



Postharvest control of mycotoxigenic phytopathogens in maize: Conventional methods and natural alternatives

Estefanía Martínez-Batista¹, Surelys Ramos-Bell¹, Edson Rayón-Díaz¹, Gerónimo Díaz-Cayetano¹, Cyndia González-Arias², Juan Antonio Herrera-González³, Javier Ireta-Moreno⁴, Porfirio Gutiérrez-Martínez^{1*}, ¹Instituto Tecnológico de Tepic, Laboratorio Integral de Investigación en Alimentos, Avenida Tecnológico 2595, Col. Lagos del Country, CP 63175, Tepic, Nayarit, México. ²Universidad Autónoma de Nayarit, Laboratorio de Contaminación y Toxicología Ambiental, Los Fresnos s/n., C.P. 63175, Tepic, Nayarit México. ³Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Campo experimental Uruapan, Av. Latinoamericana 1101, Col. Revolución, CP 60150, Uruapan, Michoacán, México, ⁴Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Campo experimental Centro Altos de Jalisco, CP 2470, Tepatitlán de Morelos, Jalisco, México.

***Corresponding Author:**
Porfirio Gutiérrez-Martínez
pgutierrez@itepic.edu.mx

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ABSTRACT

Justification. Seeds are the fundamental input for agriculture and food production. Recently, an increase in the demand for maize grain production has been observed; however, annual postharvest losses range between 10 and 40%. The objective of this review is to present the main mycotoxin-producing fungi (genera/species) associated with maize grain during storage, as well as to analyze the conventional control methods and natural alternatives that have been applied to date.

Theoretical and Experimental framework. Bibliographic information was compiled on the main fungal pathogens that develop in maize grain and the most commonly employed control methods. The principal fungal genera detected in maize grain are *Aspergillus*, *Penicillium* and *Fusarium*, all of which are important mycotoxin-producing fungi. Traditional physical and chemical control methods have been used; however, their application often fails to guarantee effectiveness and biosafety. The use of natural alternatives, as well as their combination, has shown positive effects in controlling these phytopathogens and inhibiting mycotoxin production.

Conclusions and Perspectives. One of the main causes of losses and quality deterioration in maize grain is the development of mycotoxin-producing fungi and, consequently, the generation of highly toxic secondary metabolites. To prevent the deterioration of store grain, traditional practices have been employed, such as grain cleaning, aeration at low temperatures, and the use of physical and chemical treatments (synthetic fungicides). Currently, the development of eco-friendly alternatives is one of the primary goals to reduce the use of agrochemicals on seeds and grains, in order to promote more sustainable agricultural systems.

Keywords: Maize, Fungi, Mycotoxins, Storage, Alternative control



INTRODUCTION

Maize (*Zea mays*) is the world's second most widely-grown cereal, with an annual production of 1,230,241 tons. Mexico is the eight largest producer, with a total of 24,000 tons (United States Department of Agriculture-USDA, 2024). In Mexico, maize is of great relevance, since it is the main agricultural cereal and an important component in the diets of people due to its large contribution of nutrients such as essential fatty acids, carbohydrates and proteins, mainly (United Nations Food and Agriculture Organization-FAOSTAT, 2023). Additionally, it is a prominent source of income due to the marketing of livestock feed, industrial products and biofuels.

After being harvested, maize is exposed to variable environmental conditions that jeopardize grain quality, from storage to food processing and production (Abdullahi and Dandago, 2021; Fleurat-Lessard, 2017). Losses in storage can be considerable and are usually caused by different factors such as physiological deterioration, mechanical damage, inadequate management and hygiene practices postharvest, as well as the presence of pests (Moumni *et al.*, 2023; Odjo *et al.*, 2022).

Grains constitute a favorable environment as a source of energy and a habitat for the colonization of heterotrophic organisms including fungi, bacteria, insects and mites. The main problem with the deterioration of stored maize grains is usually insect attacks. In spite of this, the presence of phytopathogenic fungi causes greater losses postharvest (SAGARPA *et al.*, 2016).

One of the main concerns behind the incidence of fungal pathogens in the grain lies in their impact on innocuousness (Carvajal-Moreno, 2022). Additionally, food security is compromised by the capacity of some strains to produce mycotoxins. These metabolites have been related to acute intoxications and chronic diseases that affect vital organs such as the kidneys, liver and lungs, as well as alterations in the immune system, nervous system, genotoxicity and carcinogenesis (Abrehame *et al.*, 2023). For this reason, there are legislations and regulations worldwide that help reduce its exposure, through maximum limits permitted in foods (USDA, 2024; Regulation (EU) 2023/915; NOM 188; NOM 247).

Traditional, physical and chemical technologies have been used to preserve the quality of grain during storage. However, recent investigations have focused on the development and application of clean technologies, natural in origin, aimed at controlling fungal species in the grain and preventing the synthesis of mycotoxins (Hamad *et al.*, 2023; Fleurat-Lessard, 2017). The aim of this review was to point out the main genera of phytopathogenic fungi related to maize grains during their storage in Mexico, with the potential to produce mycotoxins. Likewise, a bibliometric analysis of the conventional (chemical and physical) and alternative treatments that have been applied for fungal control, and the reduction or elimination of mycotoxins, in order to know and strengthen the identification of mycotoxigenic species, their implications on human health and the integrated management strategies that reduce the problems presented by maize in the postharvest stage in Mexico.

Main fungal genera related to the maize grain

The main filamentous fungi that grow on maize are widely distributed and are distinguished by their role in nature, related with the decomposition of organic matter in the soil due to their

high saprophytic capacity (Pitt *et al.*, 2012). Some of the main genera identified as maize pathogens are *Aspergillus*, *Penicillium* and *Fusarium* (Erasto *et al.*, 2023; Qi *et al.*, 2023).

