Kwigizile et al.
CABI Reviews (2025) 20:1, 0062
https://doi.org/10.1079/cabireviews.2025.0062

CABI Reviews

REVIEW

Aflatoxin production mechanisms and management in the maize cropping systems of sub-Saharan Africa

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Abstract

In sub-Saharan African countries, the maize crop is a major staple food crop, providing up to 70% of the population's total caloric intake. Aflatoxins, toxic secondary metabolites primarily produced by *Aspergillus flavus* and *Aspergillus parasiticus*, pose significant threats to food safety, public health, and agricultural economies in sub-Saharan Africa (SSA), where maize is a staple crop. This review synthesizes current knowledge on the mechanisms of aflatoxin production and its management within maize cropping systems of SSA. The occurrence and severity of aflatoxin contamination are influenced by multiple factors, including high temperatures, drought stress, insect damage, poor post-harvest handling, and inadequate storage conditions. Maize has been linked to being contaminated by roughly eighteen (18) different forms of aflatoxins, which are severely poisonous, and contribute to public health issues. The review explores the biological and environmental triggers of aflatoxin biosynthesis, highlighting molecular pathways and fungal-host interactions. Additionally, it evaluates integrated management strategies encompassing host resistance, good agricultural practices, biocontrol agents (such as *Aflasafe*), proper harvesting, drying, and storage techniques. Socio-economic and institutional barriers to effective aflatoxin control are also discussed, along with policy and research recommendations. The review also emphasizes on the necessity to apply novel and existing techniques to prevent aflatoxin. The study featured the need for a multidisciplinary and region-specific approach to sustainably mitigate aflatoxin risks in SSA. Best bet recommendations are provided given different levels of scenarios at the farmer, farm plot, maize farming systems, and eventually the nodes across the entire maize value chain.

Keywords: maize, cropping systems, SSA, aflatoxins, mechanisms, integrated management, mitigations

Introduction

Aflatoxins are a group of toxic secondary metabolites that are produced by fungi, primarily *Aspergillus flavus* and *Aspergillus parasiticus*, both from section Flavi of *Aspergillus* genus (Klich, 2007; Elias, 2016; Benkerroum, 2020). These fungi have been the subject of several studies due to their significant impact on food safety, security, nutrition, and human and animal health (Kinyungu *et al*., 2019; Mahato *et al*., 2021). They are multicellular, ubiquitous, saprophytic, and opportunistic plant-like organisms, that form long and thin filaments-like structures known as "hyphae"(Adeyeye, 2016), and known to colonize various crops, including but not limited to most cereals, ground nuts, and legumes, especially in warm and humid environments (Abbas *et al*., 2009). It is worth noting that more than 100,000 different types of fungal genera have been discovered, but only a few, including *Aspergillus* spp., *Penicillium* spp., and *Fusarium* spp., are known to produce mycotoxins that have a substantial impact on the maize cropping systems (Das and Oliveira, 2017; Benkerroum, 2020; Adeyeye and Ashaolu, 2021). Aflatoxins produced from *Aspergillus* species are potent highly carcinogenic and mutagenic types of mycotoxin compounds (Cotty and Mellon, 2006; Amaike and Keller, 2011; Assaf *et al*., 2019). Several studies have highlighted the need for increased vigilance in the monitoring and management of aflatoxins in food systems to minimize their harmful effects (Mahato *et al*., 2021; Olana, 2022;

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Submitted: 12 May 2025. Accepted: 11 September 2025. Published: 21 October 2025

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Shabeer *et al*., 2022; Tito *et al*., 2022). Therefore, it is essential to take measures to minimize their occurrence and exposure in the food chains.

Most important mycotoxins in the world are aflatoxins, cyclopiazonic acid, ochratoxins, deoxynivalenol, zearalenone, fumonisin, T-2 toxin, and T-2-like toxins (Lakkireddy *et al*., 2014; Das and Oliveira, 2017). Among these, aflatoxins, in particular, are the main mycotoxins that pose a significant threat to animal and human health (Mtega *et al*., 2020). Aflatoxins occur in different forms, such as aflatoxins B1, B2, G1, G2, and M1. Aflatoxin M1 is the metabolite of AFB1 from animal milk that consume contaminated feed (Ehrlich *et al*., 2005; Qureshi *et al*., 2015; Daou *et al*., 2021; Elkenany and Awad, 2021; Kibwana *et al*., 2023). Aflatoxin B1 and B2 are produced by *A. flavus,* whereas aflatoxins B1, B2, G1, and G2 are synthesized mostly by *A. parasiticus* (Adejumo and Adejoro, 2014; Agape *et al*., 2021). These toxins are excreted by around 24 species of the *Aspergillus* genus, which are divided into three sections *Ochraceorosei, Flavi*, and *Nidulantes* (Hussain *et al*., 2015) (Table 1). These species are capable of surviving within a wide range of environmental factors, including high temperature, high humidity, water activity, and slightly acidic soils (Tola and Kebede, 2016; Daou *et al*., 2021), though unpredicted rains can lead to pathogen propagation and production of aflatoxins. Separately from environmental factors, different cropping systems have also been reported to offer conducive environments to aflatoxins production in sub-Saharan African countries (Tédihou *et al*., 2012; Seetha *et al*., 2017; Njeru *et al*., 2019; Monda *et al*., 2020). Aflatoxin contamination in human and animals occurs when contaminated food and feed are consumed, and its effects can be acute and/or chronic, linked to liver cancer, immunosuppression, stunting growth, and death upon high-dose exposure (Tito *et al*., 2022). Thus, it is crucial to monitor and control the presence of aflatoxins in food and feed to prevent the harmful consequences they can cause (Fig. 1).

The biosynthesis of aflatoxin is a complex process that involves several enzymatic and regulatory steps (Šimončicová *et al*., 2017). Extensive research has been conducted on genes implicated in the biosynthesis of these aflatoxins, although the precise mechanism of action remains indefinable. The biosynthesis pathway comprises at least 27 enzymatic reactions, and the genes encoding these enzymes are clustered together (Cary *et al*., 2006). Two cluster-specific regulators, namely flR and aflS, regulate the synchronized expression of these genes. These discoveries (as reported by Ehrlich *et al*., 2004, 2005; Yu *et al*., 2004; Cary *et al*., 2006; Acur

Table 1. Aflatoxins- producing fungal species.

Section	Species	Types of toxins	Crops it infect	References
Flavi	*A. flavus*	B1, B2, G1, G1, M1	Maize, Groundnuts	Mili (2021)
	A. parasiticus	B1, B2, G1, G2	Maize, Groundnuts	Frisvad *et al*. (2019)
	A. novoparasiticus	B1, B2, G1, G1	Maize	Viaro *et al*. (2017)
	A. mottae	B1, B2, G1, G2	Cereals	Monda *et al*. (2020)
	A. Comenius	B1, B2, G1, G2	Wheat	Frisvad *et al*. (2019)
	A. Sergii	B1, B2, G1, G2	Cereals, oilseeds	Benkerroum (2020)
	A. pseudotamarii	B1, B2	Cereals	Ito *et al*. (2001)
	A. pseudocaelatus	B1, B2, G1, G2	Maize	Viaro *et al*. (2017)
	A. transmontanensis	B1, B2, G1, G2	Cereals	Benkerroum (2020)
	A. luteovirescens	B1, B2, G1, G2	Cereals	Frisvad *et al*. (2019)
	A. parvisclerotigenus	B1, B2, G1, G2	Peanut	Frisvad *et al*. (2019)
	A. minisclerotigenes	B1, B2, G1, G2	Groundnuts	Monda *et al*. (2020)
	A. arachidicola	B1, B2, G1, G2	Maize, Groundnuts	Viaro *et al*. (2017)
	A. austwickii	B1, B2, G1, G2	Cereals	Monda *et al*. (2020)
	A. aflatoxiformans	B1, B2, G1, G2	Cereals	Monda *et al*. (2020)
	A. pipericola	B1, B2, G1, G2	Cereals	Benkerroum (2020)
	A. cerealis	B1, B2, G1, G2	Cereals	Benkerroum (2020)
	A. Togoensis	B1, B2	cereals	Benkerroum (2020)
Nidulante	*A. astellatus*	B1	Cereals	Benkerroum (2020)
	A. miraensis	B1	Cereals	Benkerroum (2020)
	A. olivicola	B1	Cereals	Benkerroum (2020)
	A. venezuelensis	B1	Cereals	Benkerroum (2020)
Ochraceorosei	*A. rambellii*	B1	Cereals	Varga *et al*. (2009)
	A. ochraceoroseus	B1	Cereals	Varga *et al*. (2009)

