth and aflatoxin production is 85%. When storage temperatures are below 65 °F (18 °C), and the relative humidity is below 62%, the growth of *A. flavus* usually stops [8]. Sharma reported that temperature ranges from 17 to 42 °C with varying combinations of 0.90 to 0.99 water activity stimulate the production of aflatoxins in *A. flavus* during storage. The growth of fungal biomass and AFB1 production was highest at 28 °C and 0.96 water activity, while no prominent fungal growth or AFB1 production were detected at 20 °C with 0.90 and 0.93 water activity [9]. Thus, during long-term storage, improper storage conditions may result in serious aflatoxin contamination in grains.

Currently, about one-fourth of the world's population is affected by aflatoxins, which leads to serious human diseases [10]. The daily intake of low doses of aflatoxins results in chronic aflatoxicosis, impaired food digestion, stunted growth, immune system suppression, liver cancer, and cirrhosis in malnourished children. The consumption of high doses of aflatoxins results in acute high fever, vomiting, ascites, liver failure, edema of the feet, and jaundice with a high mortality rate compared to chronic aflatoxicosis [11]. Outbreaks of acute aflatoxicosis in developing countries are increasing in frequency and have led to unacceptably high numbers of deaths [12]. In 2004, more than 125 people died because of the consumption of aflatoxin-contaminated maize in Kenya [13]. One study reported that aflatoxins were responsible for causing between 25,000 and 155,000 cases of hepatocellular carcinoma each year in Asia and sub-Saharan Africa [14]. Additionally, aflatoxins cause human disease not only through the digestion of contaminated grain but also via transferral from livestock meat to humans and even from mothers to babies through breastfeeding [15]. In Iran, studies demonstrated that higher levels of AFM1 in mothers' breast milk were associated with lower infant weights and smaller lengths at birth [16,17].

As a result of the serious risks to humans, many countries have regulated the lowest threshold value for aflatoxins in crops and products by law [18]; for example, the UN set 10 μg/kg for AFB1 and 20 μg/kg for total aflatoxins in maize. However, owing to food shortages, some African countries such as Kenya have no strict regulations, which leads to serious aflatoxin exposure and health damage to humans [19,20]. Thus, the most direct method of avoiding aflatoxins is the prevention of *A. flavus* infection and aflatoxin production in storage.

Currently, some methods are in use in an attempt to control *A. flavus* and aflatoxins in grains during storage, such as irradiation, low oxygen atmospheres, chemical agents, biological agents, and aflatoxin detoxification technologies (Figure 1). These strategies promote the reduction of aflatoxins in grains during storage. However, some disadvantages have also been detected in these processes. Hence, in order to select the most effective strategies and promote their application in practice, we reviewed the recently reported methods for controlling *A. flavus* and aflatoxins during food storage and compared the advantages and disadvantages among them. This review will promote the application of effective agents in controlling plant pathogens and mycotoxins in storage.

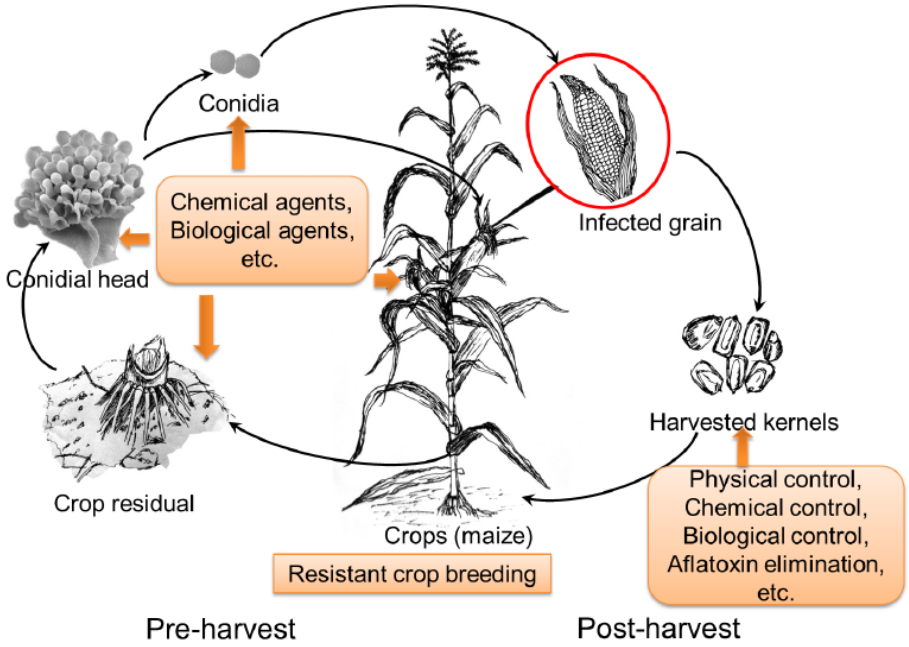

Figure 1. Current strategies used in controlling *Aspergillus flavus* and aflatoxins. The corn ear in red cycle means the infection by *A. flavus*, and then harvested in storage.