These fungi have the capacity to generate losses of dry matter and inhibit germination in the seed, causing the temperature of the grain cortex to rise, as well as a reduction in their nutritional value (Fleurat-Lessard, 2017). On the other hand, some fungal species have the ability to produce highly toxic secondary metabolites known as mycotoxins, which are biosynthesized and excreted through a set of metabolic pathways that are not essential for growth or the survival of the microorganism (García-Cela *et al.*, 2022; Bartholomew *et al.*, 2021).

The species of *Aspergillus* present fast growth and a diversity of colors, which can vary from whitish, yellowish-green, to brownish-black in color, and present granular textures and aspects (Figure 1A-D). A relevant characteristic is its ability to develop with a low humidity content (a minimum of 13% in cereals) and a relative humidity of 78 to 80%, as well as a broad interval of temperatures, which ranges from 0 up to 55 °C (Pérez *et al.*, 2021; Pitt *et al.*, 2012).

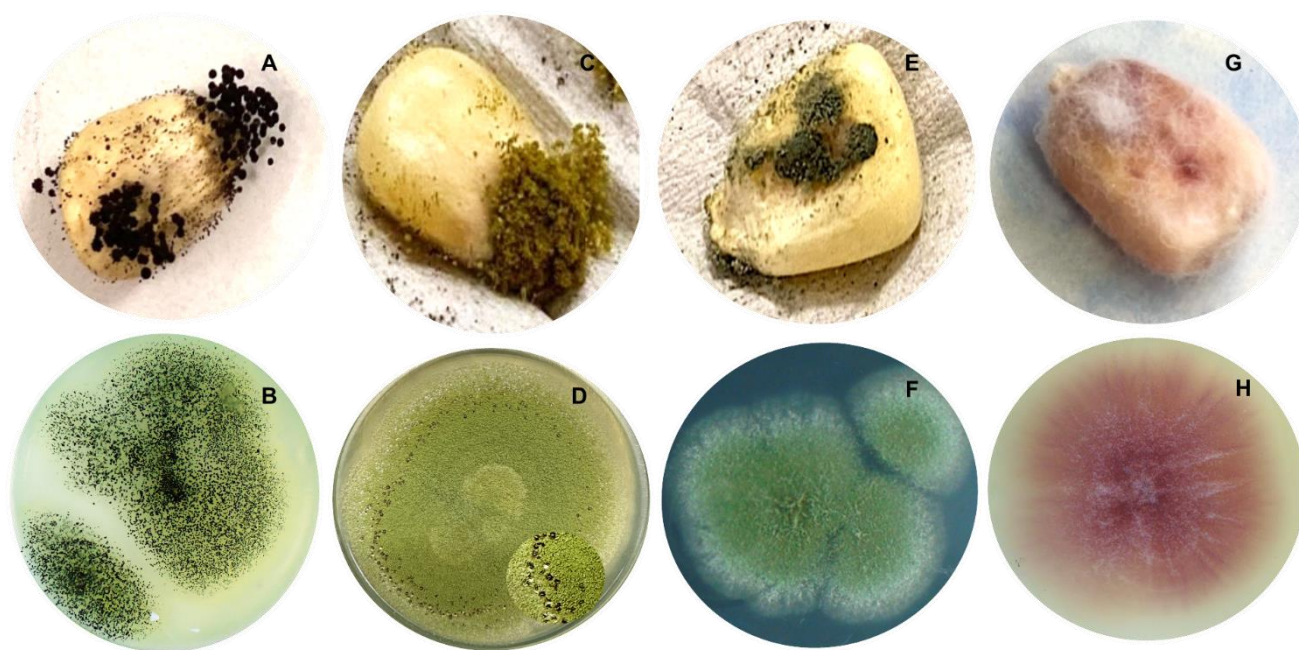


Figure 1. Mycelial characteristics in PDA medium and in maize grains of postharvest fungi; **A-D)** Genus *Aspergillus*; **E-F)** Genus *Penicillium*; **G-H)** Genus *Fusarium*.

Likewise, the species of *Penicillium* also grow quickly, developing green, bluish or gray colors and cottonlike, velvety and thread-like textures (Figure 1E-F). Its optimum growth is at temperatures between -2 to 50 °C, with a relative humidity of 85 to 90% and a humidity content of 16% (Pérez *et al.*, 2021; Pitt *et al.*, 2012). Species such as *A. flavus*, *A. parasiticus*, *P. funiculosum* and *Penicillium verrucosum* are called storage fungi, since they grow under conditions with low water activity. Unlike some *Fusarium* species, they are classified as field fungi (*F. graminearum* and *F. verticillioides*), since they invade the maize grains before harvest (Krnjaja *et al.*, 2021; Adeniji and Babalola, 2018), as well as requiring more humid conditions for their development, a relative humidity of 90 to 95%, humidity contents in the grain between

20 and 22% and a temperature range from 5-35 °C (Akbar and Alam, 2019). *Fusarium* characteristically presents mycelia with colors that can be white, beige, orange, red, purplish-pink, and others, as well as having cottonlike aerial textures (Figure 1 G-H) (Torre-Hernández *et al.*, 2014; Pitt *et al.*, 2012).

Mycotoxins

Mycotoxins are potentially toxic chemical metabolites that can cause adverse effects on human and animal health; the presence of one or more metabolites can lead to synergetic or additive effects (Carvajal-Moreno, 2022; International Agency for Research on Cancer [IARC], 2002). There are 5 groups of mycotoxins (1, 2A, 2B, 3, 4) that have an important economic and toxicological impact on the production of grains and cereals, as well as on health (IARC, 2002). The main mycotoxins are aflatoxins (AFL), ochratoxins (OTA), trichothecenes (deoxynivalenol and nivalenol), zearalenone (ZEA) and fumonisins (Wang *et al.*, 2024; Krnjaja *et al.*, 2022; IARC, 2002). Specifically, aflatoxin B1 (AFL B1) is classified as carcinogenic for humans due to its mutagenic effect and carcinogenicity in living organisms (group 1) as it binds to DNA, RNA and proteins. Unlike OTA and fumonisin B1 (FB1), they are classified as possibly carcinogenic for humans (group 2B) (Carvajal-Moreno, 2022; IARC, 2002). The presence of these metabolites has created great concern and problems, which is why diverse government regulations have been implemented to reduce and avoid the risk of contamination in the processing of cereals (USDA, 2024; Regulation (EU) 2023/915; NOM 188; NOM 247).