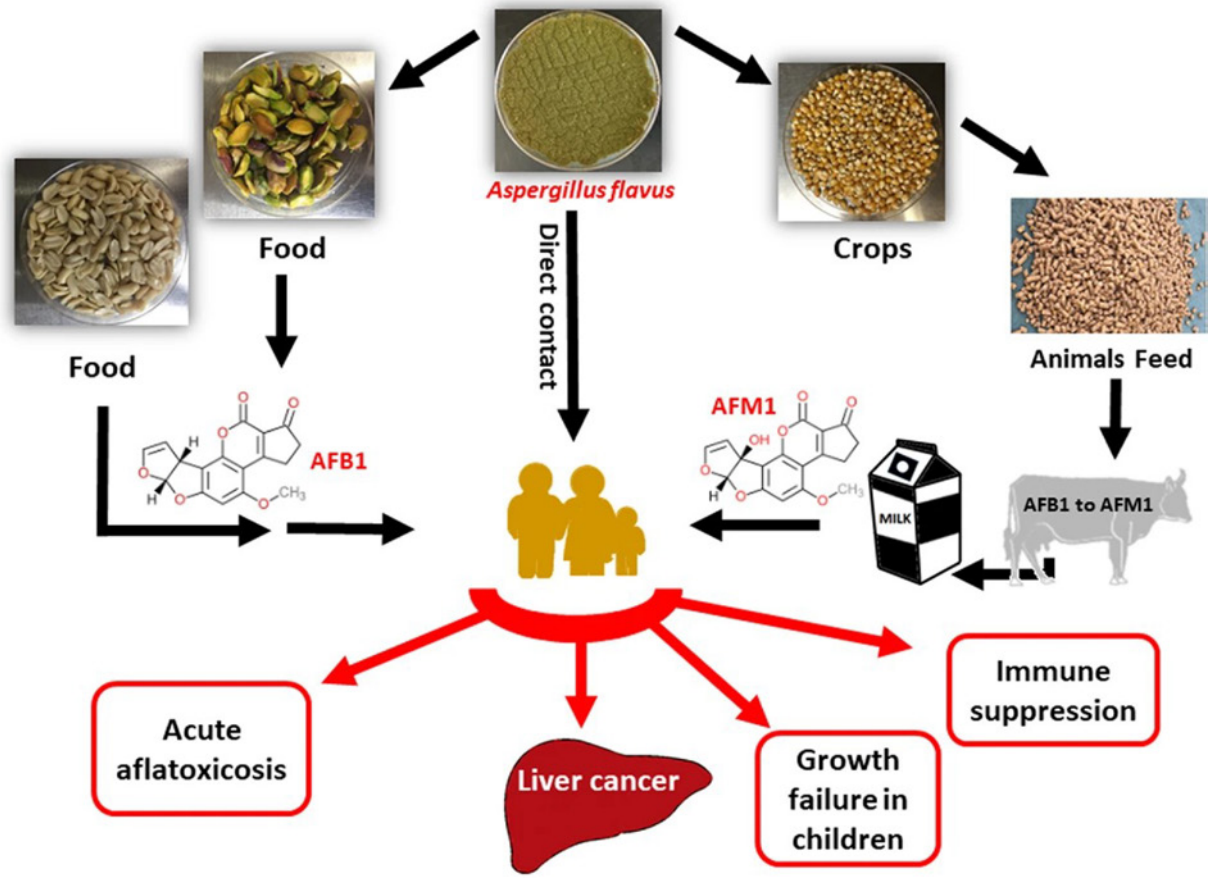

Fig. 1. Schematic presentation of the major AFB1 and AFM1 contamination/exposure routes and adverse health effects on humans and animals (Alshannaq *et al*., 2018).

et al., 2020; Caceres *et al*., 2020) shed light on the tricky back-and-forth between genetic regulation and biochemical processes essential for aflatoxin biosynthesis. This necessitates further research to fully comprehend its molecular underpinnings. Tropical SSA environments particularly in sub-Saharan African countries are known to have a significant impact on the production and prevalence of aflatoxins (Falade, 2019). The unique climatic and ecological factors in SSA create an environment that is highly conducive to the fungal growth and aflatoxin production (Manjula *et al*., 2009). These factors include but are not limited to high temperature (Temba *et al*., 2021), high humidity (Hell and Mutegi, 2011; Shehu and Bello, 2011), precipitation (Mirzabaev *et al*., 2023), host plant (Kamei and Watanabe, 2005; Cotty and Jaime-Garcia, 2007; Massomo, 2020), and biotic interaction (Fountain *et al*., 2014). Therefore, a comprehensive understanding of the relationship of various factors in tropical SSA settings is essential for devising effective strategies to mitigate aflatoxin contamination.

Among staple foods crops that strive well in the tropical environments, maize serves as a primary source of calories in sub-Saharan African countries. However, due to its biology and cropping systems, it is highly susceptible to aflatoxins contamination, which has severe implications for human and animal health and wellbeing (Kinyungu *et al*., 2019; Mutiga *et al*., 2019; Oppong *et al*., 2022). Studies have shown that countries where maize is grown in the region are particularly vulnerable to predisposing factors that accelerate and increase the risk of aflatoxins production and contamination (Gong *et al*., 2016). These factors include inadequate knowledge and skills on good agricultural practices, inappropriate storage, and favourable infection and growth conditions during harvesting, processing, transportation, and marketing (Wagacha and Muthomi, 2008; Kumar *et al*., 2021; Temba *et al*., 2021). The level of aflatoxins contamination in SSA varies depending on geographic location, farming practices, and vulnerability of the maize crop to the penetration of fungi in the field and/or during storage and processing (Shehu and Bello, 2011; Fountain *et al*., 2014; Njeru *et al*., 2019; Benkerroum, 2020; Olana, 2022). However, efforts for prevention and control of aflatoxin contamination in SSA are still not convincing due to the nature of the food production systems and technological infrastructures existing (Wagacha and Muthomi, 2008; Hell and Mutegi, 2011; Monda and Alakonya, 2016). Little is known based on the aflatoxins production environments and their implications for management in the maize cropping systems, which limits decision making support in both communities of practice and policy makers on the mitigation efforts. Thus, significance of the landscape of maize farming systems in SSA cannot be understated as it serves as a prerequisite to managing aflatoxin contamination. In order to establish best agricultural practices that ensure sustainable food production and reduced aflatoxin risks, appropriate considerations for aflatoxin accumulation in agroecosystems are decisive. In this regard, investments should be channelled towards the farms, and the adoption of the agroecosystem approaches (Fig. 2). Consequently, it is imperative that stakeholders in the agricultural sector prioritize research and development geared towards improving the management of aflatoxins in maize farming systems across SSA.

