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Fusarium in maize during harvest and storage: a review of species involved, mycotoxins, and management strategies to reduce contamination

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Abstract Maize is one of the most important crops for food and feed production worldwide. Many diseases affect maize kernels, reducing kernel quantity and quality. *Fusarium* species are the most important pathogens capable of producing diseases in maize, whose presence often results in mycotoxin contamination. These mycotoxins can produce severe diseases in consumers, leading to regulatory decisions on the maximum acceptable content of mycotoxins in consumer products. The aim of this study is to analyse the most important *Fusarium* species found in natural and storage conditions worldwide, and the associated mycotoxin content. Thus, the role of the mycotoxins, and the optimal conditions for fungal growth and mycotoxin production, have been analysed. Although maize hybrids with resistance against these diseases are not available yet, strategies that could be adopted to reduce the impact of *Fusarium* on maize crops are summarized in this review.

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Introduction

Maize importance and *Fusarium* presence

Maize (*Zea mays* L.) is one of the most important crops worldwide, with about 594 million tons (MT) produced worldwide, from 139 million hectares (ha) sown (FAO, 2020). The American continent is the main producer of maize, responsible for 50% of total maize production, distributed mainly in the USA, Brazil, and Argentina. The Asian continent is the second largest producer (31.5%), with China being the primary producer with 357 MT. Europe is the third highest producing continent (11.2%), followed by the African (6.9%) and Oceanic (0.1%) continents (FAO, 2020). Maize is used mainly for animal and human food consumption, having a similar nutritional value to wheat but being much cheaper (Czembor et al., 2015). Moreover, the demand for maize has increased due to its use in ethanol production.

Maize is a monoecious plant belonging to the *Poaceae* family. Two phases can be distinguished during its growth: a vegetative and reproductive phase. The vegetative stage begins with the germination of maize seed and culminates with the appearance of the male flower. In contrast, the reproductive phase starts with the appearance of a female flower and finishes at physiological maturity.

During the different phenological stages, pathogens can affect this crop, negatively modifying the quantity and quality of maize kernels. Among the diseases that can reduce productivity and cause economic losses, those caused by fungi, mainly *Fusarium* spp., have a key role. Although some species of *Fusarium* can affect the roots, leaves, and stems of maize plants, here we focused on these species able to damage the ear and kernels.

Two diseases can affect maize kernels: Fusarium ear rot (FER) and Gibberella ear rot (GER), the occurrence of which depends primarily on climatic conditions.

Fusarium ear rot

Fusarium ear rot, also known as pink ear rot or pink fusariosis, is mainly produced by species belonging to the *Fusarium fujikuroi* species complex (FFSC). The most predominant species is *F. verticillioides,* but *F. proliferatum* and *F. subglutinans* can also frequently be isolated (Logrieco et al., 2002). Although this disease is generally most prevalent in warmer regions, some reports suggest that *F. verticillioides* and *F. proliferatum* predominate in drier and warmer conditions, while *F. subglutinans* is more frequent in humid and cooler conditions (Goertz et al., 2010).

The high incidence of *F. verticillioides* is associated with the different entry points of this pathogen into maize: a) *systemic infection*: during maize kernel germination and seedling development; b) *cob infection:* this is the most common entry point, through silk channels during flowering by airborne inoculum; c) *mechanical damage:* some insects feeding on maize plants help *F. verticillioides* entry (de la Torre-Hernández et al., 2014). Generally, infection via the systemic pathway does not require notable mould growth, which explains the presence of *F. verticillioides* in asymptomatic maize (De la Torre-Hernández et al., 2014; Reid et al., 1999). Moreover, *F. verticillioides* has the ability to detoxify antimicrobial compounds in maize, which can explain its presence over the other *Fusarium* spp. (Bacon et al., 2008).

Regarding *F. verticillioides*' growth conditions, the minimum temperature required for germination is 4 °C, while the minimum water activity (aw) is 0.86 (Czembor et al., 2015). The classic starburst symptom on maize kernels is evidence of the presence of streaks on the pericarp radiating from the silk scar region of the kernels. Koehler (1942) reported that this characteristic symptom is a result of the disintegration of pericarp cells by the fungi.

Fusarium verticillioides is one of the most important producers of fumonisin B mycotoxins (FBs). More than ten types of FBs have been identified and characterized, however three are the most prevalent: fumonisin B1 (FB1), fumonisin B2 (FB2), and fumonisin B3 (FB3), FB1 being the most toxigenic (Musser & Plattner, 1997). Among other things, these toxins are classified as group 2B carcinogens by the International Agency for Research on Cancer (IARC, 1993). Additionally, they can cause leucoencephalomalacia in horses, pulmonary edema in swine, liver cancer in rats, and human oesophageal cancer (Marasas, 1996). Moreover, the toxicity of FB1 in the human liver plays a key role during oesophageal cancer initiation, inducting oxidation damage and lipid peroxidation as initial stages (Gelderblom et al., 2001).

Fusarium proliferatum is a mycotoxin-producing, seed-borne pathogen, causing asymptomatic infection in maize kernels (Reyes Gaige et al., 2020). This pathogen is more frequently isolated from sorghum than maize, and is also present worldwide in other food crops, including rice, millet, and several fruits such as apples and pears (Bacon & Nelson, 1994). *Fusarium proliferatum* can produce several toxins in maize kernels, including FB1 and FB2, moniliformin (MON), fusarin C, and fusaric acid. This mycotoxin production occurs under field conditions, although it also may occur during the storage process (Bacon & Nelson, 1994). The optimal temperature for *F. proliferatum* growth is 15 °C at 0.97 a_w, while a range of 15–30 °C at 0.97 a_w is optimal for FB1 production (Marín et al., 1999).