The main species with the ability to synthesize mycotoxins belong to the genera of *Aspergillus*, *Penicillium* and *Fusarium*, the main ones being *A. flavus*, *A. parasiticus* and *A. nomius* for the production of AFL B1; *P. verrucosum* produces OTA and *F. verticillioides*, as well as *F. proliferatum* produce FB1 (Wang *et al.*, 2024; Carvajal-Moreno, 2022; IARC, 2002). However, one type of mycotoxins can be synthesized by different species and a particular strain can produce different mycotoxins (Carvajal-Moreno, 2022; García-Cela *et al.*, 2022). Factors such as substrate type (maize, wheat, sorghum), dissemination of the fungal inoculum by insects and mites, the time between the harvest of humid cereals and the drying process, the initial humidity content of the grains harvested, storage time (months), accidental or environmental rehydration of the grain in storage, as well as the interactions and physiological state of the pathogens (strain variability, age, etc.) have an influence on the development of fungi and the production of mycotoxins; nevertheless, the main factor is water (García-Cela *et al.*, 2022; Akbar and Alam, 2019; Fleurat-Lessard, 2017). For this reason, an adequate management of the previously mentioned factors before and during the harvest can prevent the presence of phytopathogens and the contamination by their toxic metabolites.

Control methods

For many years, synthesis fungicides have been used to control fungi, and this practice has also been very common globally. Nevertheless, it has been shown that diverse pathogens generate resistance to these compounds, as well as the significant risks they cause in food security and the environment, since they contaminate bodies of water and soils (Fleurat-Lessard, 2017; IARC, 2002). At the same time, physical methods have been frequently implemented during postharvest handling, most notably, grain cleaning and the control of

moisture and temperature through low-temperature aeration. However, these strategies are not enough to mitigate the deterioration of the maize grain (Fleurat-Lessard, 2017).

Regarding an early detection of the growth of mycotoxigenic fungi, devices such as CO₂ microsensors have been used during storage as an effective alternative to detect the beginning of grain deterioration, although its high cost limits its accessibility (Vijaykumar *et al.*, 2024; Fleurat-Lessard, 2017). Nowadays, the use of biocontrol agents with beneficial microorganisms and basic substances such as essential oils, plant extracts and salts are frequently used, since the elimination of fungal pathogens and the prevention of toxicological problems presented by conventional pesticides has been proven (Zhang *et al.*, 2024; Hamad *et al.*, 2023).

In this sense, a bibliometric analysis was performed in order to explain recent trends in treatments applied for the postharvest control of potential phytopathogens that can potentially produce mycotoxins in maize grains. Information was gathered through the ScienceDirect data base, covering the period between the years 2019-2024. The keywords used for the search were: “maize,” “chitosan,” “biological control” and “essential oils,” which gave a total of 3,132 publications. Subsequently, using the software package VOSviewer® version 1.6.19, a bibliometric mapping was carried out based on the data obtained. As a result, a network visualization map was produced (Figure 2), which helped identify seven thematic groups or related research clusters. Every group is represented in a different color, and its size is relative to the amount of information available on it; the larger the circle, the greater the amount of information, whereas the distance between one group and another indicates how closely they are related.

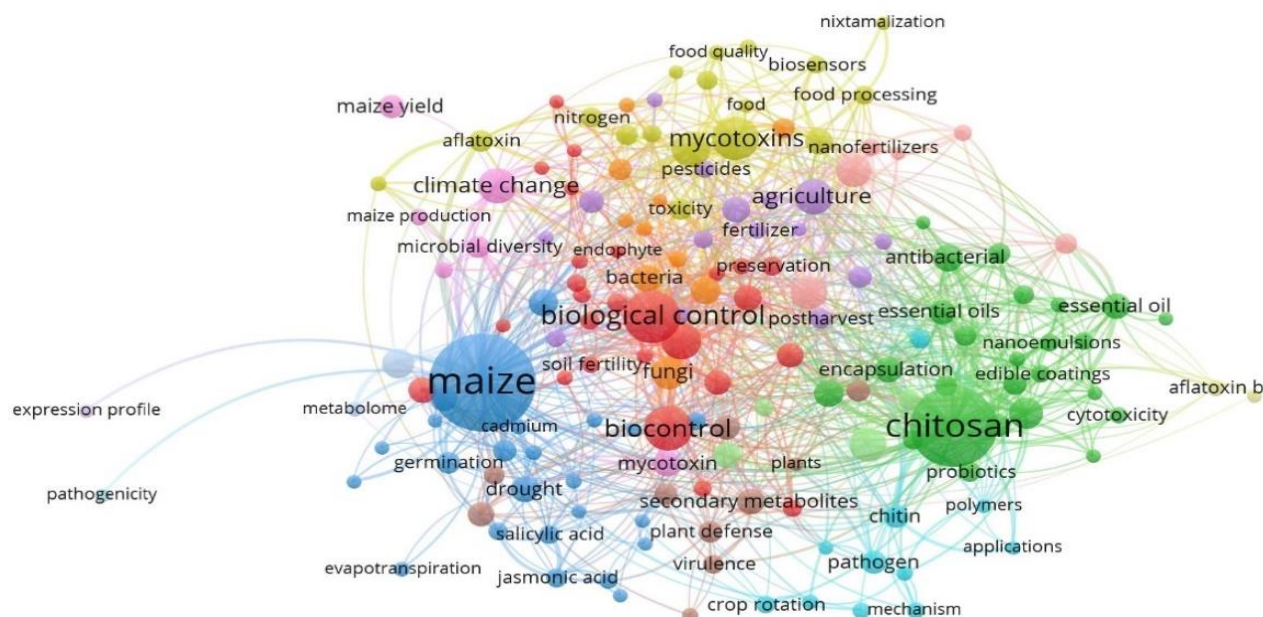


Figure 2. Visualization of the bibliometric analysis network (VOSviewer® version 1.6.19) using keywords “maize”, AND, “biological control”, OR, “chitosan”, OR, “essential oil”.