2. Physical Agents for the Control of *A. flavus* and Aflatoxins

2.1. Irradiation Methods

Irradiation as a traditional physical treatment is a non-heating sanitary process that can avoid grain damage from exposure to heat. In the past 50 years, irradiation has been established as a safe and effective treatment. It can remove microbial contamination in food and feeds and reduce mycotoxin levels without causing heating [21]. Gamma radiation, electron beams, and X-rays are three different types of radiation that are produced from different sources and have different energy levels [22]. Gamma irradiation emitted by radioactive cobalt-60 or cesium-137 has high product penetration [23]. Electron beam irradiation (e-beam) generates electrons from an electrically driven accelerator machine and has low penetration [23]. X-ray irradiation is also a kind of accelerator-based radiation with high penetration [23]. Bremsstrahlung X-rays are emitted when accelerating electrons hit heavy metal targets, such as tungsten, tantalum, or gold, and are converted into photons [23].

Ionizing radiation can reduce *A. flavus* contamination in many foods. The effects of irradiation on biomolecules and micro-organisms are mainly mediated by active intermediates formed by water radiation. Biological systems are exposed to ionizing radiation to produce reactive oxygen species (ROS), which can damage many cellular components and biomolecules such as DNA, proteins, lipids, amino acids, and carbohydrates [24]. For mycotoxins, irradiation can produce free radicals that act on the furan ring at the end of these toxins, thereby reducing the content of aflatoxins in foods [25].

The studies of Khalil et al. showed that the growth of *A. flavus* in maize was completely inhibited after gamma irradiation at a dose of 6.0 kGy, while the production of aflatoxins was significantly reduced by gamma radiation at a dose of 4.5 kGy [21]. Nurtjahja et al. found that the total number of fungi decreased significantly with increases in the gamma radiation dose [26]. Aziz et al. studied the effects of gamma radiation and corn lipids on aflatoxin B1 synthesis of sterilized maize with low water activity (a_w0.84) [27]. The results showed that the total number of *A. flavus* decreased significantly with the increase in gamma radiation dose, and its growth was completely inhibited when the radiation dose was 3.0 kGy. AFB1 was not detected in maize stored for 45 days after 3.0 kGy gamma radiation [27]. The results of Frink et al. showed that X-ray irradiation at a dose of 2.5 kGy did not allow *A. flavus* cells to survive, regardless of low or high doses of *A. flavus* spores [23].

In addition to gamma radiation, electron beams, and X-rays, ultraviolet is another irradiation technology that has germicidal effects. Ultraviolet is non-visible light with a wide range in the electromagnetic spectrum, from 100 to 400 nm [28]. Based on its wavelength, there are three kinds of ultraviolet light: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (200–280 nm) [28]. UV-C radiation has the strongest germicidal efficacy, and it can be used to reduce food contact surface contamination in postharvest storage [28]. Ultraviolet irradiation can effectively inactivate *A. flavus* without damaging food quality, but the inactivation efficiency varies greatly with different irradiation methods [29]. Byun et al. showed that UV-C can significantly reduce the amount of *A. flavus* and *A. parasiticus* on coffee beans after irradiation, but the treatment also significantly decreased the pH of the coffee beans, which may be due to the formation of organic acids [28].

2.2. Low Oxygen Atmosphere Used in Controlling A. flavus and Aflatoxins

Villers and Gummert tested an UltraHermetic storage method to control *A. flavus* and aflatoxins during storage. This method creates a low oxygen atmosphere to reduce insect and micro-organism respiration. Since molds need oxygen and high humidity, the natural respiration of insects and micro-organisms contained in harvested crops and the respiration of the harvested kernels themselves use up the available oxygen. The low oxygen atmosphere arrests mold development. Thus, even after several months, the levels of mold growth and aflatoxin enrichment do not rise. Moreover, this method does not require chemicals, fumigants, or commercial products such as electricity or water. This system proved to be useful during multi-month postharvest storage tests of maize, rice, and peanuts in hot and humid countries. It is now in use in 103 countries at varying scales [30].

3. Chemical Agents for the Control of *A. flavus* and Aflatoxins

In addition to physical methods, many chemicals have been found to effectively inhibit the infection of *A. flavus* in grain during storage. Chemical control is an important strategy for grain storage management. Lemos et al. evaluated the bacteriostatic effect of different chemicals (iodine, benzalkonium chloride, peracetic acid, biguanide, biguanide, sodium hypochlorite, and electrolyzed water agents) on *A. flavus*. The results showed that benzalkonium chloride and iodine had the best inhibitory effects, and the inhibition rate increased with the increasing compound concentration, while the inhibitory effect of electrolyzed water agents was worse for both acidic electrolytic water and alkaline electrolytic water [31].

Samapundo et al. demonstrated that 1% ammonium bicarbonate could completely inhibit the growth of *Fusarium* and *Aspergillus* isolates, and corn treated with 1% ammonium bicarbonate is still edible [32]. Therefore, using 1% ammonium bicarbonate to treat corn during storage can not only achieve a good antifungal effect but also has little effect on crop quality.