Two morphologically similar *Fusarium* species, initially named *F. subglutinans* sensu lato, were separated into two new species: *F. temperatum* and *F. subglutinans,* depending on their ability to produce the mycotoxin beauvericin (BEA) (Scauflaire, Gourgue, & Munaut, 2011). Moreover, these species can produce fusaproliferin (FP), MON, enniatins (ENNs), and FBs (Gromadzka et al., 2016). Tagele et al. (2019) have demonstrated that plants infected with *F. temperatum* produce more FB than those infected with *F. subglutinans.* These species have been found to cause seed rot, root rot, seedling blight, stalk rot, and ear rot of maize worldwide. Regarding their transmission, Wilke et al. (2001) demonstrated seed transmission and systematic infection of maize plants by *F. subglutinans.*

Moreover, other species belonging to the FFSC, such as *F. nygamai* (BEA, fusaric acid, FBs producer) and *F. ramigenum* (BEA, MON, and ENNs producer), have been isolated from maize (Leslie & Summerell, 2006; Stępień et al., 2019).

Gibberella ear rot

Gibberella ear rot (GER), also known as red ear rot or red fusariosis, is mainly produced by species belonging to the *Fusarium sambucinum* species complex (FSSC), mainly *F. graminearum*, however other species such as *F. culmorum, F. crockwellense,* and *F. avenaceum* can also be present (Logrieco et al., 2002). This disease is most prevalent in regions with frequent rainfall and moderate temperatures, as the silk channel is the most important infection pathway for *F. graminearum*. The disease is observed as pink to reddish-coloured mould on maize kernels, generally localized in the tip and spreading down the ear (Reid et al., 1999).

Fusarium graminearum growth needs a minimum temperature of 10 °C and 0.935 aw (Czembor et al., 2015). The presence of *F. graminearum* is accompanied by its ability to produce mycotoxins such as B-trichothecenes: nivalenol (NIV), deoxynivalenol (DON), and 3- and 15-acetyldeoxynivalenol (3-ADON and 15-ADON, respectively) (Castañares et al., 2014). Trichothecenes have effects on consumers causing vomiting and dietary disorders, and moreover can induce chronic effects such as immunosuppression, neurotoxicity, and teratogenicity (Piacentini et al., 2015). *F. graminearum* is, additionally, one of the most important zearalenone (ZEN) producers. ZEN is a xenoestrogen with a chemical structure similar to natural estrogens, allowing it to bind with estrogen receptors, amplifying the estrogenic effects on consumers (Mahato et al., 2021). ZEN has also been categorized as a group 3 carcinogen (IARC, 1993).

Other species belonging to the FSSC that produce GER are *F. boothi* and *F. meridionale,* more adapted to mild temperatures and sensitive to low temperatures and water stress (Belizán et al., 2019). Both species are of importance due to their ability to produce DON and NIV in maize kernels. *Fusarium crockwellense* has been reported in central and northern Europe, generally correlated with the presence of *F. poae* (Aguín et al., 2014). *Fusarium poae* is a pathogen that has been isolated sporadically from maize in Spain, never exceeding 4% of affected kernels (Aguín et al., 2014). This species is one of the most important NIV producers and other mycotoxins such as BEA, MON, ENNs, and FUS-X, among others (Dinolfo & Stenglein, 2014). Similarly, *F. venenatum* has been isolated at a low percentage from maize ears, being more frequently isolated from maize stalks (Scauflaire et al., 2011). This species can produce type A trichothecenes. *Fusarium brachygibbosum* has been isolated from maize stalks in China, and from maize ears in Iran, and is able to produce ENNs and diacetoxyscirpenol (DAS) (Fallahi & Saremi, 2019; Shan et al., 2017). *Fusarium sambucinum* has been mainly isolated from maize stalks at R6-maturity stages and, at a low percentage (<5%), from maize ears in Belgium (Scauflaire et al., 2011). This species has been reported as producing BEA, DAS, ENNs, NEO, and T-2 mycotoxins (Laraba et al., 2021). Another species that belongs to the FSSC and has been isolated from maize is *F. sporotrichioides*, being particularly prevalent in central and southern Europe. This species has been found to produce DAS, ENNs, NEO, and T-2 in vitro (Laraba et al., 2021; Scauflaire et al., 2011).

Other Fusarium species isolated from maize

Several species belonging to the *Fusarium incarnatum-equiseti* species complex (FIESC), including *F. equiseti* and *F. incarnatum,* have also been isolated from maize (Table 1). These species have the ability to produce many different mycotoxins, including fusarochromanone (FUSCHR), ZEA, and several trichothecenes (DON, NIV, T-2 toxin, FUS-X, DAS, NEO, BEA, and MON) (Avila et al., 2019).

The *Fusarium oxysporum* species complex (FOSC) involves species of *Fusarium* with a cosmopolitan life cycle and with an important impact on agriculture, horticulture, human and animal health (McTaggart et al., 2021). *Fusarium oxysporum* is the main species representing this complex able to produce fusaric acid, BEA, and FBs (López-Berges et al., 2013; O'Donnell et al., 2009).

Species belonging to the *Fusarium tricinctum* species complex (FTSC), such as *F. arthrosporoides*, F. *avenaceum, F. acuminatum,* and *F. tricinctum,* have also been found in maize (Table 1). Species of this complex are able to produce ENNs and MON (Senatore et al., 2021).