Review scope

In terms of spatial scope, this review covers the broad tropic region of SSA with a wide array of environmental settings and intensive anthropogenic activities accelerating high rates of change. The temporal scope opens with the early 1990s, a period characterized by lower impact human activities, low urbanization near farming

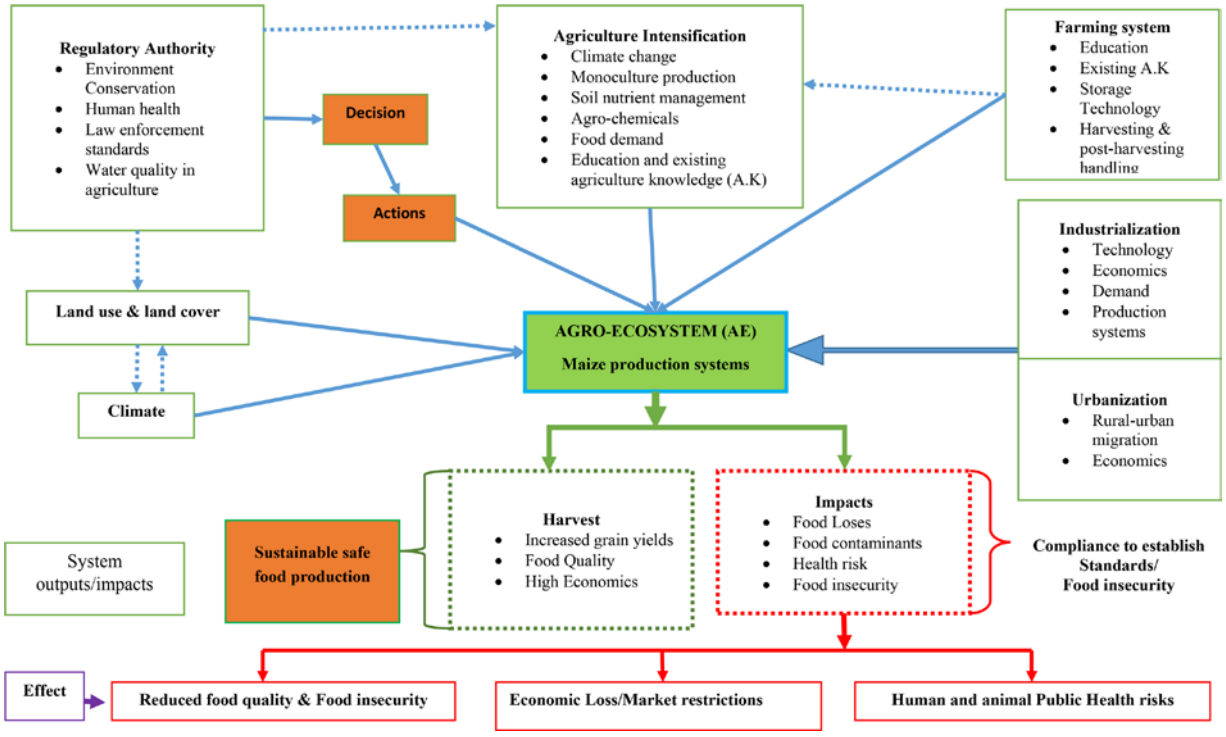

Fig. 2. Dissection of factors and drivers influencing aflatoxin accumulation in an agro-ecosystem. Bold words in a square are factors and bullets are drivers, the dotted box indicates expected system output/impacts; dotted line shows the indirect or partial influence of a factor to agro-ecosystem or other factors/driver; a solid line indicates direct influence/effect to agro-ecosystem). Adapted with modification from Mng'ong'o *et al.* (2021).

areas, high rainfall, and less cases of aflatoxin contamination reports. Then was followed around 2000 where the international maize trade increased dramatically, acceralating the exchange of maize materials in terms of seeds and products which intensified local to global connections exacerbating high food production, an increased area under cultivation but also increasing serious consideration of aflatoxin levels in maize and maize products in cross boarder trading. The SSA region is a center for food crop production, supplying even beyond its boarders, thus any food contamination to the produced grains might have detrimental effect not only in SSA but also in areas that depend on SSa as source of its food crops. At present, few effective management strategies operate to address aflatoxin contamination in maize, and other food crops and products due to an unclear unserstanding of the problem. This novel and systematic review of the SSA maize farming system aim to characterize aflatoxin-producing strains population dynamics in the tropics, and their implications on the agricultural management and public consumer health and to establish best agronomic practices and management systems to ensure sustainable food production key knowledge gaps, and recommendations for sustainable safe food production in the context of the UN Sustainable Development Goals.

Review methodology

This review was completed through a thorough search of available literature, including peer-reviewed publications and reports of ongoing studies on aflatoxin-producing strains population dynamics in the tropics, and their implications on the agricultural management and public consumer health. The magnitude, genetic diversity, adaptation of aflatoxin-producing fungi, food contamination concerns as well as impacts on consumer health and food and nutrition security. The study further explored alternative mitigation measures to be employed to inform the policy and practice to reduce aflatoxin contamination in SSA mainly in maize farming systems in SSA and other parts of the world from the 1990s to the present. Data from Science Direct, Web of Science, and other internet sources were gathered using specific keywords such as Mycotoxins, *Aspergillus, Aflatoxigenic, Aflatoxins, Food security, consumer health, and Mitigation*, genetic diversity, adaptation of aflatoxin–producing fungi, and food contamination. Also, the search included university student dissertations and government reports as grey literature from professional colleagues working in the region. Later on, the search query was narrowed down towards a new precise definition concerning aflatoxin–producing fungi and aflatoxins. Studies from different countries in the region were compared with the current status of the entire SSA to raise awareness of the aflatoxin health and economic risks on the food system.

Colonization and fungal infection mechanisms in maize

MAIZE-FUNGAL INTERACTION AND AFLATOXIN PRODUCTION

The interaction between aflatoxin-producing fungi, *A. flavus* and *A. parasiticus* with maize plays a crucial role in contaminating maize plant with aflatoxins. The process is influenced by various environmental, genetic, and physiological factors of the maize crop (Fountain *et al*., 2014; Daou *et al*., 2021; Jallow *et al*., 2021) during pre- and post-harvest practices (Shabeer *et al*., 2022). Maize-fungal colonization and toxin production starting in the field and post-harvest stages (Udomkun *et al*., 2017; Mahuku *et al*., 2019; Peles *et al*., 2021). During colonization, asexual conidia are dispersed by wind, water, and insects to the host maize plant entry points, which are either silk, tassels, and /or wounded points (Daou *et al*., 2021) (Fig. 3). On landing to the entry point of the susceptible maize plant under favourable conditions, the conidia germinate and penetrate the host cells (Mehl and Cotty, 2011; Mutiga *et al*., 2019). For a successful penetration of the conidia, there should be host-specific biochemical signals involved to trigger and establish the infection in the maize plant tissues (Soni *et al*., 2020).

Aflatoxin-producing fungi cell wall-degrading enzymes like pectinases and cellulases help them during maize host tissue penetration and then engage in competitive interactions with other microorganisms in the host environment (Fountain *et al*., 2014).

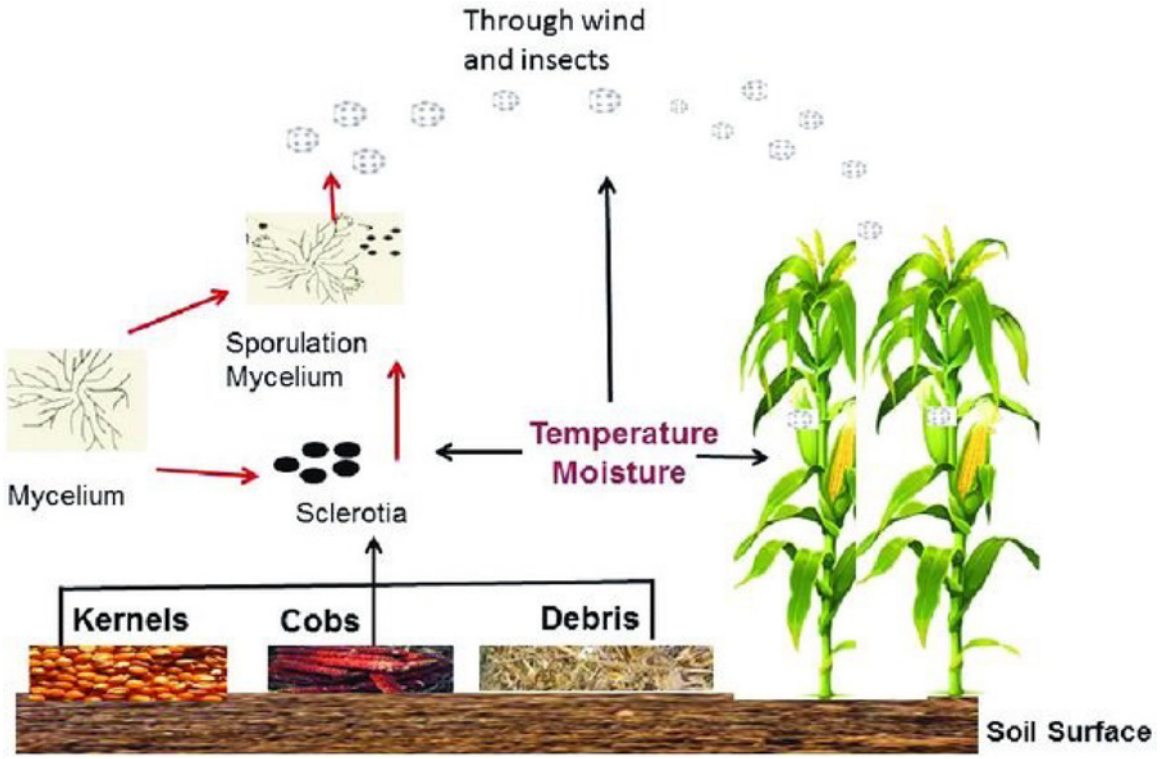

Fig. 3. Life cycle of *A. flavus* in the farm field with infection initiated through silk channel (Horn, 2003).

