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Changing climate, shifting mycotoxins: A comprehensive review of climate change impact on mycotoxin contamination

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Abstract

Climate change (CC) is a complex phenomenon that has the potential to significantly alter marine, terrestrial, and freshwater ecosystems worldwide. Global warming of 2°C is expected to be exceeded during the 21st century, and the frequency of extreme weather events, including floods, storms, droughts, extreme temperatures, and wildfires, has intensified globally over recent decades, differently affecting areas of the world. How CC may impact multiple food safety hazards is increasingly evident, with mycotoxin contamination in particular gaining in prominence. Research focusing on CC effects on mycotoxin contamination in edible crops has developed considerably throughout the years. Therefore, we conducted a comprehensive literature search to collect available studies in the scientific literature published between 2000 and 2023. The selected papers highlighted how warmer temperatures are enabling the migration, introduction, and mounting abundance of thermophilic and thermotolerant fungal species, including those producing mycotoxins. Certain mycotoxigenic fungal species, such as *Aspergillus flavus* and *Fusarium graminearum*, are expected to readily acclimatize to new conditions and could become more aggressive pathogens. Furthermore, abiotic stress factors resulting from CC are expected to weaken the resistance of host crops, rendering them more vulnerable to fungal disease outbreaks. Changed interactions of mycotoxigenic fungi are likewise expected, with the effect of influencing the prevalence and co-occurrence

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Abbreviations: 15-ADON, 15-acetyldeoxynivalenol; 3-ADON, 3-acetyldeoxynivalenol; 3ANX, 7α-hydroxy, 15-deacetylcalonectrin; AF, aflatoxin; AFB1, aflatoxin B1; AME, alternariol monomethyl ether; AOH, alternariol; a_w, water activity; ca., circa; CC, climate change; CO_2, carbon dioxide; DON, deoxynivalenol; EFSA, European Food Safety Authority; ELS, extensive literature search; FAO, Food and Agriculture Organization; FB1, fumonisin B1; FB2, fumonisin B2; FB3, fumonisin B3; FB4, fumonisin B4; FHB, Fusarium head blight; FUM, fumonisin; GM, genetically modified (organism); IARC, International Agency for Research on Cancer; IPCC, Intergovernmental Panel on Climate Change; NIV, nivalenol; NX, 7α-hydroxy, 3, 15-dideacetylcalonectrin; OTA, ochratoxin; ppm, parts per million; RCP, representative concentration pathways; RF, rainfall; T Max, maximum temperature; T, temperature; TTF, thermotolerant and thermophilic fungi; USDA-ARS, US Department of Agriculture—Agricultural Research Service; VCG, vegetative compatibility groups; ZEN, zearalenone.

of mycotoxins in the future. Looking ahead, future research should focus on improving predictive modeling, expanding research into different pathosystems, and facilitating the application of effective strategies to mitigate the impact of CC.

KEYWORDS
aspergillus flavus, fungi, *fusarium spp*, global warming, grape, maize, occurrence, pathosystem, toxins, wheat

1 | INTRODUCTION

"Expect the unexpected." This expression summarizes well how climate change (CC) will alter patterns of plant disease in ways that are sometimes difficult to predict, until they are reported for the first time (Pautasso et al., 2012; Webber, 2010). Already, rising temperatures, land and water scarcity, and extreme weather events, such as severe droughts, wildfires, and heavy precipitation, are causing unmatched damage to our food system. These variable and extreme events can introduce or exacerbate several food safety and food security hazards around the world, with major consequences for public health and international trade (Food and Agriculture Organization of the United Nations [FAO], 2020). The effects of CC will manifest both in high- and low-income countries, the former more focused on food safety, the latter being more also impacted by food security, being exposed to CC-related incidents, and lacking sufficient resources to cope with the implications of a crisis (FAO, 2020). In fact, it is projected that CC will not only impact food availability but also access to food, food utilization, and stability of the food supply (Foini et al., 2023; Nicholson et al., 2021). Changing temperature and precipitation patterns are already leading to modifications in the geographical distribution and endurance of foodborne pathogens. The Intergovernmental Panel on Climate Change (IPCC) has reported that temperate regions are incurring warmer temperatures; this can favor the expansion of pests into new suitable habitat, influence the severity and frequency of diseases, and pose novel human and animal health concerns in certain areas where they have never been present before (IPCC, 2022). Accordingly, reports already exist concerning the emergence of mycotoxins, considered playing the main role in CC impact in food safety, in areas with no prior history of contamination (Moretti et al., 2019).

Mycotoxins are secondary metabolites produced by a wide range of fungi. Though differing in structure and their biosynthetic pathway, all known mycotoxins are chemically stable and can endure most food and feed processing steps, resulting in the contamination of the final product. Consumption of such contaminated food and feed can cause harmful effects to both human and animal health, namely, hepatotoxicity, nephrotoxicity, neurotoxicity, and immunotoxicity, besides carcinogenicity (International Agency for Research on Cancer [IARC], 1993). The most important mycotoxigenic fungi are members of the *Aspergillus*, *Fusarium*, and *Penicillium* genera (Bennett & Klich, 2003) with aflatoxins (AF), ochratoxins (OTA), fumonisins (FUM), deoxynivalenol (DON), and zearalenone (ZEN) being the most relevant mycotoxins (Lee & Ryu, 2017). Mycotoxin production is influenced by temperature and relative humidity as well as pest-induced crop damage, all of which are alterable by CC. Different fungal genera and species have diverse ecological needs and optimal development conditions in term of temperature, relative humidity, rainfall (RF), and water activity. Therefore, the impact they will receive from CC will be quite variable. Till now, much research effort has concentrated on few mycotoxigenic fungi, especially *Fusarium* and *Aspergillus* species.

Within the *Fusarium* genus, *Fusarium graminearum* and *Fusarium verticillioides* are respectively involved in Fusarium head blight (FHB) and Fusarium ear rot. They are among the most important fungi associated with cereals and produce several toxic compounds, of which trichothecenes contamination of wheat and FUM contamination of maize are especially concerning (Xu et al., 2007). Within the *Aspergillus* genus, *Aspergillus flavus* is the most threatening species. It produces aflatoxin B1, which has mutagenic, immunotoxic, teratogenic, and carcinogenic effects on humans and animals, being classified as a group 1 carcinogen by the IARC (Ostry et al., 2017). In recent years, some shifts in the usual occurrence areas of those fungi were noticed. In particular, *F. graminearum* has emerged as the dominant *Fusarium* sp. in several northern European regions, replacing *F. culmorum*, and *A. flavus* has reportedly become dominant in southern European regions following dry and hot seasons outcompeting *F. verticillioides* (Battilani et al., 2016; Logrieco & Moretti, 2008; Nielsen et al., 2011).

The study of CC impacts on different pathosystems started in the 1990s (Pautasso et al., 2012). Before then, little research had been carried out on the topic. The aim of this review was to investigate how research on CC and mycotoxin occurrence has developed and evolved over time. An extensive literature search (ELS) carried out exposes the different topics on which scientific research has been focusing on in the last 20 years; research gaps and challenges are discussed to deliver guidelines on research topics that should be developed in the future.