Fusarium heterosporum was occasionally isolated on maize ears from Europe, particularly on late-maturing hybrids late in the growing season. These isolates were able to produce high concentrations of

Table 1 Species of *Fusarium* isolated from maize worldwide

Country	Isolation year	*Fusarium* spp.	References
Africa	1999–2003	*F. verticilliodes, F. proliferatum, F. incarnatum*	Fandohan et al. (2005)
Argentina	1995–1996	*F. verticillioides, F. proliferatum*	Chulze et al. (2000)
	1997–1998	*F. subglutinans, F. verticillioides, F. proliferatum, F. equiseti, F. acuminatum, F. oxysporum, F. nygamai*	Torres et al. (2001)
	2007	*F. meridionale, F. boothi*	Sampietro et al. (2011)
	2015–2017	*F. verticillioides, F. subglutinans, F. graminearum, F. proliferatum, F. crockwellense*	Castañares et al. (2019)
Belgium	2005–2007	*F. graminearum, F. avenaceum, F. crockwellense, F. culmorum, F. poae, F. temperatum,* *F. arthrosporioides, F. proliferatum, F. tricinctum, F. equiseti, F. venenatum, F. verticillioides, F. heterosporum, F. oxysporum, F. torulosum, F. redolens, F. subglutinans, F. sporotrichioides, F. sambucinum, F. lateritium*	Scauflaire et al. (2011)
Brazil	2016–2017	*F. verticillioides, F. graminearum*	Berghetti et al. (2020)
	2011–2012	*F. verticillioides, F. temperatum, F. subglutinans, F. proliferatum, F. graminearum*	Czembor et al. (2015)
	2011	*F. verticillioides, F. proliferatum*	Lanza et al. (2014)
China	2012	*F. verticillioides, F. proliferatum, F. graminearum, F. subglutinans*	Qiu et al. (2015)
Germany	2006–2007	*F. verticillioides, F. graminearum, F. proliferatum, F.crockwellense, F. subglutinans*	Goertz et al. (2010)
Iran	2015–2016	*F. subglutinans, F. temperatum, F. redolens, F. brachygibbosum, Fusarium incarnatum-equiseti* species complex (FIESC)	Fallahi and Saremi (2019)
Italy	1992–1993	*F. verticillioides, F. proliferatum*	Bottalico et al. (1995)
Nepal	1997	*F. verticillioides, F. proliferatum, F. graminearum, F. equiseti, F. incarnatum*	Desjardins et al. (2000)
Peru	1987–1988	*F. subglutinans, F. verticillioides, F. equiseti, F. graminearum, F. acuminatum, F. solani, F. oxysporum, F. culmorum*	Logrieco et al. (1993)
Poland	1985–2014	*F. graminearum, F. verticillioides, F. poae, F. subglutinans, F. avenaceum, F. crockwellense, F. proliferatum, F. tricinctum, F equiseti*	Gromadzka et al. (2016)
	2013–2016	*F. temperatum, F. subglutinans, F. ramigenum*	Stępień et al. (2019)
Serbia	2018	*F. graminearum, F. subglutinans, F. verticillioides, F. proliferatum*	Krnjaja et al. (2020)
	2008	*F. graminearum, F. subglutinans, F. verticillioides, F. proliferatum*	Krnjaja et al. (2011)
Spain and France	1999	*F. verticillioides, F. proliferatum* *F. graminearum, F. poae* (both only from Spain maize)	Bakan et al. (2002)
Spain	2016–2018	*F. verticillioides, F. proliferatum, F. graminearum*	García-Díaz et al. (2020)
	2007–2008	*F. verticillioides, F. subglutinans, F. poae, F. proliferatum, F. oxysporum, F. crockwellense, F. equiseti, F. solani, F. culmorum*	Aguín et al. (2014)

ZEN and zearalenols (Bottalico et al., 1989). As for *Fusarium lateritium,* this species was reported colonizing several substrates, which related to their presence in different regional agronomic practices (Leslie & Summerell, 2006). Although *F. lateritium* is mainly reported in crops such as wheat (Ezekiel et al., 2008), this pathogen has occasionally been isolated from maize ears and stalks in a low proportion. *F. lateritium* has been reported as producing ENNs (Scauflaire et al., 2011). *Fusarium torulosum* is a fungal pathogen infrequently encountered in maize ears (< 5%), occurring in a lower proportion in stalks during the R6-maturity stage (Scauflaire et al., 2011). *F. torulosum* produces ENNs, and also other molecules such as wortmannin and butenolide (Ryley et al., 2007; Scauflaire et al., 2011). Recently, *F. redolens* was isolated at a low frequency (1.6%) in 182 maize samples from the main producing Iranian regions. These isolates produced ENNs and a high level of BEA (Fallahi & Saremi, 2019). *Fusarium solani,* belongs to the *Fusarium solani* species complex (FSSC), is frequently isolated from soils acting as decomposers and has also been isolated from maize (Chehri et al., 2015; Table 1).

The role of mycotoxins Much research has been carried out to identify which *Fusarium* species and resulting mycotoxin compounds are present in maize (Tables 1 and 2). As observed above, *F. verticillioides* and FBs have been found worldwide (Table 2). However, some aspects of the plant-pathogen interaction and the role of mycotoxins in the plant remain to be elucidated.