The bibliometric analysis shows that there is still a limited number of studies related to maize and the use of alternative treatments. In the case of the “chitosan” and “maize” groups, there is a large amount of information. However, these are not directly connected, since the bibliographic information reported focuses on the treatment in the field and not during storage. Similarly, the investigations related to essential oils and microorganisms do not show a direct relation within the network, which suggests more studies focused on the application of biocontrol agents in postharvest for the control of fungi and the production of mycotoxins in maize grains.

Physical methods

The application of the physical methods ranges from simple procedures such as grain cleaning by brushing, abrasion and pearling, to the use of sophisticated equipment that can help control variables such as temperature and humidity (Fleurat-Lessard, 2017). Although favorable conditions can be reached for the storage of grains, keeping grains dry, healthy and clean in time is challenging (Wang *et al.*, 2024).

Some of the most noteworthy and widely used physical methods to control phytopathogens during the storage of grains include aeration at low temperatures, thermal treatments applying hot water or air and irradiation (Moumni *et al.*, 2023). Particularly, irradiation treatments (gamma, ultraviolet rays) have proven to be effective in reducing and even inhibiting pathogens by inducing damages in the genetic material and their resulting cell death, significantly reducing the production of mycotoxins (Moumni *et al.*, 2023; Tiwari *et al.*, 2022; Khalil *et al.*, 2021). However, their application has been limited due to the possible adverse effects on the quality of the grain, since its action mechanism can also affect viable maize seeds, thus compromising its nutritional and functional properties (Tiwari *et al.*, 2022; Khalil *et al.*, 2021).

On the other hand, physical methods can be used alongside other technologies such as modified atmospheres, with the application of gases such as carbon dioxide, nitrogen, ozone, noble gases (argon and helium), hydrogen, and others (Odjo *et al.*, 2022; Riudavets *et al.*, 2018). The use of ozone has been proven to reduce the growth of *Aspergillus* spp., *Fusarium* spp. and *Penicillium* spp. between 98 and 99%, respectively (Tiwari *et al.*, 2022). Despite this, its use has been affected due to the alterations caused in sensorial and nutritional properties of the grain, such as changes in color, flavor and nutritional content, as well as the high cost related to implementing this type of treatments to adapt on a large scale (Moumni *et al.*, 2023; Romanazzi *et al.*, 2022).

Chemical methods

Applying chemical compounds, such as synthesis fungicides, continues to be one of the main practices in agriculture due to its easy access and initial effectiveness (Bartholomew *et al.*, 2021). Nevertheless, its indiscriminate use at high doses has mainly caused the resistance of pathogens, contamination in grains with toxic residues and adverse effects on health and the environment. In addition, another disadvantage of these treatments is that they require the use of specialized equipment to be applied, as well as trained personnel, which can be expensive (Pereira *et al.*, 2024; Costa-Becheleni *et al.*, 2020).

Chemical products regularly change their commercial names, but their active ingredients are the same or some have the same fungicidal effect. Among the most widely-used compounds

for the control of the development of phytopathogens in maize grain during postharvest are captan, thiram, carboxin, benomyl, quintozone and chloroneb (Dell'Olmo *et al.*, 2023; Hollomon, 2015; Hernández and Carballo, 2017). In Mexico, the most widely-used fungicides are benomyl, iprodione, captan and fungicides of the carbamate group (Godínez *et al.*, 2023; Ruíz *et al.*, 2022).

Fungicides can be classified using different criteria, one of the most common being their form of action. In this sense, three main types can be distinguished: contact, systemic and translaminar fungicides (Hollomon, 2015; Hernández and Carballo, 2017). Systemic fungicides present greater toxicity, since they have a wider spectrum of activity. After being absorbed by the plant tissue, these compounds reach internal structures of the cells, which gives them the ability to act against a wide variety of organisms, from microorganisms to higher organisms. The main action mechanisms include the alteration of the cell membrane, the inactivation of enzymes, the alteration of breathing processes and the alteration of the genetic material or related structures. For example, benomyl is a systemic fungicide and its form of action is performed with the inhibition of cell mitosis through bonding with tubulin, thus affecting the cell and nuclear division, which finally leads to cell death (Hollomon, 2015; Hernández and Carballo, 2017).

It is worth mentioning that the toxicity stated in the fungicide containers is based on lethal dose 50 (LD50) taken orally (WHO, 2019). This measure reflects only acute toxicity, not considering the possible effects of chronic toxicity reported in the literature. Alongside this, the use of mixtures of active ingredients must be carefully considered, since these compounds can interact with each other and strengthen the long-term toxic effects (Godínez *et al.*, 2023; Ruíz *et al.*, 2022).

Biological methods

Control with biological methods is an important strategy to reduce the prevalence of fungal diseases in different crops. This method is based on the application of beneficial microorganisms or compounds derived from them, in order to inhibit the development of phytopathogens and prevent economic losses (Ali *et al.*, 2024; Heliyon *et al.*, 2024). In addition, they are a secure alternative to the use of synthetic fungicides, since these agents can act directly on the pathogens or contribute to the degradation of mycotoxins (Vijaykumar *et al.*, 2024; Dell'Olmo *et al.*, 2023; Orzali *et al.*, 2023; Romero *et al.*, 2022; Bartholomew *et al.*, 2021).