2 | MATERIALS AND METHODS

The ELS was performed using the Ovid search engine to collect all available studies in the scientific literature on the topic "Mycotoxins and Climate Change." In particular, we focused on research studies published between 2000 and 2023. The papers were searched for by combining the following keyword criteria: (i) mycotoxins OR OTA OR AF OR trichothecenes OR FUM OR ZEN OR vomitoxin; (ii) *Fusarium* OR *Aspergillus* OR *Penicillium* OR *Alternaria*; (iii) Forecasts OR global OR CC OR simulation models OR mathematical models OR models; (iv) (i) AND (ii) AND (iii).

An initial total of 585 scientific papers were obtained, which reduced to 81 after applying inclusion/exclusion criteria (i.e., excluding duplicates; included only those papers, conference papers, and book chapters published in English; "climate change" mandatory present in the title or in the abstract; selecting studies addressing mycotoxin contamination in relation to abiotic stress and/or CC; selecting studies considering the prediction of fungal contamination with crop and fungal models). The 81 papers were analyzed and clustered based on fungi and mycotoxins mentioned, the food-matrix, modeling studies, and CC factors. For the last of these, only papers that took into account the interaction between different abiotic factors were considered, together with papers investigating future risk scenarios. This second assessment led to the selection of 50 articles for full-text reading.

Bibliometric metadata for the selected research papers were then exported from the Ovid search engine. Metadata text files were elaborated using the scientific mapping software VOSviewer.

2.1 | Characterization of the ELS results

Figure 1 represents the logical framework of the study. Furthermore, the 585 papers gathered via the ELS were analyzed using the DrasticData Tool. Considering the 81 papers obtained after applying inclusion/exclusion criteria, a treemap was drawn that highlights how most papers were published in the *World Mycotoxin Journal*, followed by *Food Research International and Toxins* (Figure 2).

By examining the co-occurrence of keywords, Figure 3 reveals important links between *Fusarium* and various species of *Fusarium*, including *F. culmorum*, *F. graminearum*, *F. avenaceum*, and *F. poae*. Additionally, *Fusarium* showed associations with the genera *Aspergillus* and *Penicillium*, suggesting frequent discussions of these fungal genera in published mycotoxin research.

Figure 4 shows a strong connection (marked by thicker lines) between the mycotoxin DON and other mycotoxins, such as nivalenol (NIV) and ZEN. This association arose from their classification as trichothecenes, leading to their common discussion in research papers.

Our analysis of Figure 5 revealed separate connections between mycotoxins and specific host cultures. It is noteworthy that DON was linked to wheat and maize, OTA to grapes and coffee, aflatoxin B1 (AFB1) to maize, and *Alternaria* toxins to both cabbage and cauliflower.

We also explored the temporal development of research papers (2000–2023) at the intersection of CC and mycotoxins. This evolution is presented in Figure 6, encompassing only the studies selected for full reading. The most discussed commodities and mycotoxins are illustrated in Figures 7 and 8; the analysis revealed that maize has been the most frequently investigated commodity, whereas AF has been the most extensively studied mycotoxin.

3 | RESULTS AND DISCUSSION

3.1 | CC impacts and future climatic scenarios

Many factors are involved in mycotoxin contamination, but climate is now the most important one (Paterson & Lima, 2010). We have entered the Anthropocene, an era in which the environment is being changed and influenced by human activities (Paterson & Lima, 2010, 2011). According to the IPCC, a warmer planet is "*virtually certain*" and warm spells or heat waves are "*very likely*." Global warming will continue to strengthen in the near term (2021–2040), mainly due to increasing cumulative CO_2 emissions; global warming is *more likely than not* to reach 1.5°C even under the very low greenhouse gases emission scenario and *likely* or *very likely* to exceed 1.5°C under higher emissions scenarios (IPCC, 2022). Temperature and precipitation (along with sea level) are the variables most likely to be affected by future global change, and their eventual alterations are expected to have a wide array of impacts on plants and their pathogens,

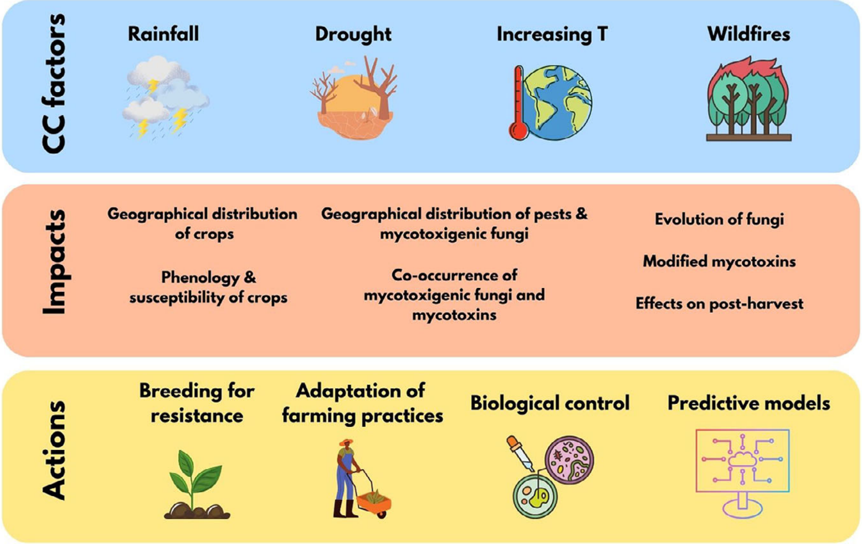

FIGURE 1 Logical framework of the study defining the climate change (CC) factors, the effects that they exert on crops and mycotoxigenic fungi, together with the strategies available to counteract mycotoxin contamination.

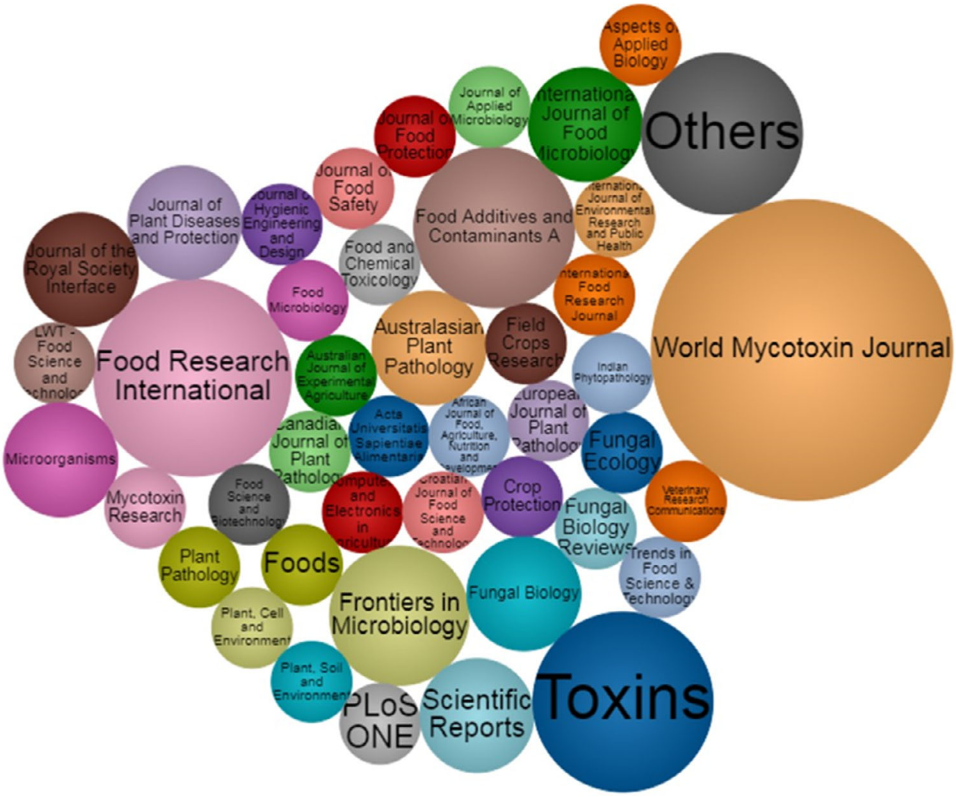

FIGURE 2 Treemap of all source titles identified during the research process. The treemap elaborated and created using DrasticData tool.