Several studies have been carried out to test the hypothesis that high levels of production of FBs was related to high levels of pathogen virulence. For instance, Desjardins et al. (1995) evaluated the role of FBs on maize seedlings by using FB-producing and FB-nonproducing *F. fujikuroi* isolates. The results demonstrated that FBs play a role in virulence, but production of FBs is not necessary or sufficient for virulence in maize seedlings. Jardine and Leslie (1999) evaluated the aggressiveness of *F. verticillioides* against maize stalk under greenhouse conditions. All tested strains showed a broad range of stalk lesions, but these were not related to the production of FBs. Later, Desjardins and Plattner (2000) evaluated isolates of *F. verticillioides* able to produce FB1, FB2, FB3, and FB-nonproducing isolates, and their ability to cause infection in maize. Field assays were performed using two inoculation pathways: silk channel injection, and the application of inoculum to the seed at planting. The results showed that FB-nonproducing isolates infect ears similarly to FB-producing isolates in both inoculation methods, indicating that FB1, FB2, and FB3 are not required for *F. verticillioides* to cause maize ear infection and ear rot. Contrary to these results, in 2008, Glenn et al. (2008) demonstrated that FB production by *F. verticillioides* was necessary for developing foliar disease symptoms in maize seedlings by using a genetic approach targeting gene disruption. Moreover, the incidence and severity were likely dependent on the amount of FB produced.

Studies with a transgenic *F. graminearum* modified to produce trichothecenes were used to inoculate maize, and measured severity, kernel yield, DON content, and fungal biomass. The results showed that although this strain was less virulent, it continues to be pathogenic in maize, suggesting that trichothecenes can act as virulence factors favouring the spread of *F. graminearum* in this crop (Harris et al., 1999). The results contained discrepancies; therefore, the role of mycotoxins related to severity and aggressiveness continues to be uncertain. The use of pathogens modified to produce mycotoxins are being used as biocontrol agents against those mycotoxin-producing isolates. But, for this strategy to be a viable control source requires confirmation that the mycotoxin plays a role as virulence factor for the pathogen.

Factors involved in determining fungal incidence and mycotoxin production The importance of fungal presence and the subsequent mycotoxin production has led several countries to establish maximum levels for mycotoxins produced by *Fusarium* spp. in food and feed to ensure that their presence does not affect human and animal health. The maximum content (μg/kg) allowed for the main *Fusarium* mycotoxins in maize flours worldwide is summarized in Fig. 1. According to the mycotoxin presence summarized in Table 2, some content exceeds these limits. For this reason, it is necessary to consider some of the factors, described below, that stimulate the fungal presence and mycotoxin production within the crop production pipeline.

Kernel development and composition

Regarding the composition of maize kernels, Bluhm and Woloshuk (2005) studied how kernel development and composition affects FB1 biosynthesis during colonization of the kernel by *F. verticillioides*. The results showed that the fungus grows well through all stages of development, reaching optimal growth in the dent and mature kernel stages. Moreover, they observed a higher level of FB1 in cultures grown in a liquid medium provided with amylopectin than those containing maltose, amylose, glucose, or dextran. Chulze et al. (1996) analyzed the occurrence of *Fusarium* and FB content in Argentinean maize. Kernels at different growth stages were sampled from 45 to 105 days after flowering. *F. subglutinans* was the predominant species in the first samples, with a low FB content. Later, *F. proliferatum* was isolated more frequently than other *Fusarium* belonging to the same section, and the highest FB content was detected 75 days after flowering, at around physiological maturity. Finally, at harvest time, *F. verticillioides* was the most frequently isolated species, and the FB content was less than that found 75 days after flowering (Chulze et al., 1996). Later, Bush et al. (2004) determined the kernels infected with *F. verticillioides* and FB contamination in harvested samples in eastern North Carolina. The results showed that the fungal presence and FBs contamination appeared near physiological kernel maturity when the kernel was in the dent stage (35–45% moisture) and

Table 2 Quantification of the main *Fusarium* mycotoxins in maize worldwide. FB: fumonisins; DON: deoxynivalenol; NIV: nivalenol; ZEN: zearalenones. Mycotoxin content is expressed in μg/kg (maximum values between parentheses)

Country	Year	Mycotoxins				References
		FBs	DON	NIV	ZEN	
Africa	2015–2016	990 (14347)	152 (1380)	14.2 (35.7)	13.6 (146)	Ekwomadu et al. (2020)
Argentina	2017–2019	–	316.58 (856.50)	–	–	Castañares et al. (2019)
Belgium	2016–2018	131.8 (6293.5)	396.4 (5322.4)	748.7 (6776.3)	159.7 (2791.6)	Vandicke et al. (2019)
Brazil	2015–2016	373.50 (1190.33)	50.77 (90.54)	–	18.39 (59.87)	Czembor et al. (2015)
Germany	2006	2370 (20690)	1780 (19570)	160 (4410)	70 (860)	Goertz et al. (2010)
Italy	2014 2015	5593 (8332) 10,993 (19371)	3669 (6818) 274 (670)	18.13 (37.8) 1.4 (1.6)	2262.5 (3491) 41 (72)	Blandino et al. (2017)
Nepal	1997	2300 (6500)	2500 (3500)	–	–	Desjardins et al. (2000)
Poland	2011 2012	488.16 (856) 1567.25 (2531)	4902.9 (8380) 1511.33 (1829)	– –	40.84 (67.77) 150.37 (232.75)	Bocianowski et al. (2019)
	2011–2012	375.50 (1190.33)	50.77 (90.54)	–	18.39 (59.87)	Czembor et al. (2015)
Russia	2016–2018	(9976)	(3300)	–	(3970)	Kokonenko et al. (2019)
Serbia	2013–20,195	(4000)* (60000)**	(1750)* (8000)**	- -	(350)* (4000)**	Kos et al. (2020)
	2018	794.98 (1202)	45.82 (64.67)	–	–	Krnjaja et al. (2020)
USA	1990	(48.5)	–	–	–	Shelby et al. (1994)
	1991	0.87 (1.82)	–	–	–	Chamberlain et al. (1993)
	1998 1999	44.4 (85.5) 2.73 (8.1)	– –	– –	– –	Abbas et al. (2006)
	2001	48.3 (56.8)	–	–	–	

*maize for human consumption; **maize for animal consumption

increased until harvest. For this reason, early harvest (at greater than 25% kernel moisture) may be a potential strategy to reduce the level of FB contamination.