Zhang et al. explored the potential antifungal effect of 1-nonanol against *A. flavus*. The results showed that 0.11 μL/mL gaseous 1-nonanol and 0.20 μL/mL liquid 1-nonanol could completely inhibit the growth of *A. flavus*. In addition, the growth of *A. flavus* in wheat, corn, and rice with 18% water content could be completely inhibited by 1-nonanol vapor at a concentration of 264 μL/L [33]. Zhang et al. speculated that 1-nonanol could destroy the cell membrane integrity and mitochondrial function of *A. flavus* hyphae and lead to their apoptosis [33].

Samapundo et al. found that phenolic compounds could not inhibit the growth of *A. flavus* under laboratory conditions but could significantly reduce the production of aflatoxin B1 [34]. The studies of De Lucca et al. showed that trans-2-hexenal could significantly inhibit the spore germination of *A. flavus* at a concentration of 10 μM, and the inhibition rate reached 95% at a concentration of 20 μM. In addition, when trans-2-hexenal was intermittently pumped into a simulated storage environment of corn, it significantly inhibited the growth of *A. flavus* and aflatoxin production [35].

Hareyama et al. studied the control effects of four isothiocyanates (ITCs) (allyl ITC (AITC), benzyl ITC (BITC), and methyl and phenylethyl ITCs) on *A. flavus* growth and aflatoxin B1 production. The results showed that BITC had the strongest inhibitory effect on the growth of *A. flavus* in a liquid state, while AITC had the best inhibitory effect in a gaseous state [36].

As well-known fungicides, azole compounds can significantly inhibit the growth of *A. flavus*. Mateo et al. showed that a very low content of *A. flavus* was observed in the presence of 0.1 mg of prochloraz or 5.0 mg of tebuconazole. The resulting antifungal effects were prochloraz > prochloraz + tebuconazole (2:1) > tebuconazole [37]. Wagacha and Muthomi pointed out that itraconazole and amphotericin B can effectively control *Aspergillus* spp. [38]. However, the use of these fungicides is hampered by economic factors and increasing concerns about the environment and food safety. In addition to the agents mentioned above, some other novel fungicides have been developed in recent years (Table 1).

Table 1. The novel fungicides used in controlling *Aspergillus flavus* and aflatoxins during storage since 2014.

Compounds	Effects	Reference
Carboxymethylation, sulfation and phosphorylation of lentinan derivatives	Lentinan at 200 μg/mL completely inhibits aflatoxin production. Sulfated derivatives led to reduced inhibition compared to lentinan. The phosphorylated derivatives showed complete inhibition of aflatoxins biosynthesis at 50 μg/mL.	[39]
5-azacytidine (5-AC)	5-AC, a DNA methylation inhibitor, decreased aflatoxin production and changed fungal cell morphology.	[40]
Vitamins A, C, and E	Vitamins A, C, and E can prevent sclerotium formation in *A. flavus*. High concentrations of these vitamins in the medium resulted in a small number of sclerotia.	[41]
Potassium sorbate and sodium benzoate	Inhibited *A. flavus* growth and its infection of peanut and other crops.	[42]
Citral	Citral caused transient transmembrane secretion of H_2O_2 and led to the inhibition of aflatoxin production.	[43]
L-Cysteine hydrochloride (L-CH)	L-CH induced glutathione (GSH) synthesis to clear intracellular reactive oxygen species (ROS), leading to hyphal dwarfing. L-CH inhibited hyphal branching by preventing the expression of cell wall and spore development-related genes.	[44]
Sub3	Sub3, over 0.15 g/L, prevented the germination of *A. flavus* spores in a potato dextrose broth medium.	[45]
Thymol	200 μg/mL thymol induced conidial apoptosis in *A. flavus*.	[46]
1-Octanol	1-Octanol can inhibit *A. flavus* spore germination in a dose-dependent manner, and 300 μL/L 1-octanol vapor could completely inhibit the growth of *A. flavus* in wheat, maize, and rice with a 20% moisture content.	[47]
Carvacrol (CV)	The spore germination rates of *A. flavus* at 50 μg/mL, 100 μg/mL, and 200 μg/mL CV treatments were reduced to 84.0%, 26.7%, and 11.3%, respectively.	[48]

4. Biological Agents Used in Controlling *A. flavus* and Aflatoxins

4.1. Biological Agents from Plants

In addition to traditional methods, novel and environmentally friendly biocontrol agents are attracting more attention today. Essential oils extracted from plants have been reported to be useful in the control of *Aspergillus* and aflatoxins in various crops, such as maize, peanut, rice, and soybeans, during storage. These plants include *Peumus boldus* Mol. (boldo), *Lippia turbinata* Griseb. (poleo) [49], *Eugenia caryophillis* C. (Spreng) [50], *Cuminum cyminum* L. [51], *Cymbopogon citratus* DC. (Stapf) [52], *Origanum vulgare* spp. *hirtum*, *Origanum vulgare* L. spp. *vulgare*, *Rosmarinus officinalis* L., *Schinus molle* L., *Tagetes minuta* L. [53], *Oxalis corniculata* L. [54], and *Glycine max* L. Merr [55]. The essential oils from these plants displayed synergistic effects. The antifungal activity was enhanced when they were used in combination compared to when they were used alone [56]. For example, a mixture of *Melaleuca alternifolia* (Myrtaceae) and *Cymbopogon nardus* (Poaceae) essential oils showed a better antifungal effect on *A. flavus* strains, and it was found that there was an additive effect with both of them [57].