Beneficial microorganisms. Biocontrol agents have been used as alternative control methods during the preharvest and postharvest stages. In Mexico, the most commonly used beneficial microorganisms are mainly fungi of the genus *Trichoderma*; and among bacteria, species such as *Bacillus subtilis*, *B. pumilus*, *B. thuringiensis*, among others (Table 1). Approximately 230 bioproducts are available, registered in COFEPRIS in the Mexican market. However, despite the significant advances in the identification and development of new biological control agents, their adoption in the field is limited due to factors such as the scarcity of information on the real efficiency of the bioproducts, or the little availability of the products, related to the limited number of active ingredients developed for each taxonomic group. These limitations contribute to the lack of awareness and the low acceptance of farmers towards the use of bioproducts

(Lahlali *et al.*, 2022; Córdova-Albores *et al.*, 2021). Table 1 shows the different microorganisms used recently in the control of phytopathogens transmitted by maize grains, such as microorganisms (fungi, bacteria and yeasts).

Basic substances. Numerous studies suggest the antifungal activity of substances derived from natural sources such as chitosan, salts, essential oils or plant extracts to extend the shelf life of various horticultural products (Minozzo *et al.*, 2023; Terefe *et al.*, 2023; Chrapacienne *et al.*, 2022; Ghule *et al.*, 2021;). However, in maize grain storage, the application of these compounds is more limited and the information available is scarce (Figure 2).

Table 1. Microorganisms used to inhibit the growth of phytopathogens transmitted in maize grains.

Microorganisms	Inhibition of phytopathogens	Result	Reference
Fungi			
<i>Trichoderma</i> sp.	<i>F. oxysporum</i> <i>A. niger</i>	73-87% mycelial inhibition	Vijaykumar <i>et al.</i> , 2024; Prasad <i>et al.</i> , 2020
<i>T. gamsi</i>	<i>F. verticillioides</i>	72% mycelial inhibition Reduction in fumonisin content	Galletti <i>et al.</i> , 2020
<i>T. asperellum</i>	<i>F. verticillioides</i>	88.71- 100% mycelial inhibition	Cuervo-Parra <i>et al.</i> , 2022
<i>Aspergillus flavus</i> (atoxigenic strains)	<i>A. flavus</i>	80% Reduction in AF	Zhang <i>et al.</i> , 2024; Fleurat-Lessard, 2017
Bacteria			
<i>Bacillus</i> sp.	<i>Talaromyces funiculosus</i> <i>P. oxalicum</i> <i>F. verticillioides</i>	 Decrease in fumonisin	Yang <i>et al.</i> , 2020 Yang <i>et al.</i> , 2020; Guimaraes <i>et al.</i> , 2020
Yeasts			
<i>Cyberlindnera jadinii</i>	<i>A. flavus</i> and <i>A. niger</i>	Reduction in growth and sporulation	Alkuwari <i>et al.</i> , 2022
<i>Debaryomyces hansenii</i>	<i>Aspergillus</i> sp. <i>F. proliferatum</i> and <i>F. subglutinans</i>	59.8% Reduction in fumonisin	Medina-Córdova <i>et al.</i> , 2016

Essential oils are extracted from aromatic plants and are composed of bioactive ingredients such as alkaloids, phenols, terpenes and organic acids, to which their antifungal activity has been attributed (Chen *et al.*, 2023). The composition and concentration of these phytochemicals can vary in each essential oil; in general terms, they can have two or three major compounds and tens of minor ones. However, applying all the compounds of the essential oil has been proven to boost the inhibiting effect against the development of the pathogens, in comparison with the use of only one compound (Taheri *et al.*, 2023; Romero *et al.*, 2022). Likewise,

essential oils have been effective to inhibit the production of mycotoxins (Chen *et al.*, 2023; Minozzo *et al.*, 2023; Qi *et al.*, 2023; Gwiazdowska *et al.*, 2022; Oliveira *et al.*, 2020). Terefe *et al.* (2023) evaluated the anti-fungal effect of different plant extracts, *Artemisia glacialis*, *Cymbopogon citratus*, *Punica granatum*, *Rosmerinus officinalis*, *Ruta chalepensis* and *Thymus vulgaris*, which inhibited the mycelial growth, sporulation and germination against *F. verticillioides*. Likewise, Iwayemi *et al.* (2024) tested cinnamon (*Cinnamomum verum*), clove (*Syzygium aromaticum*), oregano (*Origanum vulgare*) and thyme (*Thymus vulgaris*) essential oils on the mycotoxigenic fungi *Aspergillus*, *Penicillium* and *Fusarium*. The results showed that the inhibition of the anti-fungal activity and reduction in the production of aflatoxins were reliant on the increase of the concentrations, until it reached an inhibiting effect of 100% in the maize grain stored at 25 °C for 42 days.