Environmental conditions

In 2014, Cao et al. (2014) determined that the two critical periods for FB production were flowering and kernel drying. They also concluded that high rainfall and higher humidity around silking together with low temperatures limited *F. verticillioides* infection, while high temperatures increased the FB content. De la Campa et al. (2005) developed a model to predict FBs contamination by considering weather conditions and insect damage. The results showed that environmental conditions around silking were found to be more critical for FB production than insect damage, while high temperatures (Tmax >34 °C) and dry conditions (rain <2 mm) stimulate FB accumulation. In Italy, Maiorano et al. (2009) developed a risk model named FUMAgrain involving the maize-*F. verticillioides* pathosystem based on maize development, *F. verticillioides* infection, FB production, and the damage caused by the European Corn Borer (*Ostrinia nubilalis*). Considering meteorological conditions, FUMAgrain provides risk alerts at the end of the flowering and maturation. García-Díaz et al. (2020) evaluated the presence of mycotoxins and their *Fusarium* producing species in three different stages during three consecutive seasons (2016–2018). The results showed that *F. verticillioides, F. proliferatum,* and *F. graminearum* were the only species present, while FB was the only mycotoxin quantified. Moreover, high FB content was detected at the pre-harvest stage (seven days before harvest; 35% kernel moisture), mainly in the 2017 season, where humid (rainfall of 50 mm) and high temperatures (maximum of 42 °C) might have effected an increase in FB production. Furthermore, Ferreira Rosa Junior et al. (2019) showed that an environment with higher temperatures might increase FB production in hybrid maize.

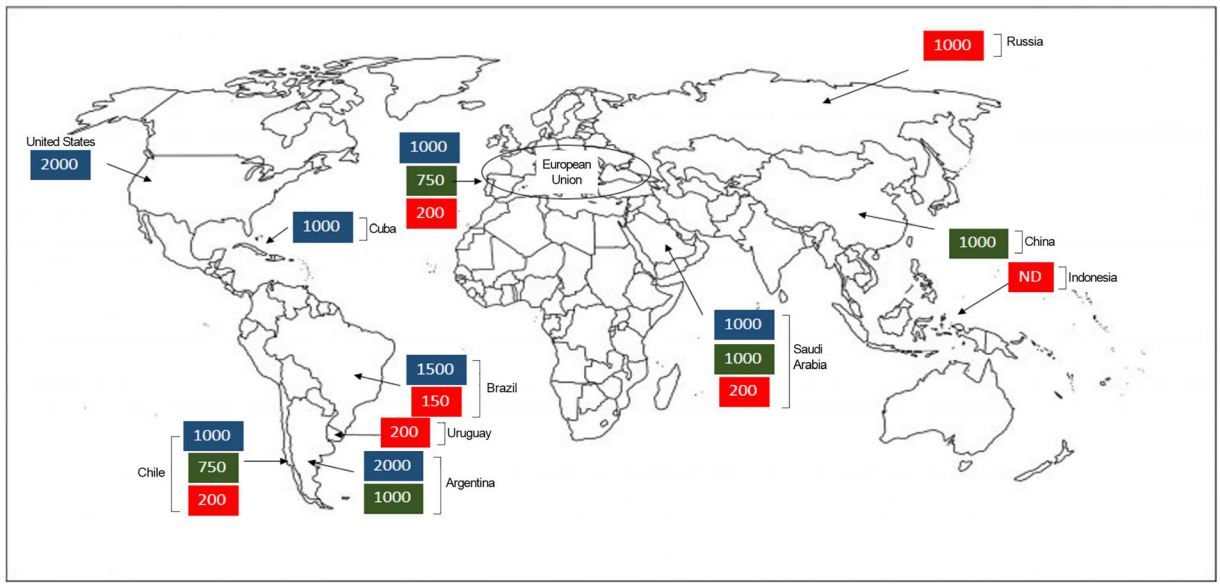

Fig. 1 Maximum levels of *Fusarium* mycotoxins allowed in maize flours worldwide. References: blue, green, and red boxes represent the maximum tolerable for FBs, DON, and ZEN content, respectively. **ND.** Not detectable

Recently, Links et al. (2020) evaluated the association of maize characteristics associated with resistance to *F. verticillioides* and FB accumulation in available commercial cultivars. For this purpose, 15 commercial cultivars were silk channel inoculated with *F. verticillioides,* and structural trait, physic-chemical properties, gene expression of defense-related genes, infection, and climate data variables were analysed. The results demonstrated that pH, N content, C/N ratio, peroxidase activity, and *PR5* expression of each cultivar evaluated correlate positively with *F. verticillioides* infection. The kernel pH value strongly influences the presence of *F. verticillioides* and the production of the mycotoxins. Flaherty et al. (2003) showed that low pH increases the presence of *F. verticillioides*, while acidic conditions favoured FB production. According to these results, several assays have been developed to understand the optimal requirements for FB production, suggesting that the optimal pH values ranged from 3 to 4, requiring good aeration for maximum FB production (Keller et al., 1997).