Successful penetration secretes secondary metabolites and antimicrobial compounds to gain a competitive advantage against maize host plant (Nasser Zohri *et al*., 2017). After the invasion by the fungal, the maize host plant activates the defences mechanism including antifungal compounds, activation of immune-related genes, and localized cell death upon recognizing the presence of the pathogen (Udomkun *et al*., 2017). Aflatoxin-producing fungi colonization and toxin production are influenced by host maize genotype temperature and humidity (Abbas *et al*., 2009). This maize-fungal interaction process implies complex processes linking a combination of physical, chemical, and genetic factors (Ojiambo *et al*., 2018). Thus, control options for both fungal colonization and aflatoxins contamination may need an integrated approach that includes a cultural approach such as fertilizer application, crop rotation, host resistant varieties (Manoza *et al*., 2017; Peles *et al*., 2021) and a biological approach such as the use of biological agents (Abdallah *et al*., 2019).

LIFECYCLE AND SPORE DISSEMINATION OF AFLATOXIN-PRODUCING FUNGI

The knowledge on the lifecycle of *A. flavus* and *A. parasticus* fungus is extreme important in devising effective control strategies to mitigate the risk of aflatoxin contamination in maize crops. This encompasses several critical stages, from spore germination to the synthesis of aflatoxins (Abdallah *et al*., 2019). The lifecycle begins with the release of asexual spores (conidia) from conidiophores that are dispersed into the environment through air currents, water, and other various vectors such as insects and animals (Horn, 2003). Upon landing on a suitable substrate, conidia germinate, producing germ tubes that penetrate the host tissue. The fungus grows and colonizes the host tissue, forming a network of hyphae (Fig. 3). Under favourable conditions, the fungi produce secondary metabolites such as aflatoxins. Thus, sorting out the complexities of this lifecycle is crucial for executing sound and evidence-based measures to combat the detrimental effects of aflatoxin exposure on human and animal health, agriculture, and food security.

Aflatoxins biosynthesis mechanisms

The genetic regulation of biosynthetic pathways in aflatoxin-producing fungi is a complex process that involves the interaction of several components (Cary *et al*., 2006). It has been extensively studied; and recent investigations indicate that it requires about 30 genes (Fig. 4) arranged in 75 kilobytes (kB) of gene clusters (Khan *et al*., 2021). The process also consists of a sequence of about 13 enzymatic reactions starting with a fatty acid synthase-hexanoate and transcription factors (Caceres *et al*., 2020). Among these, transcription factors and structural genes such as polyketides and non-ribosomal peptides play a crucial role in the biosynthesis of secondary metabolites (Table 2). Specifically, these gene clusters are controlled by specific transcription factors, including regulatory genes, which regulate the expression of structural genes responsible for enzymatic steps, including polyketide synthases (PKSs) and non-ribosomal peptide synthetases (NRPSs). These components are critical for the biosynthesis of secondary metabolites within the Aflatoxin-producing fungi (Okoth *et al*., 2018; Yu *et al*., 2005).

Aflatoxin biosynthesis processes are influenced by environmental factors such as temperature, oxygen levels, humidity, and nutrient availability in the substrate (Yabe and Nakajima, 2011; Kizis *et al*., 2014; Bandyopadhyay *et al*., 2016; Negash, 2018; Mahuku *et al*., 2019). However, it has been reported that not all *Aspergillus* species produce aflatoxins, as well as not all species invade the same types of crops portraying a level of specificity among various species (Jallow *et al*., 2021). In addition to other causal factors either singly and/or in their interactions, the levels and severity of attack are largely determined by the fungal ecology (Cotty and Mellon, 2006).

Toxin precursors undergo a series of chemical conversions to yield aflatoxins B1, B2, G1, and G2 (Fig. 4) each with unique toxicological properties (Benkerroum, 2020; Makhuvele *et al*., 2020; Daou *et al*., 2021; Habschied *et al*., 2021). Thus, understanding the genetic and environmental factors is critical. The biosynthesis process involves three critical oxygen elements, whereby (i) Monooxygenases: responsible for incorporating one oxygen atom while another is being reduced, with nicotinamide adenine dinucleotide phosphate

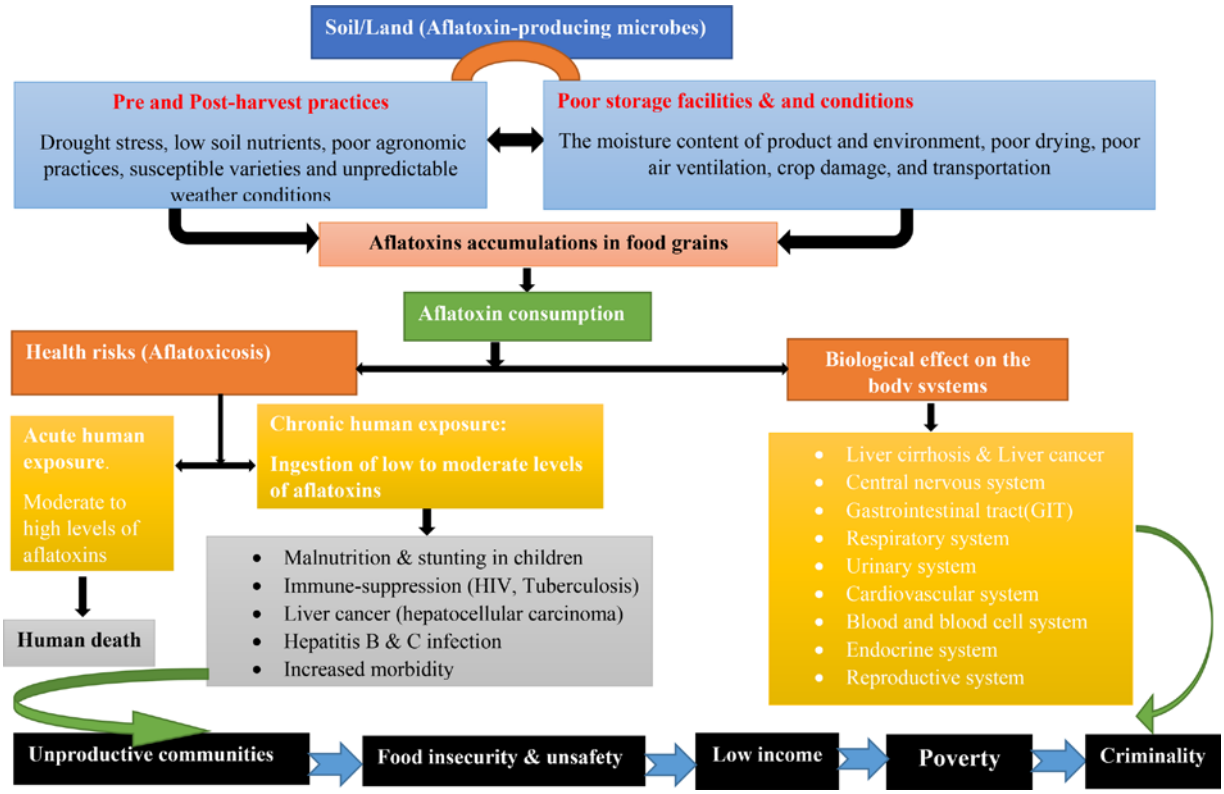

Fig. 4. Aflatoxicosis pathways in humans: showing the source, causes, and effects of contamination in tropical food crops. Adopted and modified from (Liu *et al*., 2012; Mutiga *et al*., 2019).