including their metabolites, like mycotoxins (Paterson & Lima, 2010). In fact, the traditional balanced disease triangle of the pathogen, host plant, and environment is changing because of the relative importance and pressure of the environmental component (Medina et al., 2017; Pautasso et al., 2012). This variability can impact on the growth of host plants and on their immune signaling and abiotic stress responses, as well as influencing pathogen survival, growth, and delivery of virulence factors. Therefore, the expected outcome is that host plants can range from being fully susceptible to being fully resistant to their enemies, whereas the pathogen could span from causing severe diseases to being only weakly pathogenic (Velásquez et al., 2018). In short, it is evident that prior balanced pathosys-

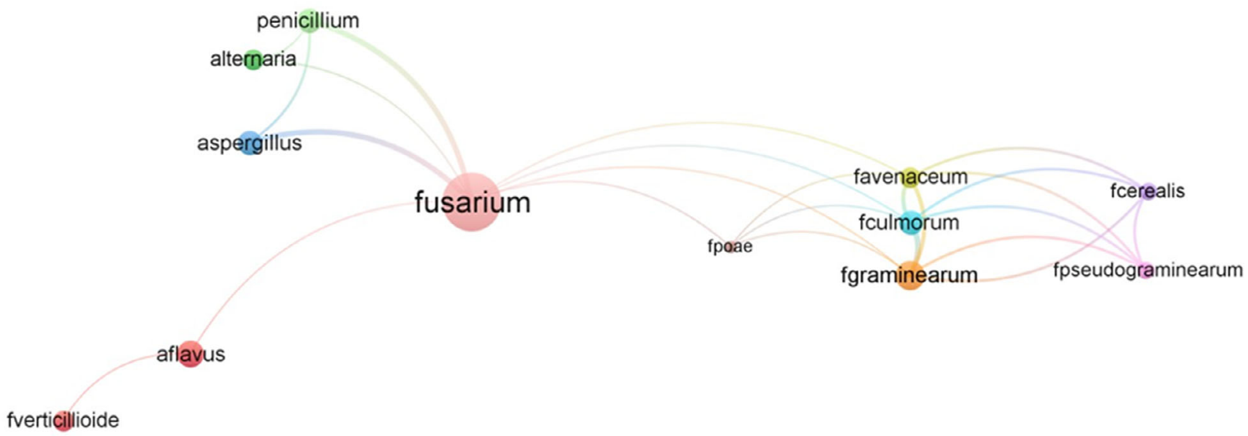

FIGURE 3 Scientific mapping of strictly linked networks for *Fusarium* as a keyword, based on papers identified during the research process. This map was elaborated and created using VOSviewer.

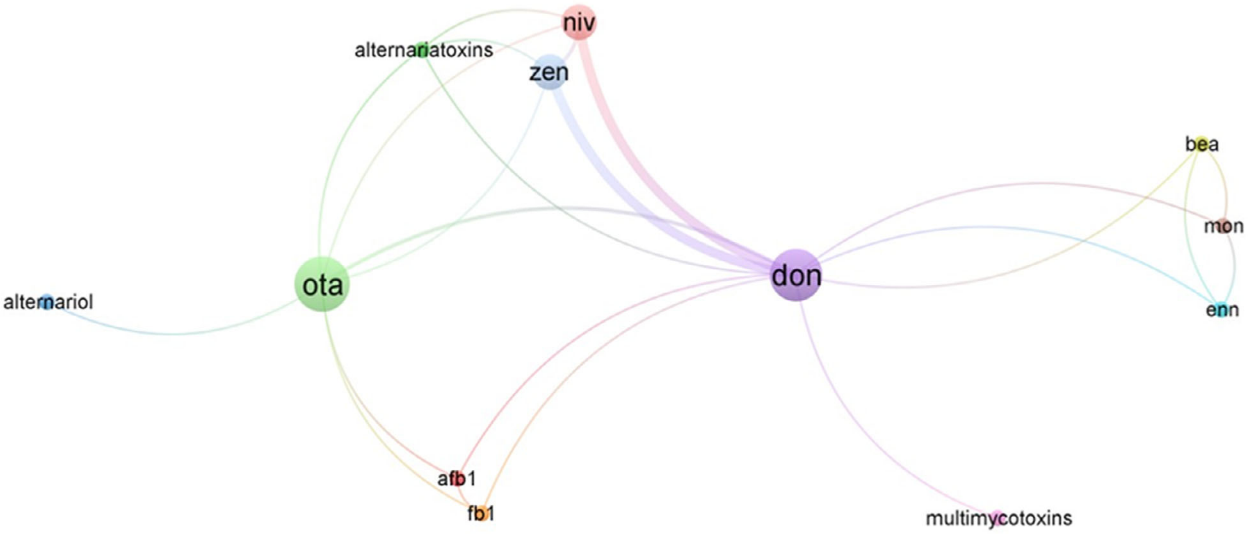

FIGURE 4 Scientific mapping of strictly linked networks for deoxynivalenol (DON) as a keyword, based on papers identified during the research process. This map was elaborated and created using VOSviewer.

tems could be disrupted, taking new and mostly unknown turns.

CC is expected to profoundly affect the landscape worldwide (Magan et al., 2011). The European Food Safety Authority examined the potential impact of CC in Europe and suggested these effects will be (a) regional and (b) detrimental or advantageous depending on the geographical region considered (Battilani et al., 2016). Hence, the impact of CC on agriculture and food safety and food security will vary among different geographical areas, but profound impacts on agriculture are likely (IPCC, 2022). For most of the globe, however, CC is expected to negatively affect agriculture; notably, crop production in semiarid (and food-insecure) regions of the world will decrease (van der Fels-Klerx et al., 2016). In African regions, hotter tropical climates and longer periods of drought stress would have a significant impact on the amount of food produced and their levels of mycotoxin contamination (IPCC, 2022; Magan et al., 2011; Paterson & Lima, 2011).