Storage factors

Farmers usually store kernels using conventional hermetic bags or silos to ensure maize supply for several months. In this condition, the main biotic factor affecting kernel quality is the level of fungal presence, whose growth and mycotoxin production depend mainly on atmosphere, kernel moisture, pH, and temperature conditions. Africa is one of the countries that widely uses maize storage for human consumption, which has been the object of several types of research.

In 1996, samples from several small-holder farm storage units from different districts of Kenya were obtained to analyze the presence of *Fusarium*. Many species were found: *F. verticillioides*, *F. subglutinans*, *F. graminearum*, *F. oxysporum*, and *F. solani*. The concentration of FBs varied from 3600 to 11,600 μg/kg, not quantifying FB in those samples that showed a lot of FB producing-*F. verticillioides* (Kedera et al., 1999). These results demonstrated that the optimal conditions for fungal growth cannot be similar to those required by mycotoxin production. In Nigeria, Akoma et al. (2019) collected 13 maize samples from various storage facilities, identifying the fungi present and mycotoxin production. *Fusarium* spp. were present in 27% of the samples. DON was detected in 92.3% of the samples with a mean value of 9.25 μg/kg, making it the most important mycotoxin found in the samples.

Similarly, the effect of three different structures used in Uganda to store maize kernels was evaluated. The kernel humidity, fungal presence, and the mycotoxins were measured. After two months of storage, the kernel humidity decreased from 19.2% to <14%. The *Fusarium* presence increased during the first two months but

decreased by the sixth month, while the FB content decreased over the storage period (Atukwase et al., 2012). Fandohan et al. (2005) also demonstrated that FB content decreased over the six months of storage, and no differences were observed among the three different storage structures used. However, the evaluation of *Fusarium* spp. in maize in Ethiopia demonstrated that the occurrence of *Fusarium* increased after six months of storage (Negasa et al., 2019). Maize samples from household maize storage units in three different agro-ecological sites were obtained. Several *Fusarium* spp., mainly *F. verticillioides*, were found and FBs were recorded, with a maximum of 10,000 μg/kg in a sample (Kankolongo et al., 2009). In 2011, Eckard et al. (2011) developed a survey to evaluate different *Fusarium* species and mycotoxin production in 17 samples of an entire plant used for silage in Switzerland. A total of 12 *Fusarium* species were identified, with *F. sporotrichioides*, *F. graminearum*, and *F. verticillioides,* being the most prevalent species isolated. DON was the main mycotoxin quantified with a mean of 1356 μg/kg, while NIV, 3-ADON, 15-ADON, HT-2, T-2, and ZEN were found in some samples.

The physiological stage of the crop at which samples are collected could determine not only the presence of a specific pathogen but also the mycotoxin detected. For instance, García-Díaz et al. (2020) sampled maize kernels in Spain in three physiological stages: anthesis, harvest, and storage. *F. verticillioides* and *F. subglutinans* were found in pre-harvest and storage, while *F. graminearum* was only present in storage. The only mycotoxins detected were FBs in the anthesis and harvest stages, but their occurrence was not detected in storage for one year of the three evaluated. Recently, Carbas et al. (2021) evaluated *Fusarium* spp. and mycotoxin production in maize from Portugal. The results showed the predominance of *F. verticillioides* over *F. subglutinans*, *F. proliferatum,* and *F. graminearum* at harvest and after six months of storage. Of the mycotoxins, only FBs were detected, increasing in their values by 20–40% during storage. It seems that storage conditions could stimulate the production of mycotoxins, but there are discrepancies regarding this conclusion. For instance, in Belgium, Vandicke et al. (2021), monitoring maize silage, concluded that the average mycotoxin content reduced during storage. According to the authors, the different results obtained could be the product of poorly conserved storage. Therefore, the entry of oxygen could modify the atmosphere inside the silage, thus favouring fungal colonization and subsequent mycotoxin contamination. In summary, the conditions that favour the presence of fungal and subsequent mycotoxins production in harvest time and storage have been described in Fig. 2.

Tools to reduce *Fusarium* impact

As climatic conditions cannot be controlled, management strategies focused on the host could be used to mitigate the impact of the *Fusarium* species and their effect on the final products as described below (Fig. 2).

Cultural practices One of the most important management practices to reduce *Fusarium* and subsequent mycotoxin production in maize is the crop rotation. Cotton and Munkvold (1998) demonstrated that isolates of *Fusarium* species producing FER can survive at least 630 days on the surface or in buried maize residue. These results demonstrate the importance of intelligently evaluating the rotation of crops, considering that maize residue acts as a long-term source of inoculum for future crops. Similarly, Chang et al. (2020) showed that a maize/soybean relay-strip intercropping system could reduce and change the diversity and aggressiveness of *Fusarium* species.

The choice of sowing date is another important tool for reducing *Fusarium* presence. Berghetti et al. (2020) demonstrated, in Brazil, that fungal incidence is lower earlier in the sowing season (September) compared to later in the season (December). In Italy, Blandino et al. (2017) investigated the effect of the combination of sowing dates and maize hybrids on the occurrence of mycotoxins. The FBs content increased in the late sowing date.

Conventional and no-tillage systems have not shown differences in the incidence of FBs, but N fertilization increased its amount (Marocco et al., 2008). In Brazil, however, Sataque Ono et al. (2011) demonstrated that FBs content correlates negatively with N content.