Table 2. Aflatoxins biosynthesis genes and intermediates adopted from (Yu *et al*., 2004).

Gene	Enzyme involved	Product of reaction
*Afl*A	Fatty acid synthase α	Polyketide backbone from acetate
*afl*B	Fatty acid synthase β	Polyketide backbone from acetate
*afl*C	Polyketide synthase	Polyketide
*afl*D	Reductase	Averantin
*afl*E	Norsolorinic acid reductase	Averantin
*afl*F	Dehydrogenase	Averantin
*afl*G	P450 monooxygenase	5´-Hydroxyaverantin
*afl*H	Alcohol dehydrogenase	Averufin
*afl*I	Oxidase	Versiconal hemiacetal acetate
*afl*J	Esterase	Versiconal
*afl*K	Versicolorin B synthase	Versicolorin B
*afl*L	Desaturase	Versicolorin A
*Afl*M	Dehydrogenase	Demethylsterigmatocystin
*afl*N	Monooxygenase	Demethylsterigmatocystin
*afl*O	O-methyltransferase B	Sterigmatocystin, Dihydrosterigmatocystin
*afl*P	O-methyltransferase A	O-methyl sterigmatocystin, Dihydro-O-methyl sterigmatocystin
*afl*Q	Oxidoreductase	AFB1, AFB2, AFG1, AFG2

(NADPH) acting as a cofactor. (ii) Dioxygenases: involved in ring-cleavage reactions. (iii) Baeyer-Villiger reactions: responsible for inserting oxygen atoms between two carbons (Caceres *et al*., 2020). Figure 5 shows the various intermediates in the biosynthesis of aflatoxin as well as the genes present in the aflatoxins gene cluster responsible for encoding the enzymes for their synthesis. The specific characteristics and interventions of the genes participating in the aflatoxin biosynthesis pathway are presented in four steps. These steps include norsoloric acid, versicolorin A, sterigmatocystin and finally, aflatoxins production.

Regulatory factors influencing aflatoxins biosynthesis in tropical environments

The production of aflatoxins varies across different fungal species and is influenced by a range of ecological and genetic factors (Cotty and Jaime-Garcia, 2007; Caceres *et al*., 2020; Monda *et al*., 2020; Daou *et al*., 2021). Research suggests that climatic conditions and genetic variability within aflatoxigenic populations play significant

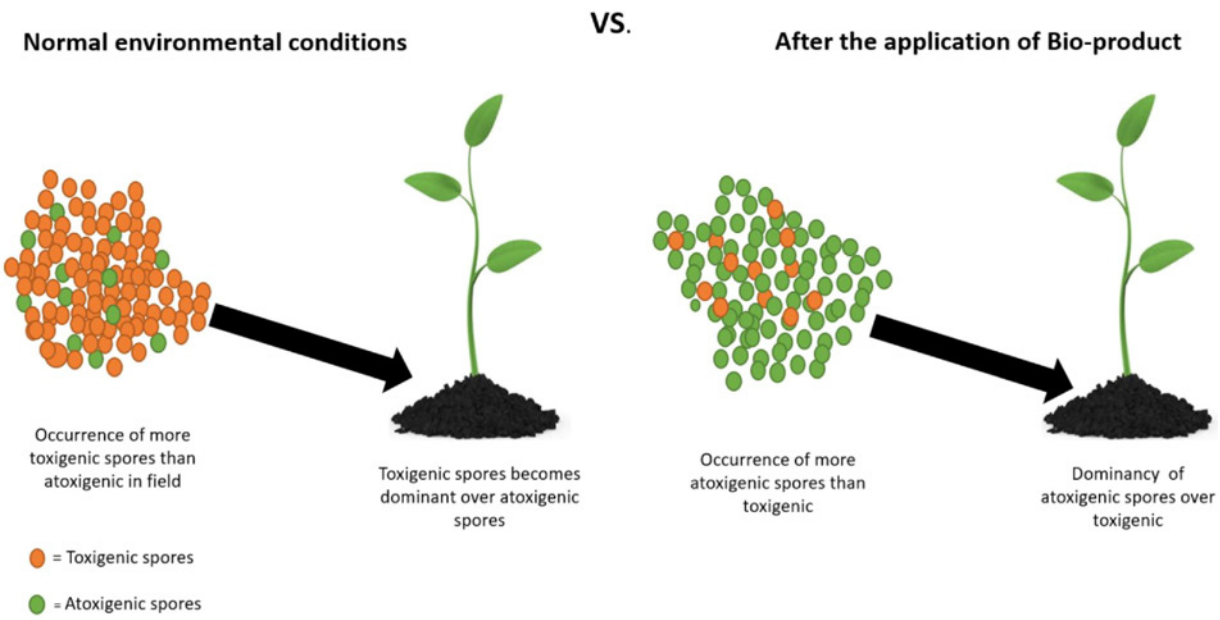

Fig. 5. Schematic illustration of the principle of biocontrol pesticides. During normal environmental conditions, usually, ratios of toxigenic spores are higher than the atoxigenic spores present in the field. After the application of bio-pesticide, the atoxigenic spores are increased and competitively exclude naturally occurring toxigenic strains (Shabeer *et al*., 2022).

roles in shaping the ability of fungal species to produce aflatoxins. Ecological interactions between species have also been found to contribute to the production of aflatoxins, with non-toxigenic strains demonstrating the ability to inhibit the survival of aflatoxigenic *A. flavus* through nutrient competitive exclusion (Jaime-Garcia and Cotty, 2006; Mehl and Cotty, 2010, 2011; Solorzano *et al*., 2014). These findings underscore the complexity of the factors that influence the production of aflatoxins by fungal species and highlight the need for further research in this area.

HOST PLANT FACTORS

Maize varieties exhibit varying levels of susceptibility to *Aspergillus* fungal infection and aflatoxin contamination. This highlights the importance of breeding for resistance and selecting resistant cultivars as a key regulatory factor in aflatoxin management. However, interactions with other organisms such as plant host pathogens are still unknown (Yabe and Nakajima, 2011). The type of crop and its composition, such as moisture content during harvesting and/or storage, together with nutrient availability, encourage fungal attacks, ultimately aflatoxins production (Tédihou *et al*., 2012; Ojiambo *et al*., 2018; Mutiga *et al*., 2019). Therefore, it is crucial to continue exploring these factors to better understand and effectively manage aflatoxin contamination in maize crops.

The cultivation of susceptible crops, such as maize and groundnuts, in SSA countries provides favourable conditions for the growth and toxin production. Additionally, crop debris serves as a potential source of carryover inoculum for subsequent crops, further exacerbating the issue. In light of this, microbial interactions, including those involving bacteria and atoxigenic species, have been identified as potential stimulants of toxin production. Furthermore, genetic mutations, additions, displacements, and deletions have been shown to affect the ability to produce aflatoxins among species, due to the presence of specific genes involved in aflatoxins biosynthesis. These findings have been documented in various studies, including Bandyopadhyay *et al*. (2016); Fountain *et al*. (2014); Kachapulula *et al*. (2017); Mahuku *et al*. (2023); Nasser Zohri *et al*. (2017); Soni *et al*. (2020), and among others.

ENVIRONMENTAL FACTORS

Temperature

Aflatoxin production is influenced by temperature, with optimal conditions ranging from 25 to 35°C. Seasonal variations with high temperatures (30–38°C) promote the growth of *A. flavus* and *A. parasiticus,* the major species for aflatoxin production (Jaime-Garcia and Cotty, 2010; Mohale *et al*., 2013; Temba *et al*., 2021). Yet, physiological stress such as drought stress on maize plants enhances susceptibility and vulnerability to fungal infection, intensifying aflatoxin production. Therefore, any alteration on the temperature and physiological stress may reduce aflatoxin production.