In southern and southeastern Europe, besides decreased agricultural yields, drought, heat waves, desertification, and greater torrential RF are also all predicted, with the Mediterranean Basin likely becoming a CC “hot spot” (European Commission, 2007; Magan & Medina, 2016; Paterson & Lima, 2011). In western, central, and Atlantic Europe high precipitation volumes, strong storms and floods are projected to become more frequent, particularly in wintertime. Milder/wetter winters, hotter/drier

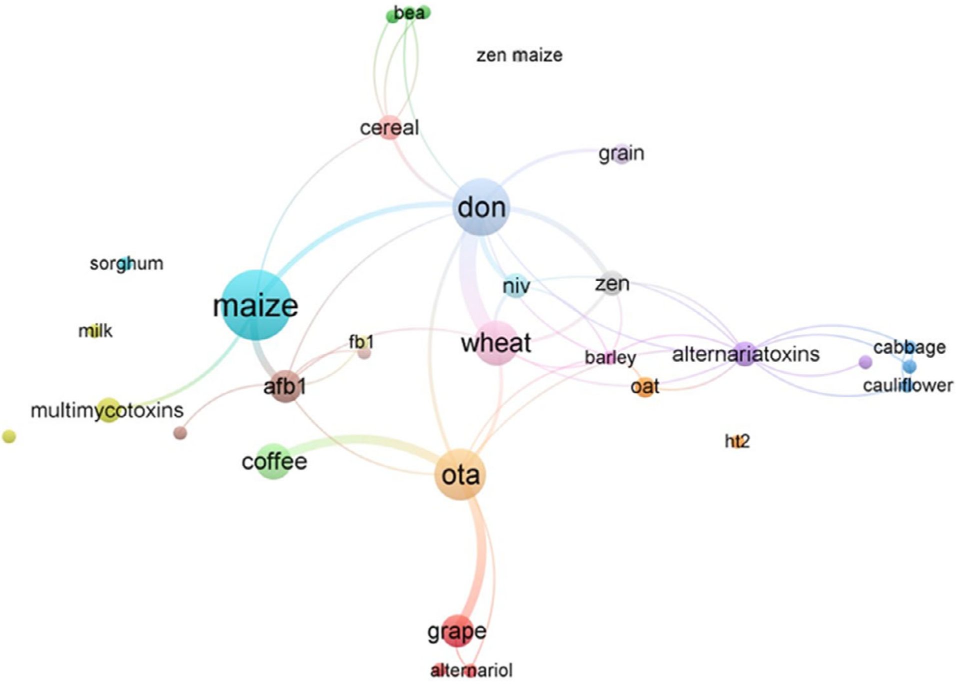

FIGURE 5 Scientific mapping of strictly linked networks for different mycotoxins and crops, based on papers identified during the research process. This map was elaborated and created using VOSviewer.

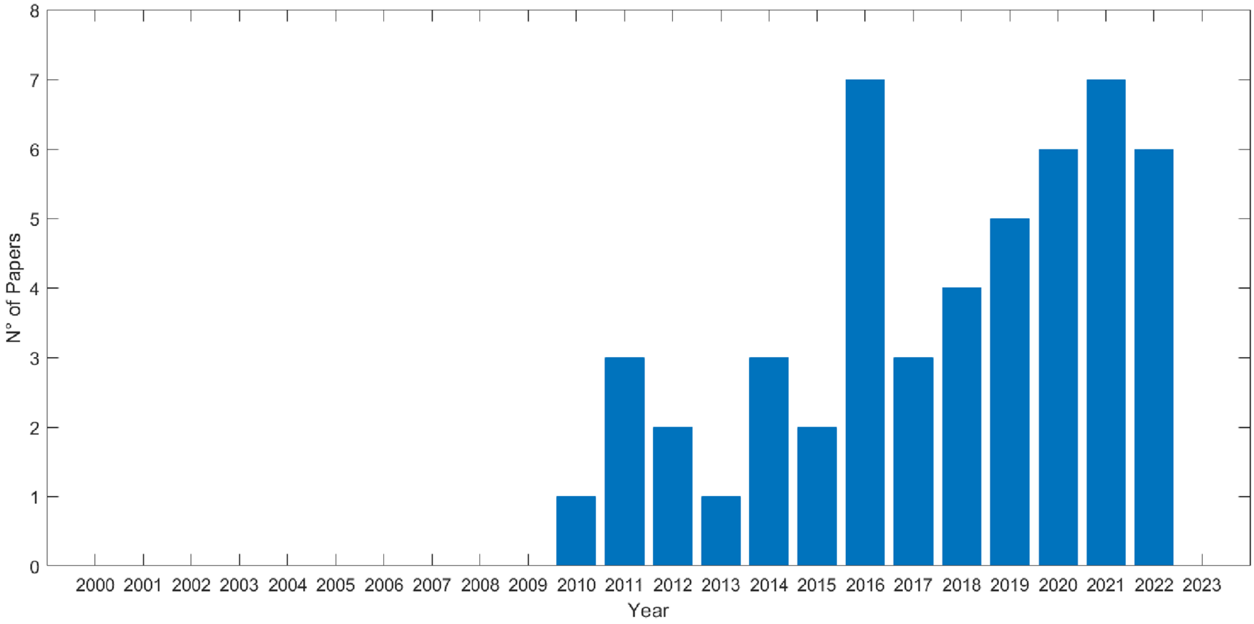

FIGURE 6 Bar graph shows the number of papers published throughout the years on the topic of climate change and mycotoxins.

summers, and generally more extreme weather incidents are all forecasted (European Commission, 2007; IPCC, 2022; Paterson & Lima, 2010). In northern Europe, an increase in yearly precipitation of up to 40%, with a higher risk of floods, is projected. Nevertheless, novel crops may be cultivated and an increase in those crop yields can be expected (European Commission, 2007; Paterson & Lima, 2011).

In Australia, temperature is projected to rise dramatically by 2100 and more hot days and heat waves are expected. Indeed, extreme events, including marine heat waves, major hailstorms, and fires, have been recorded in recent years (IPCC, 2022).

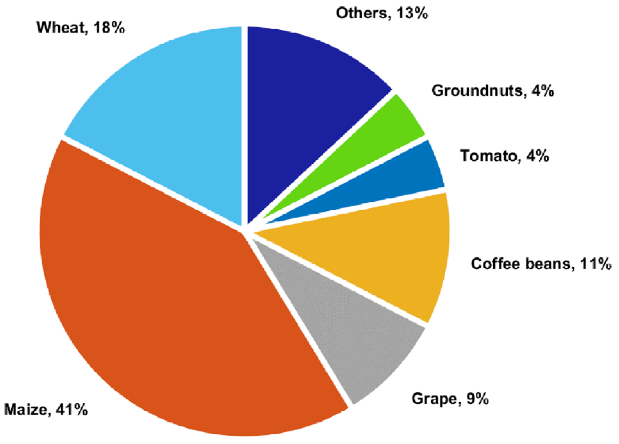

FIGURE 7 Pie chart showing the most prevalent crops in different studies.

In Asian countries, freshwater availability is projected to decrease by 2050 and coastal areas will face a higher risk of flooding. Rising temperatures are increasing the likelihood of heat waves across Asia, as well as droughts in arid and semiarid areas of western, central, and southern Asia, and leading to delays and weakening of the monsoon circulation in southeast Asia (IPCC, 2022).

In Latin America, there will be a significant increase in temperature and decrease in soil water that could reduce crop productivity (Paterson & Lima, 2011; Ponce-García et al., 2021). The risk of drought, floods, and landslides is projected to increase, together with the risk of large-scale changes and biome shifts in the Amazon (IPCC, 2022).

Finally, in USA, water resources will be stretched, and floods and drought are projected to be more common and intense, depending on the geographical area considered (IPCC, 2022; Paterson & Lima, 2011).

3.2 | Changes in geographical distribution, phenology, and susceptibility of host crops

According to Paterson and Lima (2011), there will be two predominant effects on crops due to CC: More crops may be produced in currently cool or cold regions (e.g., parts of northern Europe), and fewer will be harvested in currently hot regions (e.g., many areas within Africa). As part of the general "movement of crops to the Poles," first postulated by Pritchard (2011), the production of tropical crops, such as coconut, maize, soybeans, coffee, and cocoa, may become optimal in the world's currently subtropical regions. In particular, maize production will be reduced in certain areas, such as Africa and southern Europe, yet augmented in northern and central Europe, the USA, South America, and Asia (Battilani et al., 2016; Dovenyi-Nagy et al., 2020; van der Fels-Klerx et al., 2016; Juroszek & Tiedemann, 2013; Paterson et al., 2018; Ramirez-Cabral et al., 2017; West et al., 2012).