Another cultural practice that can increase the occurrence of *Fusarium* spp. is the choice of crop density. Krnjaja et al. (2019) compared the fungal presence and mycotoxin production at three plant densities: 55,000 (PD1), 64,000 (PD2), and 75,000 (PD3) plants/ha. The occurrence of *Fusarium* spp. increased with plant density. Comparing PD1 and

PD3, an increase in DON and FB content (from 132.06 μg/kg to 196.94 μg/kg and from 1012.69 μg/kg to 1260.25 μg/kg, respectively) were also observed.

Maize hybrid selection Although several cultural practices have been evaluated to reduce *Fusarium* presence and mycotoxin contamination, these are not efficient enough to control field infection, mainly because disease severity depends strongly on climatic conditions. Selection of maize hybrids is the primary tool to reduce *Fusarium* infection. Studies have shown that different maize hybrids develop different levels of *Fusarium* severity and mycotoxin content; hence selection of genotypes with the best features could reduce the effects of *Fusarium* on maize kernels and their subsequent mycotoxin contamination. Presello et al. (2006) evaluated a set of Argentinian maize in Ottawa, Canada, inoculated with *F. verticillioides* and *F. graminearum* to search for resistant germplasm. Those that showed the best behaviour were re-evaluated in Pergamino, Argentina. The results demonstrated that the variable with most effect was the genotype, compared with the fungus or environment. Some maize components play a crucial role in the genotypic resistance against *Fusarium.* For example, Bily et al. (2003) found that dehydromers of ferulic acid, the primary cell wall phenolic acids, may play an important role against *F. graminearum*. It has been shown that maize with high content of phlobaphenes, a phenolic compound of the pericarp, results in a decrease in mycotoxin accumulation (Landoni et al., 2020). Moreover, transgenic maize hybrids expressing *cryIA* genes that reduce kernel damage by insects reduce *Fusarium* infection, preventing one of the possible entryways of the fungus (Bacon et al., 2008). The use of Bt maize genotypes seems to reduce fungal growth and mycotoxin contamination (Bakan et al., 2002; Magg et al., 2002). Gasperini et al. (2021) evaluated the fungal and mycotoxin presence in several of Brazil's genetically modified (GM) non-GM maize cultivars. The number of fungal species and quantity of mycotoxins were significantly lower in GM maize than non-GM maize. Another important trait to consider when selecting the maize hybrid is the kernel dry-down rate (KDD) which could decrease GER disease development (Kebebe et al., 2015).

Biological control Several biological control strategies have been shown to have positive effects on *F. verticillioides* endophytic growth and FB production.

The endophytic bacterium *Bacillus subtilis* occupies the *F. verticillioides* ecological niche within the plant, reducing its growth and subsequent mycotoxin accumulation (Bacon et al., 2001). Cavaglieri et al. (2005) evaluated bacterial populations from the maize rhizoplane and their capacity to inhibit *F. verticillioides* root colonization and FB1 accumulation in vitro. *B. subtilis* CE1 strain was the most effective in reducing *F. verticillioides* growth parameters and toxin production in greenhouse assays.

Trichoderma viridae, isolated from maize root, has also been used against *F. verticillioides*, suppressing radial extension of colonies on PDA plates as well as FB1 production (Yates et al., 1999). It has also been demonstrated that treatment with *Trichoderma* agents has advantages for controlling pathogen infection and promoting maize seedling growth (Lu et al., 2020).

Recently, the use of the biological control agent (BCA) *Clonostachys rosea* was demonstrated to be effective at suppressing the development and release of primary inoculum of *F. graminearum* from maize stalks (Gimeno et al., 2020).

The use of essential oils to inhibit fungal growth and mycotoxins has also been demonstrated. Perczak et al. (2020) tested the capacity of cinnamon, palmarosa, orange, and spearmint essential oils against *F. graminearum* and *F. culmorum,* demonstrating that these could inhibit fungal growth and reduce mycotoxin production. Cinnamon and oregano essential oils have been shown to be effective against *F. proliferatum* and its FB production (Velutti et al., 2003).

Chemical control Although research into the chemical control of epidemics of *Fusarium* species has mostly been carried out on wheat (Nicholson et al., 2004), fungicides can be an important tool for managing FER, GER, and mycotoxin contamination in maize kernels. In vitro studies have demonstrated that sufficiently high doses of carbendazim and prochloraz reduced both the growth rate of *F. graminearum* and 3-ADON production. However, low doses of thiabendizole, tebuconazole, and fluquinconazole increased mycotoxin production relative to mycelial growth (Matthies et al., 1999). In addition, Simpson et al. (2001) observed that the application of azoxystrobin in field trials may