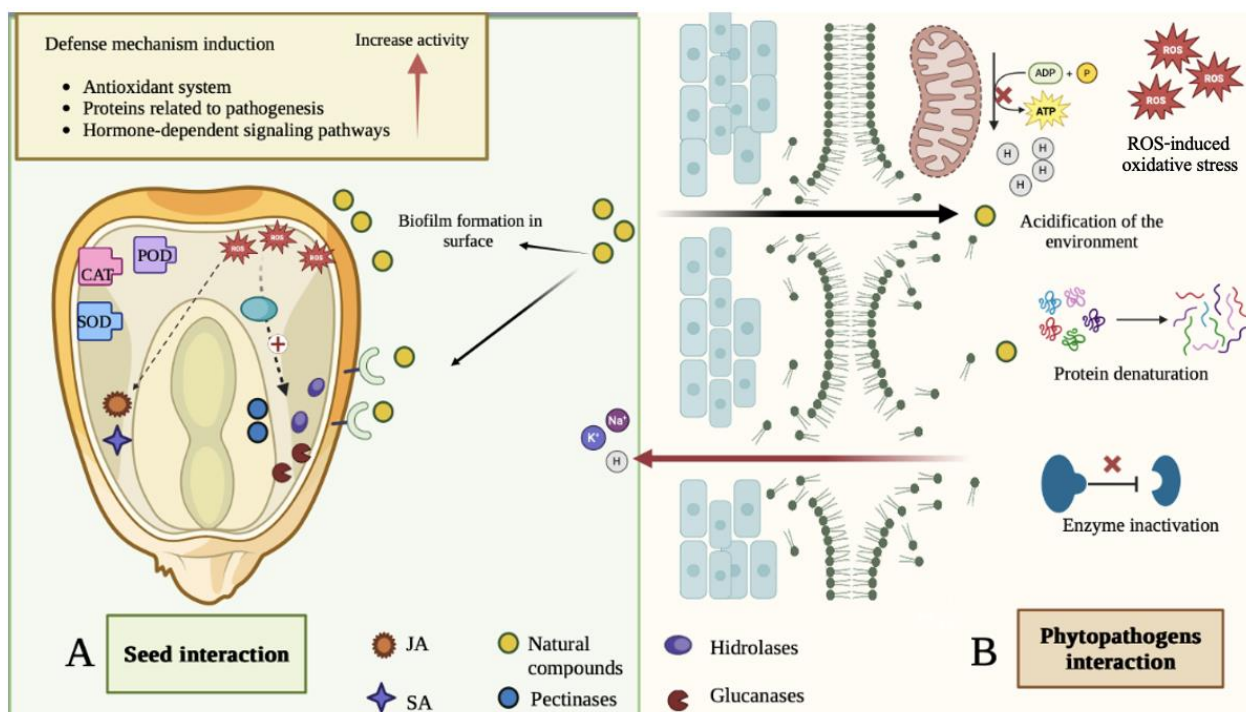
In recent years, broad-spectrum essential oil-based botanical fungicides have been developed and registered in Mexico for agricultural use. An example of this is the fungicide Sporan (Registered: RSCO-MEZC-FUNG-0910Q-X0073-009-38.00), which contains a mixture of bioflavonoids of the essential oils of clove, rosemary (*Salvia rosmarinus*), thyme and mint (*Mentha piperita*). The registration and marketing of this botanical fungicide responds to the need to search for the development of safe and eco-friendly alternatives.

Another compound that stands out as a control agent, alternative to the use of synthetic fungicides in maize is chitosan; its efficiency has been proven on diverse crops such as avocado (*Persea americana*), mango (*Mangifera indica*), cranberry (*Vaccinium corymbosum*), cereals, and others (Rayón-Díaz *et al.*, 2025; Romanazzi *et al.*, 2024; Ramos-Bell *et al.*, 2023; Herrera-González *et al.*, 2022; Ghule *et al.*, 2021). Its application not only contributes to the control and inhibition of phytopathogenic fungi, but also improves seed quality, induces defense mechanisms, favors germination and vigor in seedlings (Martínez-Batista *et al.*, 2024; Saberi *et al.*, 2024; Carvalho *et al.*, 2020; Gutiérrez-Martínez *et al.*, 2020). Chitosan is a biopolymer composed of long N-acetyl-glucosamine and D-glucosamine chains, and is obtained from the partial deacetylation of chitin, a polysaccharide found in the exoskeleton of insects and crustaceans, as well as in the cell wall of fungi (Mukarram *et al.*, 2023; Debnath *et al.*, 2022). This compound is characterized for being biodegradable, biocompatible, non-toxic, with the ability to form semi-permeable films, as well as for displaying anti-microbial activity for both its direct interaction with phytopathogens and its ability to stimulate metabolic pathways and the expression of genes related to the defense mechanisms in fruits and grains. Its antimicrobial efficiency is mainly related to its physio-chemical characteristics, such as the degree of deacetylation and molecular weight, although other factors can also have an influence, such as the type of chitosan (native or modified), the host, the pH of the medium and weather conditions (Saberi *et al.*, 2024; Mukarram *et al.*, 2023; Debnath *et al.*, 2022). The molecular structure of chitosan is versatile, allowing its chemical modification to generate certain derivatives of chitosan, thanks to the presence of active functional groups such as hydroxyls and aminos (Saberi *et al.*, 2024; Mukarram *et al.*, 2023). These modifications are an efficient way to optimize its physio-chemical characteristics, without compromising its unique biological properties (Jiménez-Gómez and Cecilia, 2020). The current study of chitosan has been extensive, and has led to searches for new application techniques, as well as the combination with other additives such as beneficial microorganisms, essential oils and other

natural compounds, with the purpose of obtaining a more efficient control during the storage of grains (Vijaykumar *et al.*, 2024; Godana *et al.*, 2020; Wu *et al.*, 2019).

Action mechanism of biocontrol agents

The previous application of biocontrol agents has proven to prevent the growth, sporulation and germination of the spores of pathogens such as *Fusarium*, *Aspergillus* and *Penicillium*, due to them being directly involved in the antifungal activity and indirectly in the activation of the grain defense system, which helps reduce the infection with a highly toxic effect (Figure 3) (Chen *et al.*, 2023; Sharma *et al.*, 2023).