Supporting this latter statement is the work by Ramirez-Cabral et al. (2017) indicating that one of the most relevant changes for maize cropping is greater suitability in large areas of Europe, especially toward its northern regions (England, France, Germany, Denmark, the Netherlands, Poland, Slovakia, and the Czech Republic). Furthermore, Nordic countries are expected to shift from a state of unsuitability to one of marginal suitability. Considering grape production, falling productivity is projected in southern Europe, USA, and Australia, whereas northern European regions (e.g., Mosel Valley, Alsace, Champagne, and the Rhine Valley) could become more suitable for warmer-climate varieties of grapevine (Paterson & Lima, 2011; Paterson et al., 2018). Moreover, coffee production will be reduced in various tropical regions, such as Mexico, Brazil, and Vietnam, with the migration of suitable habitat to higher altitudes (Adhikari et al., 2020; Baca et al., 2014; Jassogne et al., 2013; Moat et al., 2017; Paterson et al., 2014; Zullo et al., 2011). Overall, CC could exert a profoundly negative impact on Arabica plantations, with a projected 65% reduction in the number of preexisting suitable localities and, at worst, an almost 100% reduction by 2080 (Paterson et al., 2014). At the same time, southern regions in the USA could become more bioclimatically suitable for coffee plantations (Paterson et al., 2014).

Additionally, host susceptibility to fungal infections could be altered under CC conditions (Paterson & Lima, 2010). Key crops, such as maize and peanuts, are especially prone to infection when they incur water stress. Specifically, pistachios and peanuts can develop hull cracking under heat and drought stress, and maize kernel integrity can be compromised by a more pronounced "silk cut" problem (Cotty & Jaime-Garcia, 2007; Magan et al., 2011). Moreover, it is proven that phytoalexin production may be reduced under heat stress, thereby increasing peanut's susceptibility to fungal infection and mycotoxin production by, for instance, *A. flavus* (Paterson & Lima, 2010).

Furthermore, CC will affect plant physiology, modifying stomatal patterns on leaf surfaces, with the effect of influencing transpiration and photosynthetic capacity and thus possible invasion by pathogens (Magan et al., 2011). Another effect from CC is an earlier onset of anthesis (advanced by ca. 2 weeks by 2050) and maturity for harvest (by 3 weeks) for some cereals, like wheat (West et al., 2012). For maize, Battilani et al. (2016) found evidence for a shorter growing season, with earlier flowering and harvesting dates. Given rising CO_2 concentrations, several positive aspects that can be distinguished are the enhanced metabolism of crops and higher yields, with positive repercussions for crop growth dynamics. Still,

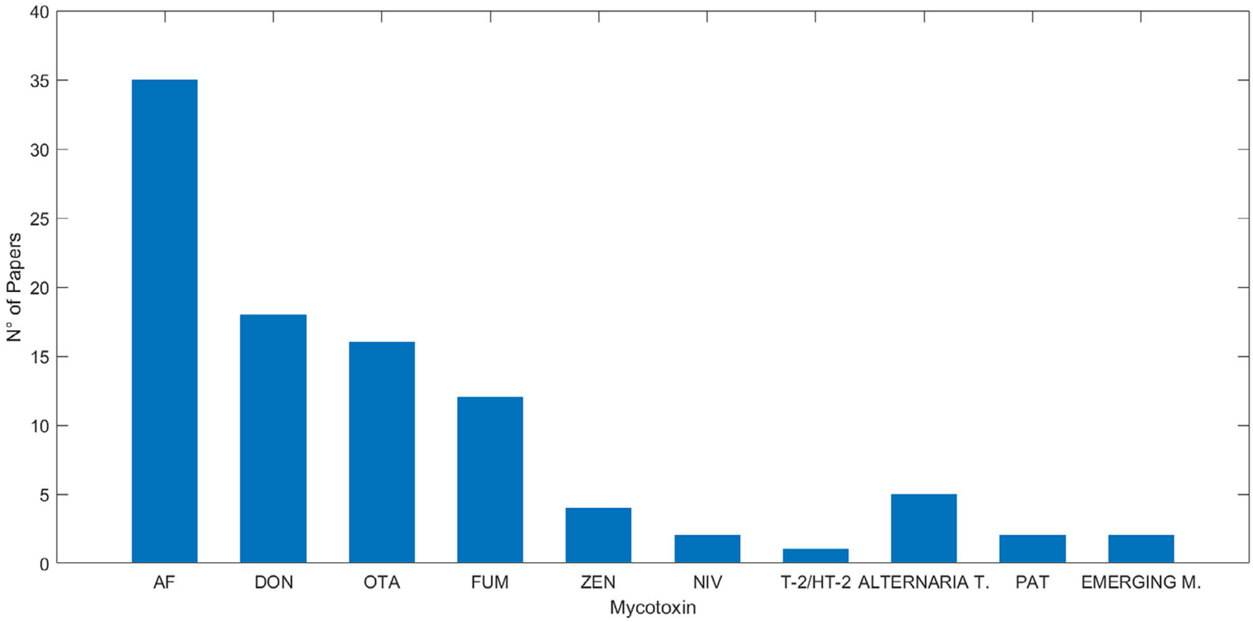

FIGURE 8 Bar graph showing the most prevalent mycotoxins in different studies.

abiotic stress factors such as those associated with CC have been shown capable of reconfiguring plant defense signaling pathways; this can reduce or augment plant susceptibility to a specific biotic stress. According to Vaughan et al. (2016), phytohormone signaling pathways seem particularly sensitive to elevated CO_2 levels, with salicylic acid biosynthesis and signaling enhanced, but jasmonic acid and lipoxygenase pathways suppressed in both soybean and tomato. These changes resulted in bolstered resistance against biotrophic pathogen infection but greater susceptibility to necrotrophic pathogen infection and insect herbivory. An elevated CO_2 level of ca. 800 ppm (about 2× the current value) increased the susceptibility of maize to *F. verticillioides* proliferation, although fumonisin B1 (FB1) contamination was not proportional to the biomass increase (Vaughan et al., 2014). Moreover, both maize and wheat crops are confirmed as being more susceptible to *Fusarium*-related diseases when CO_2 concentrations increase (Adhikari et al., 2020).

The effects of CC on crops include shifts in crop production regions due to changing temperatures and RF patterns. Production could increase in some areas, while being reduced in others. Maize is an accurate example of this phenomenon, with potential reductions in production in Africa and southern Europe but increases in northern and central Europe. Moreover, increased susceptibility to fungal infections under CC conditions, affecting key crops like maize and peanuts, is expected. Modifications in plant physiology, including stomatal patterns and flowering times, are already visible effects. Research should continue to investigate the correlation between abiotic stresses and crop susceptibility to fungal diseases and whether they can lead to a reconfiguration of plant defense signaling pathways. In particular, how elevated CO_2 levels can impact phytohormone signaling pathways, leading to enhanced resistance against some pathogens but increased susceptibility to others.