Some other natural plant products have also been proven effective in controlling *A. flavus* or aflatoxins in recent years (Table 2). The only factor that requires elucidation is the logistics of the mass production of these oils. The growing season of the plants is very long, and early harvest reduces the production of their essential oils. Hence, the commercial production of these essential oils requires finding a more acceptable and less time-consuming approach.

Table 2. The novel natural plant products used in controlling *A. flavus* or aflatoxins since 2014.

Plant	Products	Mechanism	Reference
Seaweed	Alginate oligomer	Could disrupt fungal biofilm formation, increase cell surface roughness to disrupt fungal growth.	[58]
Litsea cubeba	Essential oil containing (Z)-limonene oxide (30.14%), (E)-limonene oxide (27.92%) and D-limonene (11.86%)	Controlled *A. flavus* growth and aflatoxin B1 production in licorice.	[59]
Callistemon citrinus and *Ocimum canum*	Major components in *C. citrinus* are 1,8-cineole (60.6%), α-pinene (18.5%). *O. canum* containing 1.8-cineole (20.8%), linalol (14.3%), and eugenol (11.9%)	Used as a fumigant in *Ethmalosa fimbriata* preservation against *A. flavus*.	[60]
Neem and bitter kola seeds	Methanolic and ethanolic extracts	Inhibited the growth of *A. flavus* with antifungal compounds in the extraction.	[61]
Pistachio nut	Carvacrol and allyl isothiocyanate	Controlled conidia germination and mycelial growth of *A. flavus*.	[62]
Curcuma longa	Curcumin	Curcumin inhibited the mycelial growth and sporulation of *A. flavus*, inhibited the biosynthesis of ergosterol, and enhanced the permeability of cell membranes.	[63]
Oregano variety Mendocino (OMen), Cordobes (OCor), and Compacto (OCom)	Essential oils	The compounds of thymol in OCor (18.66%), OMen (12.18%), and OCom (9.44%) showed the best antifungal activity.	[53]
Zanthoxylum schinifolium pericarp	Linalool	Linalool vapor at 800 μL/L prevented *A. flavus* growth, and linalool at 10 μL/mL caused *A. flavus* spore death.	[64]
Pterocarpus indicus Willd., *Vaccinium* spp. and *Vitis vinifera* L.	Pterostilbene	Pterostilbene inhibited mycelial growth of *A. flavus* with EC50 (the concentration that causes inhibition by 50%) at 15.94 μg/mL. Pterostilbene at 250 and 500 μg/mL effectively inhibited *A. flavus* infection in peanuts.	[65]
Buckwheat hull	Polyphenols, tocopherols, phytosterols, and fatty acids	Lipophilic extract at 10 μg/mL and polyphenol extract at 100 ng/mL inhibited the growth of *A. flavus* by 74% and 38%, respectively. A mixture of the two inhibited the growth of *A. flavus* by 86%.	[66]

4.2. Biological Agents from Animals

Animal derivatives refer to substances extracted from wild animals or products processed by wild animals, including wildlife hair, bone, viscera, meat, stratum corneum and its secretions, odors, and other special substances. Studies have shown that propolis and chitosan can effectively control *A. flavus* in vitro and effectively decrease the infection of *A. flavus* in crops [67]. Propolis, a natural sticky substance, is made by bees that collect saps, resins, and mucilage from various parts of the plant and then mix them with beeswax and several honeybee enzymes [68]. In general, the raw propolis is mainly composed of resin and vegetal balsam (50%), wax (30%), essential oil (10%), and pollen (5%), as well as debris, minerals, polysaccharides, and proteins [69]. Although propolis exhibits variations in its components across regions, plant species, and bee species, they all have similar qualities, such as antibacterial, antifungal, antiviral, antiparasitic, anti-inflammatory, antiproliferative, and antioxidant effects [70]. Although the antibacterial mechanism of honey is not clear, it is speculated that it may be related to high osmotic pressure due to its high sugar content; low moisture content; gluconic acid, which creates an acidic environment; hydrogen peroxide; and phytochemical components [71].

Chitosan is a linear polymer of 1,4-D-glucosamine that is formed by the deacetylation of chitin [72]. Chitin is a naturally occurring biopolymer, the second most abundant polysaccharide after cellulose. Chitin exists in the exoskeletons of crustaceans such as crabs, shrimp, lobsters, crayfish, and insects [73]. Chitosan and its derivatives inhibit the growth of microbials by affecting the activity of endogenous chitinase. In addition, chitosan possesses the capability to aggregate spores, resulting in the abnormal morphology of *A. flavus* spores. This aggregation induces swelling, bud tube polarization and leakage of intracellular contents [74], and finally inhibits the germination and growth of *A. flavus* spores.