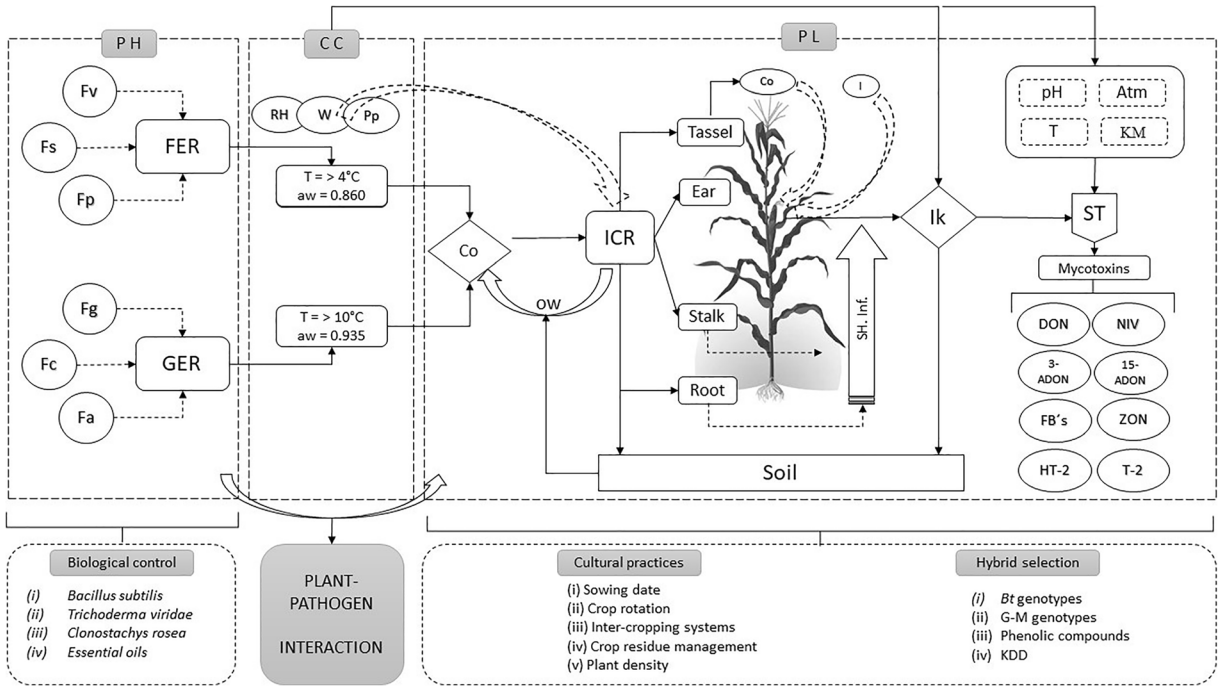

Fig. 2 Diagram of the life cycle of Fusarium ear rot (FER), Gibberella ear rot (GER), and their interaction with host plant (*Zea mays* L.). Above: disease triangle composed by PH (pathogens), CC (climatic conditions), and PL (host plant). Below: management strategies such as biological control, cultural practices, and hybrid selection. References: (i) PH: Fv = *F. verticillioides*, Fs = *F. subglutinans*, Fp = *F. proliferatum*, Fg = *F. graminearum*, Fc = *F. culmorum*, Fa = *F. avenaceum*; (ii) CC: RH = relative humidity, W = wind, Pp = precipitations, T = temperature, aw = water activity; (iii) PL: Co = conidia, ICR = infected crop residues, ow = infected residues that overwinter in the soil, I = spore-carrying insects, SH. inf = systemic hyphae infection, IK = infected kernels, ST = kernel storage, Atm = atmosphere, KM = kernel moisture. (iv) Others: GM = genetically modified, KDD = kernel dry-down rate

stimulate the production of mycotoxins, increasing the risk of grain contamination in susceptible wheat cultivars. This result was due to the differential control of FHB pathogens, allowing greater colonization by toxigenic *Fusarium* species, increasing the levels of DON.

The effectiveness of fungicides in field conditions for maize crops depends on the active ingredients, doses, and timing of application (Eli et al., 2021), suggesting the need for an integrated approach (Ferrigo et al., 2016). For instance, application of a mixture of azoxystrobin + cyproconazole (0,3 L/ha, Priori Xtra®) and carbendazim (1 L/ha, Derosal®) at two days around flowering could reduce GER severity (Andriolli et al., 2016). In addition, Masiello et al. (2019) evaluated in vitro 11 fungicides belonging to eight chemical classes with five different modes of action, selected from the most effective molecules used to control diseases caused by ascomycetes fungi. In artificially inoculated field trials, applications of prothioconazole (0.8 L/ha, Proline®) and thiophanate-methyl (1.25 L/ha, Enovit Methyl®) during flowering reduced contamination with *F. graminearum* (52% and 48%, respectively) and *F. proliferatum* (44% and 27%, respectively). However, none of the fungicides evaluated in field conditions was effective at controlling *F. verticillioides*. Recently, Eli et al. (2021) reported that the application of a novel carboxamide (pydiflumetofen), conventional triazole fungicides, and mixtures at full silk under field conditions reduced GER symptoms and the accumulation of DON and DON-3-glucoside, but did not affect FB concentrations in the kernel. Considering the research reported for small grain cereals, more detailed studies are required to design chemical control strategies that minimize the risk of contamination with mycotoxins in maize kernels.

Conclusion

The importance of the *Fusarium* genus as a maize pathogen has been well established. The capacity of this species to produce mycotoxins is well documented, both in vitro and under natural conditions. However, some aspects of the role of these mycotoxins in the life cycle of the fungus and their effect on plants are still uncertain.

Storage of maize kernels is commonly practised worldwide, and monitoring the *Fusarium* presence and mycotoxin content within the storage process is necessary. Several countries have set maximum levels of *Fusarium* mycotoxins for consumers; however, there is a lack of legislation in most countries. In the coming years, maize production is likely to increase to produce food and feed worldwide. The presence of *Fusarium* spp. and mycotoxin contamination make it difficult to achieve these objectives without compromising food safety. Hence a significant effort in disease mitigation through crop management is necessary to reduce future risks, using some strategies described above.

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Declarations

Conflicts of interest/competing interests The authors declare that they have no conflicts of interest.

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