Humidity

Elevated humidity of 80 to 90% during crop development and post-harvest storage favours fungal growth and development, eventually leading to toxin production. However, moist conditions create an environment conducive to spore germination and aflatoxin production, this makes the tropics a good environment for aflatoxins production (Hell and Mutegi, 2011; Shehu and Bello, 2011). To control this, processing practices such as drying, sorting, packaging and storage of maize and maize products must be observed and maintained.

Climate change and variability (rainfall pattern)

Hot and dry conditions encourage fungi spores to be airborne which increases their chances of contaminating crops. Adequate or excessive rainfall during the growing season leads to stress on the maize crop, creating entry points for fungal infection and subsequent aflatoxin production (Temba *et al*., 2021). Weather changes alter the geographical distribution of *A. flavus* which may increase or decrease the prevalence of the pathogen, thus, impacting the timing and severity of aflatoxins contamination. Understanding the relationship between climate change and aflatoxin production is crucial for food safety and sustainable agriculture.

INSECT PESTS

Insects, birds, and other factors causing physical damage to maize create entry points for *Aspergillus* spores. For instance; insect pests particularly maize earworm *Lumbricus spp.* and sap beetles are known to cause damage that creates channels that act as entry points for fungal infection (Hell and Mutegi, 2011; Tédihou *et al*., 2012); thus, controlling some insect pest attack may reduce *A. flavus* colonization and aflatoxins contamination since fungi colonize the damaged tissue, initiating the infection process.

CHARACTERISTICS

Aflatoxin production is influenced by soil pH, with optimal conditions often found in slightly acidic to neutral soils. The pH of the substrate has a significant impact on *A. flavus* growth and aflatoxins production (Amaike and Keller, 2011; Fountain *et al*., 2014). Yet, contaminated soil and crop management practices, including irrigation, fertilization, and plant density, influence *A. flavus* growth and aflatoxins contamination (Manjula *et al*., 2009; Mutiga *et al*., 2019; Daou *et al*., 2021). Nutrient imbalances in soil nutrients, particularly excessive nitrogen, can contribute to increased susceptibility of maize crops to *Aspergillus* infection (Manoza *et al*., 2017). Thus, pre-harvest practices in the maize cropping systems remain key in reducing aflatoxin contamination levels. Generally, aflatoxins biosynthesis is highly influenced by a multifaceted complex, iterating biophysical and agronomic dynamics. Managing these factors is essential for reducing contamination in susceptible crops, especially effective interventions encompass pre-harvest measures, such as crop management practices, and post-harvest strategies, including proper storage and processing techniques. From these influencing factors, peasantry in the maize cropping systems, ecological perturbations, poverty, and farmers' limited access to information, knowledge, inputs, lifestyle, and feeding habits are among the factors that make aflatoxins endemic in SSA. Thus, suggest a key entry point in the problem tree to manage aflatoxin contamination sustainably and effectively.

Significance and impact of aflatoxins contamination on food safety, security, economic loss and consumer health

SSA region is characterized by high levels of food insecurity and malnutrition, despite comprising a significant portion of the world's productive land area (Adeyeye, 2016; Eskola *et al*., 2019; Adeyeye and Ashaolu, 2021). According to the Food and Agriculture Organization (FAO), reported food contamination by mycotoxins is about 25% of all crops produced worldwide, whereby aflatoxins contamination plays a large part (HLPE, 2014; Eskola *et al*., 2019), exacerbating the insufficiency of food safety and food loss in terms of quantity, quality, nutritional; hence, influencing food systems, health, and overall well-being. Evidence of food contamination has been reported worldwide, especially in SSA countries like Tanzania, Uganda, Nigeria, Benin, Ethiopia, Kenya, and many others (Kaaya, 2005; Norlia *et al*., 2019; Benkerroum, 2020; Mtega *et al*., 2020; Adeyeye and Ashaolu, 2021). Although more attempts to increase food production in the SSA countries have been expanded (Udomkun *et al*., 2017), the supreme goal remains on aflatoxins-free food and feed production (Negash, 2018; Gichohi-Wainaina *et al*., 2023), because it poses a grave threat to food safety. Ingesting aflatoxin-contaminated food leads to acute and chronic health issues. Vulnerable populations, including children and immunocompromised individuals, suffer disproportionately. However, public health campaigns must raise awareness about aflatoxin risks and promote safe food practices. Contaminated crops result in reduced market value, trade restrictions, and lost revenue. Therefore, based on risks associated with aflatoxins contamination, plans would promote farm investment and the adoption of novel agricultural techniques, leading to increased environmental sustainability, reduced hunger and malnutrition, rural development, economic stability, social stability, and poverty reduction, as well as improved health and well-being and resilience to biophysical stresses (Fig. 5). Integrated approaches that address both crop and livestock sectors are vital for sustainable livelihoods. This must be employed to address aflatoxin contamination, ranging from post-harvest management and agricultural practices to consumer education and compliance with regulations. This would support food systems, safeguard human and animal health, as well as build resilient communities to ward off this silent menace.

Mitigating aflatoxins contamination in SSA

Inhibiting the growth of aflatoxin-producing fungi, particularly *A. flavus* and *A. parasiticus,* is vital to prevent and control the contamination of food crops and animal feeds with aflatoxins. Various agricultural-based techniques have been advocated, such as timely planting, use of resistant crop varieties, best crop management practices, irrigation, insect pest control, crop rotation, proper soil fertility management techniques, timely harvesting, and appropriate post-harvest practices (Jallow *et al*., 2021). However, post-harvest strategies involve proper drying to the required product moisture content, good sorting, grading, and packing, recommended storage ambient conditions (i.e. humidity and temperatures), and enough ventilation have been proven as basic effective aflatoxins preventive measures (Klich, 2007; Das and Oliveira, 2017; Udomkun *et al*., 2017; Mahuku *et al*., 2019; Safari *et al*., 2020; Soni *et al*., 2020). Generally, effective preventive interventions are the first line of defence against the risks of food contaminated with aflatoxins. However, various interventions, including physical, biological, and chemical means, have been recommended to degrade, detoxify, or remove aflatoxins from already-contaminated foods. Each intervention possesses its benefits and drawbacks suggesting that no single method could solve the problem alone (Agric, 2022).

PHYSICAL CONTROL

Physical techniques involve density segregation, irradiation, mechanical sorting, heat inactivation, steaming, boiling, and washing or thermal treatment to kill fungal pathogens that may lead to aflatoxin production (Sipos *et al*., 2021). Although aflatoxins are resistant to heat treatments, dried fruits, and nuts have reportedly been successfully decontaminated using heat (Cheng *et al*., 2016). For instance, roasting almonds at 200°C effectively lowers the quantity of aflatoxins accumulated. Ultraviolet light and ionization are used to break fungal cell walls, ultimately inhibiting fungal growth and limiting aflatoxins contamination (Xu *et al*., 2013; Tahir *et al*., 2018). Sipos *et al*. (2021) reveal a reduction of aflatoxins concentrations by 9–39% using thermal treatments, but this depends on the treatment and the commodity being treated. For example, autoclaving fruits and other species for 30 min at 120°C could reduce aflatoxins (Al-Meamar *et al*., 2017), on the other hand, autoclaving peanuts for 90 min at 1.5 atm may reduce aflatoxins by up to 100% (Xu *et al*., 2013). The use of gamma rays effectively reduces aflatoxin contamination in fruits and vegetables by up to 60%. There have been other methods employed as well, like treating aflatoxins with an adsorbent (Assaf *et al*., 2019). The use of sorbents, clays, and activated carbons may help detoxify food items containing aflatoxins, such as B1 and G1 (Falade, 2019). A variety of inorganic substances and their by-products, including silicates, bentonite, zeolite, hydrated sodium calcium aluminium silicates, and phyllosilicates, have also been reported to be effective aflatoxins detoxifiers (Yin *et al*., 2008; Xu *et al*., 2013). Nevertheless, techniques like sorting, handpicking, and floating

are effective but only appropriate for small-scale applications that match most of the crop producers and processors at household and aggregate levels in SSA.