3.3 | Changes in geographical distribution of pests and mycotoxin-producing fungi

The so-called "movement of crops to the Poles" is combined with the "movement of pests to the Poles." As described by Vaughan et al. (2016), with their shifting or expanding geographical range of suitable weather conditions, the diversity and distribution of organisms within a community will be redefined. For instance, insect outbreaks are expected to increase in frequency and to move northward, confirming the "movement of pests to the Poles" (van der Fels-Klerx et al., 2016). Aphids are predicted to migrate to more temperate-like regions, leading to greater damage in cereal crops cultivated there. Moreover, they may act to suppress plant defenses in wheat when this crop is simultaneously exposed to them and *F. graminearum*, showing an accelerated FHB progression and greater mycotoxin accumulation (Drakulic et al., 2015; Vaughan et al., 2016).

Considering mycotoxigenic fungi, every fungal species has its own range and optimal environmental conditions—particularly in relation to air temperature and relative humidity and the amount and distribution of rain—for crop infection, host colonization, toxin production, and survival. Accordingly, changes in climatic conditions will lead to shifts in fungal populations and mycotoxin patterns, with fungal species migrating to those areas with the best environmental conditions for their growth; thermophilic fungi will be prevalent at lower latitudes and psychrophile ones at higher latitudes (van der Fels-Klerx et al., 2016). Therefore, one of the most anticipated effects of CC is that warmer temperatures will enable the migration, introduction, or establishment of more thermophilic/thermotolerant species, but in parallel, the higher frequency of extreme weather events will diminish the number of species with low phenotypic plasticity (Vaughan et al., 2016).

3.3.1 | CC impact on fungal dynamics

Bebber et al. (2013) predicted that, on a global scale, pests and diseases are moving to the poles at a rate of 3–5 km/year. However, that study did not focus on the spread of mycotoxigenic fungi or mycotoxins with respect to CC (Medina et al., 2014). Anyhow, there is mounting evidence that CC and extreme weather regimes are already impacting the geographical distribution of mycotoxigenic fungal species and their related toxins. This is exemplified in the 2003/2004 and 2012 seasons in northern Italy (Leggieri et al., 2015; Medina et al., 2015; Piva et al., 2006). Very hot and dry seasons occurred in northern Italy where maize is largely grown. Drought and elevated temperatures resulted in a switch from *F. verticillioides* and FUM contamination to *A. flavus* and AF contamination. *A. flavus*, a tropical and drought-tolerant mycotoxigenic fungus, tolerates a wide range of temperatures (19–35°C) with about 28°C being optimum for its growth and 28–30°C for AF production (Medina et al., 2014). AFs are a major concern in areas such as Sub-Saharan Africa but, since the Mediterranean area is becoming warmer, with a significant risk of drought phenomena in countries such as Spain and Italy, shifts in fungal and mycotoxin patterns are expected to happen more often (Fapohunda & Adewunmi, 2019). Based on a multi-mycotoxin long term monitoring survey of maize from 2011 through 2021, Locatelli et al. (2022) confirmed that *Fusarium* spp. are the most frequently present fungi, with FUMs being the predominant mycotoxins; nevertheless, AF contamination is becoming more common and widespread.

The increasing prevalence of *A. flavus* on maize crops was not only identified in Italy but also in the Balkan regions (i.e., Serbia and Croatia) and Hungary (Dovenyi-Nagy et al., 2020; van der Fels-Klerx et al., 2016). It is predicted that *A. flavus* will outcompete other fungi whose optimal temperatures are lower. To cite some supporting examples, it was isolated more frequently than *A. ochraceus* in Brazil nuts and pepper from Brazil (Freire et al., 2000). Moreover, *A. flavus* may outcompete *Aspergillus carbonarius*, with AF then posing a greater risk than OTA, in grapes grown in northern Portugal (Serra, Lourenço, et al., 2006; Serra, Mendonça, et al., 2006). Once established, it is unlikely that *A. flavus* will lose dominance to *Alternaria*, *Fusarium*, other *Aspergillus* conspecifics, or *Penicillium* spp.; hence, we may infer that AF will not be supplanted by alternariol, DON, FUM, and OTA in staple crops, such as peanuts, maize, and wheat (Paterson & Lima, 2011).

Not only *A. flavus* but also other fungi part of the genus *Aspergillus* section *Flavi* could become relevant in the future. *A.* section *Flavi* involves more than 20 species, of which *Aspergillus parasiticus, A. nomius, A. pseudotamarii, A. bombycis, A. toxicarius, A. parvisclerotigenus, A. minisclerotigenes, A. arachidicola, A. pseudonomius*, and *A. pseudocaelatus* have been proven to produce AF (Varga et al., 2011).

As fungi present in *A.* section *Flavi* can be favored by warmer environmental conditions, it can be assumed that also other aflatoxigenic species different from *A. flavus* could be detected in a higher extent because of CC. As an example, in a 5-year study (2012–2016) carried out by Nikolić et al. (2021), *A. parasiticus* was detected on maize kernels under field conditions in Serbia. Before, in Serbia as well as in other European countries, the occurrence of *A. parasiticus* in maize seemed quite rare (Giorni et al., 2007). Nevertheless, new studies are needed to eventually relate this report with CC.

F. graminearum is considered the main DON producer in central and southern Europe, whereas *F. culmorum* is reportedly dominant in Nordic regions. However, a decline in the presence of *F. culmorum* coupled with an increase in that of *F. graminearum* has been reported in some areas of central and northern Europe, like in the Netherlands, Germany, Poland, and the United Kingdom (Logrieco & Moretti, 2008; Moretti et al., 2019). These two *Fusarium* spp. have different temperature optima for growth, namely, 24–28°C for *F. graminearum* and 20–25°C for *F. culmorum*. This discrepancy may explain why *F. graminearum* has historically prevailed in regions where the summers are relatively hot, such as the USA, Canada, Australia, and parts of continental Europe, whereas *F. culmorum* is prevalent in cooler maritime regions such as northwestern Europe (West et al., 2012). That said, the northern European climate is predicted to become milder and more humid toward the year 2050, such that the subsequent associated CC effects will benefit *F. graminearum* growth (Moretti et al., 2019; Paterson & Lima, 2011). Consistent with that view, recent work by Martínez et al. (2022) conducted in Argentina revealed how warm nights can favor the growth of *F. graminearum* over *F. poae* in cereal crops, namely, barley and wheat, this decreasing the quality of grain and significantly its increasing mycotoxin contamination. The recent shift in dominance in favor of *F. graminearum* has also coincided with an increased occurrence of FHB on wheat in southern England (West et al., 2012) and central China (Zhang et al., 2014). Other changed fungal dynamics include the following: *Fusarium langsethiae*, now more common in oats and barley grown in the UK, with a correspondingly greater contamination level of T-2 and HT-2 toxins (Paterson & Lima, 2017); *Aspergillus steynii* and *Aspergillus westerdijkiae*, which are becoming more relevant OTA producers in coffee (Gil-Serna et al., 2014); the black *Aspergilli*, which are increasingly prevalent on onions and grapes from Hungary (Farkas et al., 2011); *A. niger*, along with *A. tubingensis*, which can prevail over *A. carbonarius* on grapes from southern Spain (Paterson et al., 2018). Moreover, Valverde-Bogantes et al. (2019) documented fungal population shifts, such as the more aggressive and toxigenic *F. asiaticum* 3-acetyldeoxynivalenol (3-ADON) replacing the existing NIV population in China and a highly toxigenic population composed mainly of *F. graminearum* 3-ADON isolates replacing the existing 15-acetyldeoxynivalenol (15-ADON) population in North America. Additionally, those authors reported on the introduction of *F. asiaticum* outside of Asia, on *F. graminearum* NIV isolates in the USA and Luxembourg, on *F. graminearum* 15-ADON in Norway, and on *F. graminearum* in South Korea.