Ventura-Aguilar et al. blended propolis, chitosan, and pine resin extracts, combining them in varying ratios to create distinct solutions, and studied the inhibitory effect of them on *A. flavus*. The results showed that the inhibitory rate of chitosan + propolis + turpentine extract on *A. flavus* mycelium growth was about 75%. After treatment, conidia germination was completely inhibited on the surface of corn grains [67]. Similarly, Hassanien et al. showed that propolis and propolis nano-preparations could significantly inhibit the growth of *A. flavus* and aflatoxin production [75]. Cortés-Higareda et al. demonstrated that a combination of chitosan nanoparticles (30% propolis nanoparticles and 40% propolis extract) significantly inhibited the growth of fungi. This evidence indicates that a synergic effect formed among the components in the formulation [76]. Aparicio-García et al. smeared a combination of chitosan and propolis on the surface of figs. This treatment greatly reduced the infection degree of *A. flavus* on figs in storage and significantly decreased the content of aflatoxins [77]. In summary, the application of wild animal derivatives such as propolis and chitosan on crop surfaces can evidently inhibit *A. flavus* infection, and these animal derivatives have no effect on the quality and taste of food, and cause no harm to human health.

4.3. Biological Agents from Micro-Organisms

Micro-organisms, as rapidly proliferating and easily cultivable entities, have been proven as valuable resources in the production of economical and efficient antifungal agents against *A. flavus* and aflatoxins during food storage. Reddy et al. showed that *Pseudomonas fluorescens* and *Bacillus subtilis* had obvious inhibitory effects on the growth of *A. flavus*; their inhibition rates reached 93% and 68%, respectively [78]. Another bacterium strain, *Bacillus pumilus* HY1, isolated from Korean soybean sauce, showed strong antifungal activity against *A. flavus* and *Aspergillus parasiticus* in soybeans. This inhibitory effect is based on the production of the lipopeptide iturin [79].

Additionally, micro-organisms not only produce a steady supply of antifungal compounds, but they can also produce volatile antifungal compounds, which may be more acceptable for postharvest disease control. For example, Gong et al. screened one bacterial strain, TR-1, from the rhizospheres in the soil of tea plants. The TR-1 strain, identified as *Bacillus flexus*, was found to produce volatiles that had a strong antifungal effect against *Aspergillus* pathogens. The TR-1 volatiles also completely inhibited aflatoxin biosynthesis in stored peanut samples with high water activity. TR-1 also showed broad antifungal activity against six other fungal pathogens [80]. Additionally, the authors screened other bacteria, which were proven to be efficient in controlling *A. flavus* and aflatoxins in grains during storage. These bacteria include *Alcaligenes faecalis*, *Pseudomonas stutzeri*, *Serratia marcescens*, *Enterobacter asburiae*, *Staphylococcus saprophyticus*, and *Shewanella algae*. (Table 3).

Some studies also demonstrated that the bacteria could inhibit aflatoxin production by reducing gene expression in the aflatoxin biosynthesis pathway. *Bacillus megaterium* isolated at 10^9 CFU/mL exhibited efficacy in reducing the rot of peanut kernels caused by *A. flavus* during storage. This strain reduced the expression of *aflR* and *aflS* genes and significantly decreased the biosynthesis of aflatoxins [81]. In addition to these bacteria, some other micro-organisms with antifungal effects against *A. flavus* and aflatoxins in the past 10 years are also listed in Table 3. These bacteria, as well as their varied antifungal compounds, could provide materials for the production of novel antifungal agents.

Table 3. The micro-organisms used in controlling *A. flavus* and aflatoxins since 2014.