BIOLOGICAL CONTROL

By using naturally occurring atoxigenic strains through competitive exclusion, aflatoxins could be effectively controlled in the field (Table 3). Many organisms have been screened for their suitability as aflatoxins bio-control agents, including atoxigenic *Aspergillus* fungi (Cotty, 1990; Kinyungu *et al*., 2019; Mfaume, 2019; Peles *et al*., 2021; Xu *et al*., 2021). Proven methods have been obtained from research investments, including the complete exclusion of toxigenic fungal strains from survival in the field, preventing growth, colonization, and eventually inhibition of aflatoxins production (Mwakinyali *et al*., 2019). This intervention has been successfully commercialized in West and East African countries as Aflasafe (Plateaux *et al*., 2014; Massomo, 2020; Jallow *et al*., 2021) and in the United States as Aflaguards (Abbas *et al*., 2009). Although product formulation, inoculation rate, application time in the field, and site specificity are still determinant factors to realize full success. The diversity and genetic complexity with the ability to exchange genetic materials, mutations, deletions, and being site-specific, could be enabling to development of aflatoxins production capacity (Ren *et al*., 2020a).

CHEMICAL CONTROL

The ability of several chemical products to degrade and detoxify aflatoxins has been explored (Yang, 2020). The method, among other chemical products, includes oxidizing agents, reducing agents, acids, and bases. Ammonia treatment is widely utilized and has frequently been reported with high degradation rates (Weng *et al*., 1994). However, the method has challenging concerns, especially on the residual effects of environmental issues, food safety, food quality, and trade. In this regard, popularizing and deploying the technology that could detect and estimate both aflatoxins concentration and residual chemical effects, becomes relevant in SSA. Other chemical methods are proven by studies to control aflatoxins in the food and feed systems. Citric acid and lactic acid are more effective in controlling aflatoxins than other acids, with inhibition rates of up to 92% and 67%, respectively (Ghanbari *et al*., 2018). Other organic and inorganic acids that have been tested include tartaric acid, propionic acid, citric acid, and hydrochloric acid. Aflatoxin control can be achieved with sodium bisulfide at varying rates, contingent on the method employed (Hell and Mutegi, 2011). For example, applying 0.2% H_2O_2 for 10 min before applying sodium bisulfide is possible to 65% control rate; applying 45°C heat for up to 1 h after applying sodium bisulfide can achieve a 48% control rate; and applying 65°C heat can achieve a 68% control rate.

Ozone and chitosan nanoparticles have also been successfully used in some experiments to lower aflatoxins concentration. Other fruit derivatives that can be employed to stop the development of aflatoxins include hexane and chloroform. *A. flavus* was suppressed by antioxidants, such as propylparaben, butylated hydroxyanisole, and butylated hydroxytoluene, which resulted in a decrease in aflatoxins contamination (Ghanbari *et al*., 2018; Sipos *et al*., 2021). Adsorbents such as zeolites, activated charcoal, complex carbohydrates (polysaccharides, cellulose, etc.), activated charcoal, aluminous (clay, yeast, bentonite, diatomaceous earth, etc.), and active carbon can be employed to reduce aflatoxins contamination (Tahir *et al*., 2018).

Nixtamalization, a traditional alkaline cooking method widely practiced in Latin America, has shown high efficacy in reducing

Table 3. Global status of development and use of aflatoxins control bio-pesticides.

S. No	Product/strain name	Country
1.	AF36	The U.S.
2.	Afla-Guard(strain NRRL21882)	The U.S.
3.	CT3 (unregistered)	Southern U.S.
4.	K49 (unregistered)	Southern U.S.
5.	AF-X1	Italy
6.	Aflasafe SN01	Senegal and The Gambia
7.	Aflasafe GH01	Ghana
8.	Aflasafe GH02	Ghana
9.	Aflasafe	Nigeria
10.	Aflasafe KE01	Kenya
11.	AR27 (unregistered)	Northern Argentina
12.	AR100G (unregistered)	Northern Argentina
13.	AFCHG2 (unregistered)	Northern Argentina
14.	FS10 (unregistered)	China
15.	AF051 (unregistered)	China
16.	BN30 (unregistered)	Africa
17.	Aflasafe BF01	Burkina Faso
18.	Aflasafe TZ01	Tanzania
19.	Aflasafe TZ02	Tanzania
20.	Aflasafe ZM01 & ZM02	Zambia
21.	Aflasafe MW01 & MWMZ01	Malawi
22.	Aflasafe MZ01 & MWMZ01	Mozambique

Adapted and modified from: Ren *et al*. (2020b); Mahuku *et al*. (2023).

aflatoxin levels in maize. This process involves boiling maize in a lime solution (calcium hydroxide), steeping, and washing, which leads to the degradation of aflatoxin B1 into less toxic compounds like aflatoxin D1. Studies have reported reductions exceeding 90%, making it a promising chemical control technique. However, its adoption in African settings remains limited due to differences in culinary practices and cultural acceptability. Nonetheless, its scalability in institutional feeding or food processing industries could offer potential for aflatoxin risk mitigation in maize-based diets.

PLANT BREEDING TECHNIQUES

Plant breeding is currently deployed to manage fungal growth and aflatoxins production (Mahato *et al*., 2019, 2021). The technique involves the development of resistant crop varieties to aflatoxins contamination. Nonetheless, there are still no commercially viable cultivars that are resistant to the aflatoxins though real research progress has been made to study host genes involved in resistance in peanut crops (Nigam *et al*., 2009) and maize crops (Warburton and Williams, 2014). Fast-tracked approaches for host plant resistance such as molecular breeding techniques such as proteomics, genomics, transcriptomics, quantitative trait loci (QTLs), and Genome-Wide Association Studies (GWAS), are being applied to identify resistant traits in maize (Brown *et al*., 2003; Nigam *et al*., 2009; Oppong *et al*., 2022). However, aflatoxin resistance and grain yield are negatively correlated, which suggests using techniques that would take advantage of win-win and trade-off cases.

Developing and using aflatoxins-resistant varieties are much more difficult in SSA. In addition to the interaction of biophysical stresses in tropical areas the R&D and regulation systems in SSA complicate the use and benefit of host plant resistance by farming communities. Some of the present challenges include investments in research, testing, regulatory processes, and political will. Yet, resistant varieties are recognized as a sustainable solution to aflatoxins management, integrating different mitigation efforts that are compatible is suggested.

USE OF PLANT EXTRACTS

Plant extracts are proven measures to manage aflatoxin contamination in agricultural products (Kumar *et al*., 2017). The inhibition of *A. flavus* and the synthesis of aflatoxins is effectively suppressed by bio-active plant chemical extracts such as carvacrol, cinnamaldehyde, eugenol, limonene, terpineol, and turmerone (Udomkun *et al*., 2017; Olana, 2022). The mechanisms involve tampering with the cell membrane and inhibiting cytoplasmic and mitochondrial proteins. This helps impair the fungal ability to secrete enzymes necessary for the synthesis of cell wall components, weakening its ergosterol metabolism, and causing ultra-structural changes in cell compartments (Loi *et al*., 2020). However, plant extracts could be a limitation in their application due to their instability, volatility, availability, and means of preparation together with other environmental issues. Worth noting, plant extract methods are believed to be less aggressive, more specific, environment-friendly, and cost-effective compared to other methods of detoxifying aflatoxins.

USE OF MICRO-ORGANISMS

In addition to atoxigenic fungi to control aflatoxins, studies recommend other microorganisms. However, the non-fungal beneficial microbes are becoming popular as biocontrol agents. Yet elsewhere trials are underway to avail commercially available non-fungal agents that are specifically designed to control aflatoxins. If this innovation succeeds, it will widen the scope of managing aflatoxins as currently, many studies demonstrate that most bio-fungicides aflatoxins have a limited span of active control. Nevertheless, issues with ecological balance vs aflatoxins control would attract more studies.

USE OF YEASTS SPP.