Antifungal activity takes place mainly due to the interaction between the compound and the phytopathogen. Because phytochemical compounds have liposoluble characteristics, they can join and damage the cell wall and membrane of the pathogen (Minozzo *et al.*, 2023; Qi *et al.*, 2023; Shabir *et al.*, 2023). Similarly, due to its polycationic nature, chitosan can interact, through its amino group, with the groups of the cell wall, negatively charged (glucans, chitin) or in the cell membrane (phospholipids) of the pathogen (Vijaykumar *et al.*, 2024). This interaction causes membrane permeability, affecting the transportation of ions and the absorption of nutrients (Figure 3). Damage to the shape and integrity of the fungal cells, such as severe contraction, rugged surface and partial collapse of the membrane, can trigger a

cascade effect on other cell structures, such as the cytoplasmic vacuolization, enzyme deactivation, the denaturation of cellular proteins and changes in the endoplasmic reticulum and mitochondria (Vijaykumar *et al.*, 2024; Terefe *et al.*, 2023; Ghule *et al.*, 2021; Saberi *et al.*, 2014). In particular, the phytochemical compounds have been related to the mitochondria for being the target structure, with effects such as mitochondrial dysfunction, which leads to a reduction of the activity of the ATPase accumulating protons within the cell and an intracellular acidification (Figure 3) (Taheri *et al.*, 2023; Terefe *et al.*, 2023; Gwiazdowska *et al.*, 2022; Oliveira *et al.*, 2020; Boukaew *et al.*, 2017). After the chitosan enters the cell, it can interact with the nucleus of the pathogen and join the DNA, and thus affect its replication, and consequently, the protein and mRNA synthesis. All these effects finally lead to the cellular death of the pathogen (Saberi *et al.*, 2024; Mukarram *et al.*, 2023). In terms of beneficial microorganisms, the main inhibition mechanism in the growth of phytopathogens is due to the competition for space-nutrients (Figure 4A) (Oztekin *et al.*, 2023; Romero *et al.*, 2022).

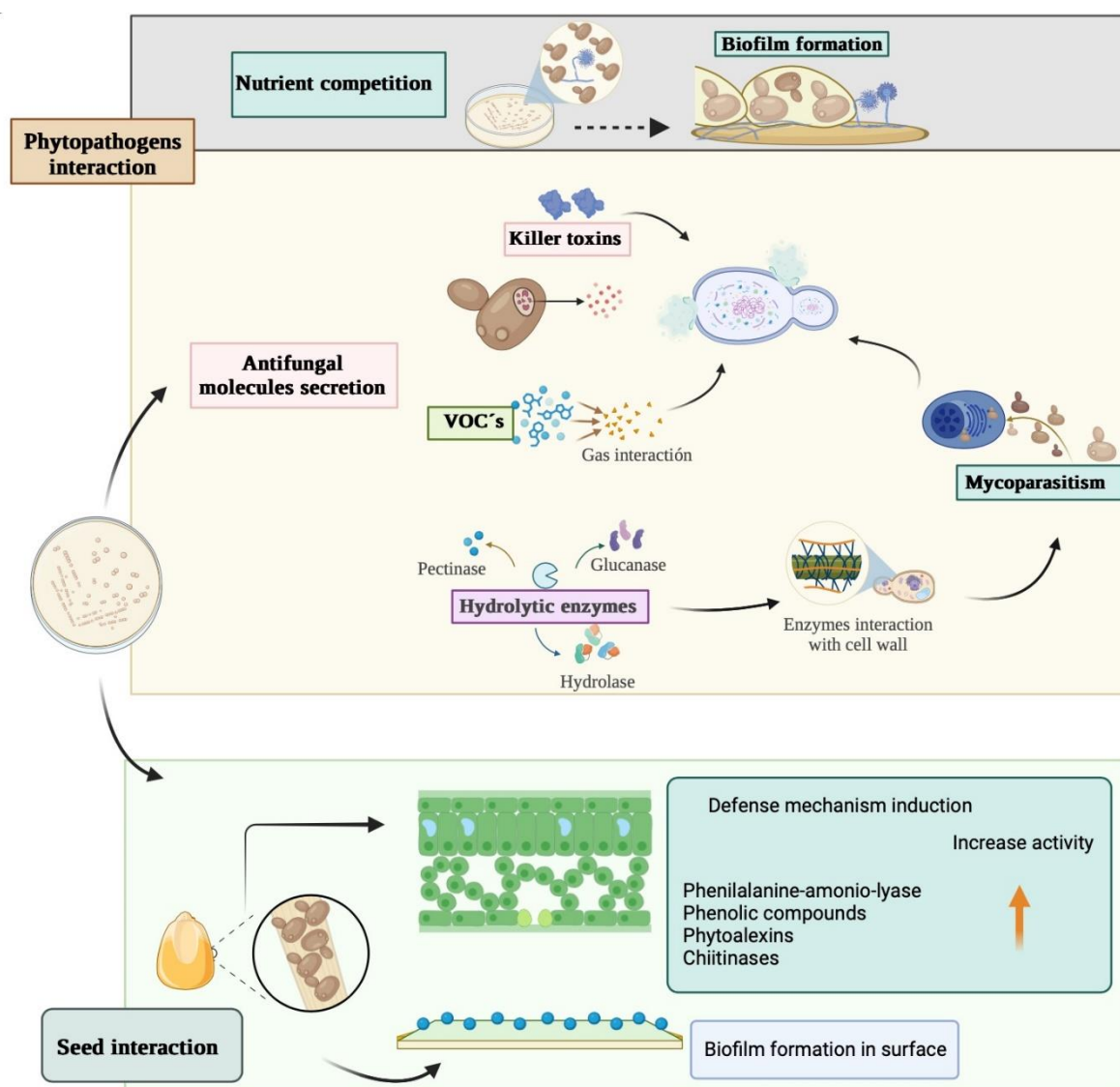


Figure 4. Action mechanisms Beneficial microorganisms. **A)** Interaction with phytopathogens. **B)** Interaction with seeds. Image created using the program BioRender.