Micro-Organisms	Habitat	Antifungal Effects	Reference
Lactobacillus plantarum	Fermented Kenyan milk and maize products, etc.	(a). Produces antifungal biomolecules and other metabolites, inhibits fungal growth. (b). Adheres to the olive surface, produces a biofilm, competes for oxygen with *A. flavus*, and finally inhibits growth.	[82,83]
Bacillus subtilis fmbJ	Unknown	Produces bacillomycin D, injures the cell wall and cell membrane, prevents mycelial growth, sporulation, and spore germination.	[84]
Leuconostoc mesenteroides DU15	Unknown	Produces peptides due to fungal cell lysis.	[85]
Bacillus subtilis UTBSP1	Unknown	Produces fengycin and surfactin, which can reduce *A. flavus* growth and aflatoxin B1 content in pistachio nuts.	[86]
Pseudomonas sp. 4B	Effluent pond of a bovine abattoir located in southern Brazil.	Reduced fungal growth by 53.8–69%. The aflatoxin concentration reduced from 1472 ng/mL to 42.3 ng/mL.	[87]
Zygosaccharomyces rouxii	Unknown	Degraded AFB1 to new products; the detoxification rate reached 97%.	[88]
Hanseniaspora opuntiae L479 and *H. uvarum* L793	Unknown	L479 produced a lot of acetic acid compounds, while L793 produced a lot of esters and alcohols compounds. These compounds could inhibit the growth of *A. flavus*.	[89]
Wickerhamomyces anomalus and *Metschnikowia pulcherrima*	Unknown	*W. anomalus* inhibits the growth of *A. flavus* through the production of volatiles and lytic enzymes, while *M. pulcherrima* performs biological control through competition for iron.	[90]
H. uvarum and *H. opuntiae*	Unknown	*H. uvarum* and *H. opuntiae* inhibit the growth of *A. flavus* by producing three volatiles, namely octanoic acid, 2-phenethyl acetate, and furfuryl acetate.	[91]
Saccharomyces cerevisiae	The Western and Eastern Ghats of India	Produces ethyl acetate, hexanal, 1-propanol, 1-heptanol, 1-butanol, benzothiazole, and other volatiles to inhibit the growth of *A. flavus* mycelia and AFB1 production.	[92]
Bacillus megaterium BM344-1	Strawberry jam (imported from Turkey) marketed in Qatar	Produces hexadecanoic acid methyl ester (palmitic acid) and tetracosane to inhibit the growth of *A. flavus*.	[93]
B. megaterium and *Pseudomonas protegens*	Stored rice grains in Korea	Produces volatile organic compounds to inhibit the growth of *A. flavus* and aflatoxins production.	[94]
B. subtilis SV36-2	Different cooked food (meat and vegetables)	Produces high quantities of carbon disulfide and 1,3-pentadiene to reduce mycelia and conidiation in *A. flavus* MG09.	[95]
Pichia kudriavzevii and *Lachansea thermotolerans*	Soil and pistachio nuts	Prevents *A. flavus* growth in dual culture, volatile, and non-volatile compounds reached 32–60%, 13–31% and 40–61%, respectively, while the inhibition rate of AFB1 production was 90.6–98.3%.	[96]
Pichia anomala WRL076	Unknown	Produces the volatile compound 2-PE to inhibit the growth of *A. flavus*.	[97]
Candida nivariensis DMKU-CE18	Leaves of rice, sugarcane, and corn in Thailand	Produces the volatile compound 1-pentanol to inhibit mycelial growth (64.9% inhibition) and conidial germination (49.3% inhibition) of *A. flavus*.	[98]
Streptomyces philanthi RL-1-178	Chili pepper rhizosphere soil in southern Thailand	Produces the volatile compounds geosmin (13.75%), L-linalool (13.55%), 2-mercaptoethanol (9.71%), and heneicosane (5.96%) to inhibit the growth of *A. parasiticus* and *A. flavus*.	[99]
Streptomyces yanglinensis 3-10	Rice (*Oryza sativa*), Huazhong Agricultural University, Wuhan, China	Produced 19 volatiles, including methyl 2-methylbutyrate, 2-phenylethanol, and β-caryophyllene, which can inhibit mycelial growth, sporulation, conidial germination, and expression of aflatoxin biosynthesis genes in *A. flavus* and *A. parasiticus* in vitro.	[100]
Alcaligenes faecalis N1-4	Rhizosphere of tea plants	Produces dimethyl disulfide (DMDS) and methyl isovalerate (MI) to prevent conidial germination and mycelial growth of *A. flavus*.	[101]
Pseudomonas stutzeri YM6	Sea sediment in the Yellow Sea of China	The main volatile organic compound dimethyl trisulfide (DMTS) at 200 μL/L can completely inhibit the growth of *A. flavus*.	[102]
Serratia marcescens Pt-3	Rhizosphere of tea plants	Produces dimethyl disulfide (DMDS) to inhibit the growth of *A. flavus*.	[103]
Enterobacter asburiae Vt-7	Rhizosphere of tea plants (North: 32°11′56.03″, East: 113°46′36.95″)	Produces 1-pentanol and phenylethyl alcohol to inhibit the growth of *A. flavus*.	[104]
Staphylococcus saprophyticus L-38	Yellow Sea marine sediment	Produces 3,3-dimethyl-1,2-epoxybutane (3-DE) to inhibit the growth of *A. flavus*.	[105]
Shewanella algae strain YM8	Yellow Sea marine sediment	Produces volatile organic compounds such as dimethyl trisulfide (DMTS), 2,4-bis(1,1-dimethylethyl)-phenol to reduce mycelial growth and conidial germination in *A. flavus*.	[106]

5. Aflatoxin Elimination Methods

The aflatoxins produced by *A. flavus* can cause great damage to human health [6]. Notably, aflatoxins possess the capability to create the 8,9-epoxide structure through cytochrome P450-dependent epoxidation within human cells. Subsequently, this resulting product has been identified as a causative agent of substantial harm in humans, attributable to its interaction with DNA. Specifically, the formation of an adduct has been observed, playing a pivotal role in the carcinogenic activity associated with aflatoxins. Thus, to reduce

aflatoxin contamination in grains, scientists have developed several methods to eliminate these mycotoxins.

AFB1, one of the most toxic mycotoxins, is highly resistant to heat, solvents, and radiation [107]. Studies are urgently needed to determine how to eliminate AFB1 contamination in crops. In the 1990s, Mukendi et al. [108] tested the effect of chemical agents to detoxify AFB1 in crops, such as sodium sulfite, sodium hydrogen sulfate, sodium hydroxide, ammonia, sodium hypochlorite, and hydrogen peroxide. The results showed that sodium sulfite is the most effective for eliminating AFB1 contamination. Recently, Safara et al. [109] tested aflatoxin detoxification with aqueous citric acid in 275 rice samples. After treatment with 1 N citric acid, aflatoxins at concentrations of <30 and <4 ppb in the rice samples were completely degraded, and 97.22% degradation occurred in rice contaminated with ≥30 and ≥4 ppb [109]. Several additional chemical techniques have been confirmed to be effective in degrading AFB1, including lactic acids [110], an alkali-refining method [111], and ozone [112]. Some of these treatments have been shown to have indirect detoxification effects. Jardon-Xicotencatl et al. [113] confirmed that the detoxification effect of neutral electrolyzed oxidizing water (NEW) did not directly act on the aflatoxins. Aflatoxin-contaminated maize at a concentration of 360 ng/g was soaked in NEW (60 mg/L available chlorine, pH 7.01) for 15 min at room temperature. NEW showed no detoxification effect on aflatoxins. However, the aflatoxin-associated cytotoxicity and genotoxicity effects were markedly reduced in hepatic cells by the detection of IC50 (50% inhibitory concentration) values at different exposure times [113]. In addition to the agents mentioned above, some other novel aflatoxin detoxification agents have been obtained in recent years (Table 4).