Moreover, according to Magan and Aldred (2008) and Leong et al. (2011), xerophilic fungi, such as *Wallemia sebi*, *Xeromyces bisporus*, and *Chrysosporium* spp., could become more important colonizers of food because they can grow under dry conditions, with new toxic compounds occurring in consequence. Both walleminol and walleminone harbor toxigenic potential to animals and humans and are produced by the *W. sebi* fungus (Fapohunda & Adewunmi, 2019).

Paterson and Lima (2010, 2011) addressed the possibility that, under certain CC scenarios, some mycotoxigenic fungal species could go extinct, representing a CC benefit. For example, temperatures in Pakistan have reached a staggering 53.7°C (Iqbal et al., 2011); this could drive the extinction of fungal species, or at least inhibit xerophilic fungi like *A. flavus* and *A. parasiticus*. The prospect of aflatoxigenic fungi going extinct in currently hot regions is thus highly advantageous for tropical countries, as their food will have a low AF content and could be easily exported (Paterson & Lima, 2017). In any case, two points deserve attention: first, temperatures of 40°C or above also pose a challenge to crops' health. Should aflatoxigenic fungi go extinct, yet some crops persist, it does not prevent those aflatoxigenic fungi from being substituted by other more thermophilic fungi.

The "Parasites Lost phenomenon" hypothesis, whereby crops could experience a release from their associated pests as they move into new geographical regions, could lead to potential advantages in terms of enemy fungi and mycotoxin contamination (Mitchell & Power, 2003; Paterson & Lima, 2011). However, if temperatures do not become extremely high and drought conditions recur more often, then a stimulation of AF contamination may ensue (Fapohunda & Adewunmi, 2019). Further, it is plausible that crops will diminish in quality due to the stress-related effects of CC and thereby come to harbor more mycotoxins per unit weight of crops (Paterson & Lima, 2011).

3.3.2 | CC impact on mycotoxin dynamics

In the past, serious AF contaminations were detected particularly in the tropical climatic zones of developing countries. For instance, Benkerroum (2020) reported on past major outbreaks of aflatoxicosis associated mainly with maize-based foods, which occurred in West-India (1974), Kenya (1981 and 2004), and Tanzania (2016 and 2017). Nevertheless, such outbreaks are no longer limited to tropics anymore (Dovenyi-Nagy et al., 2020). AFs are increasing in the Mediterranean Basin, especially in crops such as maize and, more recently, in almonds, peanuts, and pistachios grown in southern Europe (Paterson & Lima, 2017). On the contrary, AFs may be of little or negligible concern in countries with currently very cold climates (e.g., Norway, Canada, and Russia), where even global warming will not result in temperatures warm enough to sustain the growth of *A. flavus* and *A. parasiticus* populations (Paterson & Lima, 2010).

Regarding OTA contamination, it is more commonly associated with *A. ochraceus* in warm regions, such as west and central Africa, and with *P. verrucosum* in temperate climates such as northern European countries and Canada (Fapohunda & Adewunmi, 2019). Given that OTA is optimally produced by *A. ochraceus* between 25 and 30°C but only at 25°C by *P. verrucosum*, it is likely the latter will become less prominent in OTA production due to CC, especially in currently warm regions (Adhikari et al., 2020). In general, according to Adhikari et al. (2020), AF will tend to supersede OTA as the major mycotoxin found in grapes and coffee, because temperatures will become more suitable for the thermotolerant *Aspergilli* that produce AF (Adhikari et al., 2020). Conversely, OTA will increase its presence in currently cold regions because *P. verrucosum* can thrive in those areas as temperatures become warmer (Magan et al., 2011; Paterson & Lima, 2010). Nonetheless, OTA contamination driven by OTA-producing *A. westerdijkiae* and *A. steynii* will probably continue affecting coffee beans grown in tropical regions (Gil-Serna et al., 2014).

With respect to FUM contamination, it is present in temperate climates and has a production peak at ca. 30°C. Therefore, a general increase in the FUM contamination of crops is anticipated, namely, maize, wheat, rice, and soybeans (Fapohunda & Adewunmi, 2019). Yet displacement by AFs is also possible in certain areas. *Fusarium* spp. are in fact tolerant of higher temperatures but they are not as xerotolerant as *A. flavus*; hence, in areas where RF is predicted to decrease, FUM may be replaced by AF. However, in crops like coffee, with their higher RF requirements, drought is unlikely to be an issue and *Fusarium* spp. are likely to continue thriving (Adhikari et al., 2020). Depending on the year and climatic conditions that develop, AFs and FUMs could alternate in dominance, as AFs thrive during hotter seasons and FUMs thrive during wetter seasons, as the study by Akello et al. (2021) highlighted, even if their co-occurrence is the most likely outcome. Therefore, unlike for OTA, FUM contamination seems capable of withstanding adverse climatic conditions brought about by CC. Although OTA contamination is generally expected to decline, giving way to AF contamination in many staple crops, FUM contamination is expected to be steady or even increase in the future.

An important effect tied to CC that cannot be overlooked is a possible switch in dominant mycotoxins produced to other related compounds, which could then become the predominant toxic contaminants. It is known that *F. verticillioides* is able to produce different FUM toxins (FUM B1, B2, B3, and B4); under a CC scenario the ratio of these toxins can significantly change. In fact, as shown by Medina et al. (2017), at levels of a_w of 0.97 and 0.95, with higher temperatures (15–30°C), the ratio of FB1/ fumonisin B3 (FB3) changes in favor of FB3. The same behavior was detected for the ratio fumonisin B2/ fumonisin B4 (FB4), where FB4 was favored at increasing temperatures.

Concerning DON contamination, in the cold and humid areas of northern European regions, these expected to warm up, the incidence and level of mycotoxins produced by *Fusarium* spp. (DON, but also ZEN) will increase (Gagiu, 2018). Both DON and ZEN are projected to increase in coastal savannah and humid rain forest regions, because *Fusarium* and *Penicillium* spp. thrive under conditions of high humidity and warm temperatures that are forecast for these areas (Fapohunda & Adewunmi, 2019). In addition, as West et al. (2012) highlighted, the incidence of FHB has been increasing in recent years in northern European regions such as the UK. As such, DON contamination should continue rising in future years in these regions, whereas its presence can be considered negligible in currently warm and hot areas.

Moreover, it is worth mentioning *Alternaria* toxins. According to Perre et al. (2015), these toxins may become more common in currently cold regions such as Poland, less prevalent in currently warm regions such as Spain. This geographical shift is expected to occur because the environmental conditions of southern European countries will become too extreme for the fungi to grow and produce toxins, whereas the conditions in central and northern European countries will become progressively optimal for that.

Furthermore, CC may cause changes in mycotoxin prevalence within the same species. As an example, *A. alternata* produces the mycotoxins alternariol (AOH), alternariol monomethyl ether (AME), and altenuene. Although AOH's maximum production is at 21°C and 0.95 a_w, AME's production is maximal at the same a_w level but requires much warmer conditions of 35°C. Thus, higher temperatures may lead to shifts from AOH to AME (Medina et al., 2017).