Several yeast strains have been reported to exhibit a considerable reduction in aflatoxins generation and *Aspergillus* spp. Growth and development, including *Candida maltose*, *Pichia anomala, Debaryomyces hansenii* strains, *D. hansenii* (native yeast), *Kluyveromyces* spp., and *Saccharomyces cerevisiae* (Ren *et al*., 2020b). *Trichoderma* spp. is thought to be a useful biocontrol agent for a variety of fungal species. It has been discovered that *T. harzianum* and *T. viridae* are the most efficient species of *Trichoderma* against aflatoxins, with an inhibition rate of over 80%. Studies indicate that aflatoxins levels were also halved by two other species, *T. longibrachiatum* and *T. auroviride*. Additionally, it was noted that, *Trichoderma* spp. effectively decreased the aflatoxins contamination in sweet corn and groundnuts by up to 65% and 57%, respectively (Alshannaq *et al*., 2018; Mahato *et al*., 2019; Shabeer *et al*., 2022; Mahuku *et al*., 2023). *Penicillium* spp inhibits the growth of toxic *Aspergillus* strains. In a similar vein, *P. nalgiovense* is regarded as a common biocontrol agent against a wide variety of plants, pathogenic fungi, and the secondary metabolites that they produce.

USE OF BACTERIA SPP.

Numerous bacterial species have demonstrated effective *in vitro* prevention of aflatoxins formation by preventing *Aspergillus* spp. from growing. These bacteria include various strains of *Bacillus*, *Pseudomonas*, *Ralstonia*, *Burkholderia*, *Streptomyces*, and *Lactobacilli* (Table 4).

Integrated aflatoxin management strategies in maize cropping systems

Based on the nature and mechanisms of aflatoxin production, effective management requires more than a single intervention, as contamination can occurs at multiple points along the production and supply chain of maize. Integrated Aflatoxin Management (IAM) strategies offer a holistic and coordinated approach by combining preventive and control measures from pre-harvest to post-harvest, storage, processing, and policy enforcement. Pre-harvest interventions include the use of aflatoxin-resistant maize varieties (Massomo, 2020; Soni *et al*., 2020; Oppong *et al*., 2022), crop rotation (Wang *et al*., 2023), timely planting (Hell and Mutegi, 2011), and proper fertilization (Hell and Mutegi, 2011). Biological control using non-toxigenic strains of *Aspergillus flavus* (e.g., *Aflasafe*) has also proven effective in outcompeting aflatoxin-producing strains in the soil (Mahuku *et al*., 2023); drying maize to safe moisture levels (≤13%) immediately after harvest (Hell and Mutegi, 2011; Kortei *et al*., 2021), using hermetic bags (e.g., PICS bags) or metallic silos to protect maize from moisture, insects, and fungal contamination (Mutiga *et al*., 2019); processing and detoxification using binders or microbial enzymes that degrade or adsorb aflatoxins in animal feed or processed products (Abbas, 2019; Farghl *et al*., 2023); education and awareness through building farmers capacity and engaging local communities in participatory approaches (Hell and Mutegi, 2011; Kenngott *et al*., 2022). However, policy and regulation support would add value to implementation; this would include setting and enforcing standards on aflatoxin limits in food and feed systems. Generally, IAM is most effective when personalised to local agro-ecological and socio-economic perspectives, combining scientific evidence, field practical, and policy tools to safeguard health, food security, and trade.

Conclusions and recommendations

This review presents a complex interplay between environmental conditions, fungal biology, agricultural practices, and socio-economic factors with a focus on the development of effective management strategies to mitigate its occurrence. Aflatoxins, predominantly produced by *Aspergillus flavus* and *A. parasiticus*,

Table 4. Bacterial species with potential to control aflatoxins conidia growth and production.

	Description	References
Bacillus spp.	*Bacillus* species are the most researched pathogen in terms of aflatoxins management. *Bacillus megaterium* completely stopped the formation of aflatoxins in the broth medium. *B. subtilis* can suppress *A. parasiticus* development by up to 92% and the formation of aflatoxins by up to 100%. The most effective *Bacillus* species against aflatoxins contamination are thought to be *B. megaterium, B. subtilis*, *B. amyloliquefaciens, B. mojavensis, B. cereus, B. mycoides, and B. Pumilus*	Monda *et al*. (2020); Ren *et al*. (2020b); Kumar *et al*. (2021)
Pseudomonas spp.	The most common pathogenic group in soil is pseudomonas. Aflatoxins B1 was inhibited by *Pseudomonas fluorescens* in peanut medium by 99.4% and the germination of *A. flavus* conidia reduced 20. Several *P. chlororaphis* strains isolated from maize completely stopped *A. flavus* from growing. *P. protegens* strains isolated from rice grains may suppress aflatoxins by up to 82.5% and reduce *A. flavus* growth by 68.3%.	Abdallah *et al*. (2019); Monda *et al*. (2020); Kumar *et al*. (2021)
Lactobacillus spp.	*Lactobacillus* spp., also known as lactic acid bacteria (LAB), is a group of bacteria that produce lactic acid through fermentation. These bacteria are being widely used in food technology. In this group of bacteria, several species, such as *L. delbrueckii* subsp. *Lactis*, *L. reuteri*, *L. plantarum*, *L. acidophilus*, *L. paraplantarum*, *L. rhamnosus*, *L. fermentum*, *L. pentosus*, and *L. casei* have been reported to be effective against aflatoxinss	Ghanbari *et al*. (2018); Abdallah *et al*. (2019); Wang *et al*. (2023)
Streptomyces spp.	Some of the *Streptomyces* species, including *S. yanglinensis, S. anulatus, S. alboflavus,* and *S. roseolus*, showed very good results when used against aflatoxigenic fungi as biocontrol agents. A strain of *Streptomyces* is reported to have the capacity to completely control *Aspergillus flavus* growth and conidial production.	Abdallah *et al*. (2019)

are highly toxic and pose serious health risks, particularly in regions where maize is a dietary staple. Drought stress, insect damage, poor agronomic practices, and inadequate post-harvest handling influence their production. Despite increased awareness, aflatoxin contamination continues to hinder food security, trade, and public health efforts across the region. To effectively manage aflatoxins, a multi-pronged, integrated strategy are recommended. Pre-harvest control measures such as the use of resistant maize varieties, biological control agents (e.g., *Aflasafe*), and improved agronomic practices should be promoted. Post-harvest interventions, including timely harvesting, effective drying, grain sorting, and hermetic storage, are equally critical to reducing contamination. Chemical control methods, such as nixtamalization and innovative novel technologies like RNA interference and nanotechnology, also offer promising avenues for aflatoxin detoxification and prevention. Policy support and investment in research, infrastructure, and capacity building are essential to scale up these interventions. Governments, researchers, and development partners should collaborate to establish strong regulatory frameworks, support farmer education initiatives, and promote adoption of best practices at all levels of the maize value chain. With coordinated and sustained efforts, it is possible to significantly reduce aflatoxin risks and ensure safer, more productive maize systems in SSA countries. To achieve this, research efforts should focus on innovations in genomics, agronomy, and biotechnology to develop sustainable solutions for aflatoxin management. By doing so, we can ensure the safety and security of our food systems and improve public health outcomes.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in the paper.

ETHICS STATEMENT

Not applicable.

ACKNOWLEDGEMENTS

The authors wish to thank all collaborators at Nelson Mandela African Institution of Science and Technology (NM-AIST), Arusha, Tanzania, Department of Crop Science and Horticulture, College of Agricultural Sciences and Technology, Mbeya University of Science and Technology, Mbeya, Tanzania and Tanzania Agricultural Research Institute, Kilosa, Morogoro, Tanzania for their technical and guidance support during the development of this article.

AUTHOR CONTRIBUTIONS

OHK, MM, AM, MP, and EM contributed in conceptualization and methodology; OHK, MM, and AM performed writing original draft preparation; OHK, MM, AM, MP, and EM contributed in writing review and editing. All authors have read and agreed to the published version of the present manuscript.

FUNDING STATEMENT

This study was supported by the Government of United Republic of Tanzania, Through the Ministry of Agriculture under the Tanzania Initiative for Prevention of Aflatoxins Contamination (TANIPAC) project funded by African Developent Bank.

DATA AVAILABILITY

The datasets used and analyzed during the current study are available from the corresponding author upon request.

CONSENT TO PARTICIPATE

Not applicable.

CONSENT FOR PUBLICATION

Not applicable.

CODE AVAILABILITY

Not applicable.

Reference

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