Likewise, the secretion of antimicrobial as killer toxins, volatile organic compounds (VOCs) and hydrolytic enzymes (pectinases, glucanases and chitinases) is considered another important mechanism of beneficial microorganisms (Figure 4A) (Oztekin *et al.*, 2023; Sharma *et al.*, 2023). VOCs are being widely studied for their ability to inhibit the development of fungal pathogens, even at low concentrations. Their volatile nature helps them diffuse easily in different environments, without the need for direct contact with the pathogen (Vijaykumar *et al.*, 2024). VOCs are produced as a competition strategy and its antimicrobial activity is related to its easy absorption or interaction in the cell membrane of the pathogen (Figure 4A). This interaction increases membrane permeability, the diffusion of ions and metabolites, resulting in the loss of homeostasis (Vijaykumar *et al.*, 2024; Oztekin *et al.*, 2023). Likewise, the hydrolytic enzymes secreted by beneficial microorganisms act directly on the cell wall of the pathogen, causing irreversible structural damage that results in cell lysis (Figure 4A) (Sharma *et al.*, 2023). The production of these enzymes is also associated to mycoparasitism (Figure 4A), a mechanism through which the beneficial microorganism colonizes and invades the hyphae of the pathogen, using them as a source of nutrients (Vijaykumar *et al.*, 2024; Oztekin *et al.*, 2023; Sharma *et al.*, 2023).

On the other hand, some biocontrol agents can act as a coating or form biofilms on the surface of the grain (Figure 3A and 4B). This mechanism affects the development of the phytopathogen by limiting the availability of nutrients, as well as preventing the entry or its establishment in the grain (Debnath *et al.*, 2022). An example of this is applying yeasts, which can form biofilms in a short amount of time, favoring the colonization and ability to efficiently absorb carbon sources found in the medium; thus, they limit the disposition of nutrients for the optimum development of fungal pathogens (Vijaykumar *et al.*, 2024). Likewise, the coatings form a physical barrier on the grain that controls the humidity by reducing water loss, reduces respiration rate, regulating the gas exchange (low oxygen availability) and activates the defense mechanisms (Saber *et al.*, 2024; Debnath *et al.*, 2022). Regarding the activation of the defense mechanisms in the maize grain, the application of biocontrol agents improves the resistance against phytopathogens (Prusky and Romanazzi, 2023). At a systematic level, the interaction of the agent with the surface of the grain unleashes multiple signaling pathways that positively regulate the expression of genes related to the induced resistance (Figure 3A y 4B) (Sharma *et al.*, 2023). During this mechanism, secondary metabolites with protective functions are synthesized, including pathogenesis-related (PR) proteins such as chitinase and glucanases, phytoalexins, phytohormones (jasmonic acid [JA], ethylene [ET], salicylic acid [SA]), as well as enzymatic antioxidants (superoxide dismutase [SOD], peroxidase [POD], catalase [CAT], polyphenol oxidase [PPO] and phenylalanine ammonia-lyase [PAL]) that help alleviate oxidative stress (Chen *et al.*, 2023; Shabir *et al.*, 2023; Taheri *et al.*, 2023). These physiological changes give the grain the protection against a broad spectrum of pathogens and help maintain its quality during storage (Prusky and Romanazzi, 2023; Lahlali *et al.*, 2022).

The effect on the production of mycotoxins has been associated with ancillary effects related to inhibiting the phytopathogen; however, research shows that fungal growth effects do not always correlate with the inhibition of mycotoxin synthesis (Haggag *et al.*, 2023; Jian *et al.*, 2022). Its reduction can also be related with a low expression of genes related to biosynthesis, the activation of metabolic processes such as the generation of ROS (reactive oxygen species) or the catabolism of carbohydrates that are associated with the biosynthesis of

mycotoxins (Zhang *et al.*, 2024). Jian *et al.* (2022) proved that essential oils can completely inhibit the production of mycotoxins, inhibiting mycelial growth very scarcely.

Another way to decontaminate mycotoxins in the maize grain by applying biocontrol agents is with its degradation; this means that the interaction of some compounds can degrade or modify the structure of mycotoxins, generating less-toxic metabolites (Wachowska *et al.*, 2023). For example, Anjum *et al.* (2020) report that some bioactive compounds, when interacting with aflatoxin, can remove the double bond of the furan ring and modify its structure, which will generate new non-toxic compounds. Particularly, with beneficial microorganisms, the inhibition of mycotoxins can also be achieved with the adhesion of the toxin to the components of the cell wall of the antagonist (Oztekin *et al.*, 2023). Adsorption is a reversible physical-chemical process, but its effectiveness depends largely on structural, physical morphology and composition of the cell wall (Zhang *et al.*, 2024; Oztekin *et al.*, 2023; Papp *et al.*, 2021).

CONCLUSIONS AND PERSPECTIVES

The deterioration of the maize grain during storage, particularly due to the action of fungi and the production of mycotoxins, continues to be a challenge for food security. The main fungi related to this problem belong to the genera *Aspergillus*, *Penicillium* and *Fusarium*, which stand out for their ability to synthesize mycotoxins, and some of these are classified by IARC for their toxicological importance. Among these, aflatoxin B1 is especially relevant for its high toxicity and classification as a human carcinogen. Despite the efforts aimed at ensuring safe maize production and storage in Mexico—including the implementation of official standards that establish the sanitary requirements and specifications that must be met during the postharvest stage, the permissible limits for mycotoxin concentrations, and the application of Hazard Analysis and Critical Control Points (HACCP) in control systems—contamination by fungi and mycotoxins remains a recurring problem. Conventional technologies used to mitigate these effects present limitations that derive from factors such as microbial resistance, the persistence of chemical residues and environmental impact. In this context, alternative control technologies, particularly those based on biocontrol agents, have become increasingly relevant as innovative and promising approaches. Not only do these technologies offer an effective control of phytopathogens, but also contribute to the prevention of the synthesis of mycotoxins, without compromising the innocuousness and nutritional quality of the maize grain. The bibliometric analysis shows that the investigations on this area focus on the preharvest stage and very few focus on postharvest. Similarly, the research that incorporates the combination of different biocontrol agents to identify a more efficient control method is very scarce. Therefore, the systemic and integral understanding of agrobiotechnological strategies, as well as identifying the most prevalent mycotoxigenic species in Mexico must be strengthened to sustainably improve plant health and ensure food safety. Progress in this field is a priority research line, particularly towards the design of integrated management systems that combine different methods to provide a more effective control of phytopathogens, as well as reduce mycotoxin contamination in maize grain.

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