Table 4. Novel aflatoxin detoxification agents since 2014.

Aflatoxin Detoxification Agents	Detoxification Effects	Reference
Vasaka leaf extract (*Adhatoda vasica* Nees)	Alkaloid extracted from leaves showed strong aflatoxin B1 (AFB1) detoxification activity. The degradation rate was ≥98%.	[114]
Manganese peroxidase from white rot edible mushrooms *Pleurotus ostreatus*	The degradation efficiency of AFB1 was the highest (90%) when incubated under 1.5 U/mL enzyme activity for 48 h.	[115]
Ozonation	The detoxification rates of ozone (6 mg/L applied for 30 min at room temperature) to the total aflatoxins and AFB1 were 65.8% and 65.9%, respectively.	[116]
Ultraviolet irradiation	The optimal enzymatic reaction occurred in 0.1 M of citrate buffer containing 20% dimethyl sulfoxide at 35 °C, a pH of 4.5, and a laccase activity of 30 U/mL.	[107]
Ultraviolet irradiation	AFB1 was decreased from 51.96 to 7.23 μg/kg in 10 min and reduced by 86.08% in peanut oil.	[117]
Pulsed light (PL)	PL treatment (80 s) reduced AFB1 and aflatoxin B2 (AFB2) in rough rice by 75.0% and 39.2%, respectively; treatment for 15 s reduced AFB1 and AFB2 in rice bran by 90.3% and 86.7%, respectively.	[118]
Extracellular extract of *Cladosporium uredinicola*	Thermostable enzyme in the extract of *C. uredinicola* can eliminate AFB1 by 84.5% at 37 °C.	[119]
Nitrogen gas plasma	Nitrogen gas plasma degrades AFB1 (200 ppb) by 90% within 15 min.	[120]
Ozone	In red pepper samples containing AFB1 treated with ozone 80 mg/L for 40 min, the reduction in AFB1 was 74.1%. Additionally, the mesophilic bacteria and mold/yeast counts decreased by 7–22.1% and 27.2–33.7%, respectively.	[121]
Magnetic carbon nanocomposites	The equilibrium times at pHs 7 and 3 were 96 and 180 min, respectively, and nearly 90% of AFB1 was removed in both adsorbents.	[122]
Fifty-nine *Streptomyces* isolates and Mycostop®'s *Streptomyces griseoviridis* K61	After 10 days of culture, most strains in 59 *Streptomyces* isolates were able to degrade AFB1 on solid medium (mean = 33%, median = 32%), while the *Streptomyces griseoviridis* strain degraded it to undetectable levels.	[123]
Aspergillus oryzae M2040 strain	In peanuts, the 1% inoculation level of *A. oryzae* M2040 could secrete inhibitory compounds and effectively inhibit AFB1 production and *A. flavus* growth.	[124]

In addition to these chemical and physical methods, biological agents have also proven useful in the degradation of aflatoxins such as micro-organisms and plants and their extracts or enzymes. Ciegler et al. tested the detoxification activities of different micro-organisms, such as yeasts, molds, bacteria, actinomycete, algae, and fungi [125]. They confirmed that the bacterium *Flavobacterium aurantiacum* NRRL B-184 could remove aflatoxins in

contaminated milk, oil, peanut butter, peanuts, and corn. Additionally, after NRRL B-184 treatment, aflatoxins in these materials were completely detoxified and no toxic products were formed [125]. Since then, many other micro-organisms have been screened and have proven useful in reducing aflatoxins, including *Armillariella tabescens* [126], *Saccharomyces cerevisiae* [127], *Bacillus* spp. [128], *Enterococcus faecium* [129], *Serratia marcescens* [130], *Streptomyces* sp. [131], *Lactobacillus casei* and *Pichia anomala* [132], edible mushrooms including *Trametes versicolor* [133] and *Pleurotus ostreatus* [115], and even plants [114] and insects [134].

The aflatoxin degradation activity of some micro-organisms relies on enzymes within their cells. They can convert aflatoxins to less toxic compounds or small molecules and eventually reduce or eliminate aflatoxin damage. Several effective AFB1 degradation enzymes have been found, such as laccase [107], aflatoxin-detoxifying enzyme [135], glutathione S-transferases [136,137], manganese peroxidase [115,138], and co-expression of human glutathione S-transferases (GSTs) with GSTA1-1 or GSTP1-1 in *Salmonella typhimurium* strains [139]. Other enzymes, such as β-naphthoflavone (BNF), are inducers of various detoxification enzymes. Enzyme BNF and CYP450 mono-oxygenases increased GST activity by 133% in animals fed 50 μg/kg AFB1, and by 48% in animals pre-exposed to 50 μg/kg AFM1 [137].

However, because of protein instability, the activity of the aflatoxin detoxifying enzymes is weakened in a variety of natural environments due to heat, light, and pH. Moreover, because aflatoxins are fat-soluble compounds, the aflatoxin detoxification activity is always better in the oil phase. Therefore, it is important to determine how to improve the stability and activity of these aflatoxin detoxifying enzymes (detofizymes). Several studies have analyzed the immobilization of detofizymes. Liu et al. [140] identified one aflatoxin detofizyme (ADTZ), which was isolated from the edible fungus *Armillariella* sp., and analyzed the activity after immobilization using a hydrophobic adsorption method (n-alkyl or n-octyl amino-agar beads as the carrier). The results indicated that the pH stability, the thermostability, and the freezing stability of ADTZ were improved after immobilization. Thus, immobilization provides a useful and available method to develop aflatoxin detofizyme agents [140].

6. Discussion

Global climate changes have heightened the damage caused by aflatoxins and decreased the efficacy of the currently used control methods [19]. The threat of aflatoxins to humans has become increasingly serious all over the world. The control of *A. flavus* and aflatoxins is now one of the most rapidly developing areas of research [6].

In this review, we summarized different types of methods used in the control of *A. flavus* and aflatoxins during food storage. The advantages and disadvantages of these methods are compared and listed in Table 5. Of these methods, chemical-based controls have been studied for the longest time and play important roles in the control of *A. flavus* and aflatoxins. However, owing to the requirements for food security, environmental protection, and human health, chemical agents are not sufficient. Physical methods, as well as irradiation treatments, have also been broadly used in practice. However, these technologies are not always economical or effective in the control of *A. flavus* infection of crops during storage. Moreover, some of them are laborious and expensive during long-term storage [141]. Biological agents can achieve effective and useful results in the experimental setting, there are still some important questions that have not been successfully answered. Some biological agents, such as essential oils, extractions, and volatiles are also not completely safe to humans and other organisms. Safe, environmentally friendly, and effective biological agents are still urgently needed. Additionally, these biological technologies require more research to increase their acceptability for application in varied environments. This includes the urgent need to understand the positive and negative effects on micro-organism biodiversity and the environment, the reasons for the unstable activity of micro-organism in varied environments, and the interactions between these agents and pathogens. Moreover, the difficulty in timing the application or control of

inoculum stability, the potential damage to crops, and the adverse effects of fungicides on microbial strains in applications should also be addressed and tested in future studies [142].

Table 5. Advantages and disadvantages of the methods of inhibiting *A. flavus* infection.

Approach	Advantages	Disadvantages
Irradiation	It leaves no residue, has no legal restrictions, is easy to use, and is lethal to a wide range of hazardous micro-organisms [143].	The application of irradiation in long-term storage is laborious and uneconomic. The effect is not obvious in dry crops [21].
Low oxygen atmosphere	Minimizes the use of chemical preservatives and integrated control of both microbial growth and insect infestation [144].	May not control or prevent fungal growth and possible production of mycotoxins because some fungi can grow under facultatively anaerobic conditions [144].
Chemical agents	It has great antifungal efficiency [145].	Some of these agents can adversely affect the nutritional, sensory, and functional properties of foods, produce harmful toxic residues, contaminate the environment, and create resistant fungal pathogens [146,147].
Phyto materials	A variety of compounds are present in essential oils, and their antibacterial activities may be due to the interaction of several mechanisms of action in different parts of microbial cells, which may result in the bacteria not developing resistance [148].	The application of these essential oils from plants is always dose-dependent [149]. These substances are difficult to produce in a short period of time owing to large planting areas needed, long growth cycles, daily management, etc. [149].
Animal derivatives	Cheap and natural origins [75].	Often results in a strong taste that can change the character of the food [75]. These substances are also difficult to produce in a short period of time owing to livestock scales, standardized management, and long breeding periods. [75].
Microbial agents	Low in toxicity, biodegradable, and environmentally friendly [150]; they also have high efficiency and specificity [151].	The method is in the research and experimentation stage; there are still many questions to answer, and currently few microbe strains can commercially be used in practice for aflatoxin degradation [11].

In conclusion, with the rapid changes in climate and environment, outbreaks of acute aflatoxicosis in the world are increasing and resulting in unacceptably high mortality rates. In this report, we reviewed the current strategies used for controlling *A. flavus* and aflatoxins during food storage during the past 10 years. Some physical and chemical agents are laborious, uneconomic, or environmentally hazardous. They do not satisfy the needs of sustainable development in modern society. Among potentially sustainable methods, biological agents as have mostly been studied in the laboratory, but they have not successfully been applied in production; their safety and effectiveness require more evaluation and testing. Thus, with the increasing requirements relating to environmental protection and low energy consumption, these environmentally friendly and sustainable agents will become more broadly used in controlling *A. flavus* and aflatoxins during food storage. Moreover, the integrated utilization of these effective methods will become more and more common in production. This topic opens exciting perspectives for the screening of novel agents to control fungal pathogens and mycotoxins during food storage.

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