Finally, in tropical countries, where temperatures of 40°C and above could ensue under CC, aflatoxigenic fungi may get outcompeted by thermotolerant and thermophilic fungi (TTF). In fact, AF production is optimal at 28–30°C but ceases altogether at 37°C (Paterson & Lima, 2017). Many TTF produce secondary metabolites that could contaminate food crops. Some TTFs are currently present on crops, but they are rarely isolated because they are outgrown by mesophilic fungi at a normal incubation temperature of 25°C (Paterson & Lima, 2017). Paterson and Lima (2017) also suggested that *A. fumigatus* is a TTF that could become of interest in the future. This fungus has been isolated from tobacco, as well as hazelnuts and walnut seeds, in experiments where the cultures were incubated at 45°C (Abdel-Hafez & Saber, 1993). Gliotoxin is its most well-known metabolite, and this could become more common in crops under extreme CC conditions. Patulin may also become increasingly pertinent under CC given its production by some TTF fungi, such as *Byssochlamys nivea* and *Paecilomyces saturatus* (Paterson & Lima, 2017).

The movement of pests toward the poles due to changing weather conditions will impact organisms' diversity and distribution. Insects are expected to migrate northward, causing increased damage to crops. CCs will influence fungal populations and mycotoxin patterns, with thermophilic fungi moving to warmer regions and psychrophile fungi to colder regions. Warmer temperatures may introduce more thermophilic species, whereas extreme weather events could reduce species with low adaptability. Therefore, future research should expand studies beyond the few mycotoxigenic fungi and crops that have been hot topics in the past to include other fungi and related mycotoxins that may become relevant due to CC. In particular, investigate other fungi besides A. flavus, including other aflatoxigenic species that could be detected at higher levels, together with TTF species.

3.4 | Co-occurrence of mycotoxigenic fungi and mycotoxins

Co-occurrence of mycotoxins has been associated with CC (Bertuzzi et al., 2014; Leggieri et al., 2020; Palumbo et al., 2020). Several reports mentioned more than 85% of maize samples being co-contaminated with ≥2 mycotoxins (Ibáñez-Vea et al., 2012; Locatelli et al., 2022).

Evidently, several fungi can contaminate the same crop at the same time. In the past, the contamination of food commodities, and therefore its effect on human and animal health, was studied by examining one fungus at a time. The germination, growth, and mycotoxin production were analyzed considering only the relation between that pathogen, its host plant, and the environment. However, fungi are members of fungal communities and are subjected to their dynamics. The presence of more fungi in the same environment can influence the growth of a single member species or strain and eventually mycotoxin contamination. Moreover, most fungi are not specialized in the production of a sole type of mycotoxin but rather can produce several mycotoxins. It follows that the co-occurrence of mycotoxins would be an obvious consequence (Smith et al., 2016).

The co-occurrence of mycotoxins can cause additive and eventually synergic effects, resulting in a modification of their toxicity to humans and animals in a not well-defined manner. Leggieri et al. (2019) investigated in vitro the co-occurrence of *A. flavus* and *F. verticillioides*, finding each fungus affected by the presence of the other. Notably, *A. flavus* and *F. verticillioides*, respectively, exhibited 10% and 44% decrease in colony diameter when grown together; however, that same influence was not detected for mycotoxin production. In fact, the dynamics of toxin production under differing temperature regimes followed a similar trend whether the two fungi grew alone or together (Leggieri et al., 2019). This was the first attempt to describe the impact of mycotoxigenic fungal co-occurrence under different temperature regimes on fungal growth and mycotoxin production. It is critical to continue investigating the interactions between mycotoxigenic fungi because CC does not influence the pathogen singularly, in modulating its virulence and pathogenicity. Rather, CC can also influence the dominance of fungi in a changing environment and their interactions in general. The first study conducted in field with artificially inoculated co-occurring fungi in maize revealed a relevant impact on both fungal incidence and mycotoxins' production, this strictly dependent on weather conditions. In particular, main interactions were noted between *A. flavus* and *F. verticillioides* and between *F. verticillioides* and *F. graminearum* (Giorni et al., 2019). More research is needed to better evaluate how fungal dynamics, and their mycotoxins' prevalence, may change under CC conditions in field trials (Leggieri et al., 2019).

Co-occurrence of mycotoxins in crops is a common phenomenon, with multiple fungi contaminating the same crop simultaneously. This can influence mycotoxin production and toxicity levels. Studies show interactions between fungi like *A. flavus* and *F. verticillioides* and how that can affect each other's growth. Anyhow, research is ongoing to understand how fungal dynamics and mycotoxin prevalence change under co-contamination conditions and in the future it should be investigated more the effect of co-occurrence of mycotoxigenic fungi under different temperature regimes on fungal growth and mycotoxin production, not only through in vitro studies but also in the field.

3.5 | Evolution and adaptation of fungi

Plant pathogens will most likely evolve and adapt to the new environmental conditions brought about by CC. This adaptation will probably proceed much faster than that of host crops, resulting in more efficient fungi and more vulnerable crops (Juroszek & Tiedemann, 2013). Accelerated evolution, increased disease incidence, changes in pathways or pathology, and infections in new host species or populations are all predicted to occur (Medina et al., 2017; Paterson & Lima, 2011). The ability of a mycotoxigenic fungus to mutate and hence respond to opportunities arising from environmental change is a key factor when assessing the potential impact of CC (Paterson & Lima, 2010). Several successive years of a favorable climate could cause a build-up of inoculum, leading to epidemics that are much more severe than when a single favorable year occurs. A greater survival of inoculum is also expected when CC leads to reduced competition between fungi (West et al., 2012) and the aggressiveness of fungi may mutate too. For example, 3-ADON isolates of *F. graminearum* are more resilient to extreme temperature events, and in response to heat or cold, they become more aggressive by producing more DON and ZEN than do fungal isolates from the 15-ADON subpopulation (Vaughan et al., 2016). Historically, studies examined morphological changes in response to temperature and water activity stresses. For example, Sabburg et al. (2015) showed that with an increased temperature the fungus *F. pseudograminearum* exhibited decreased fitness after host inoculation, whereas *A. niger* featured an abnormal spore morphology and reduced germination rates. Moreover, Gilbert et al. (2016) found a positive correlation between temperature increasing and the level of toxin production; 28–30°C were optimal conditions for the expression of AF cluster genes and toxin biosynthesis between, with AF biosynthesis undergoing a pronounced increase as temperatures rose between 20 and 30°C. Another critical issue is acclimatization; Akbar et al. (2016) noted how the acclimatization of *F. graminearum* cultures for 10–20 generations under CC conditions prior to infection of wheat exposed to CC conditions led to a significant increase in FHB, although the mycotoxin production level was not itself determined. Work by Medina et al. (2017) described how strains of *A. flavus* reacted differently when acclimatized to conditions of 37°C, 0.98 a_w, and 1000 ppm CO_2 for five generations on a pistachio nut-based medium. For one of the strains, acclimatization influenced its growth, yet for the other strain there was no significant effect on its colonization of pistachio nuts; further, for one strain its AFB1 production was significantly stimulated, whereas for the other strain there was no significant increase. This certainly suggests that intra-strain differences could emerge via the effects of acclimatization, and this may influence mycotoxin production since mixed populations of contaminant fungi commonly occur in food crops (Medina et al., 2017). On this matter, Paterson and Lima (2017) argued why and how adaptation of mycotoxigenic species will be important in the future. Overall, a succession of fungal species through their optimal growth temperature ranges is the most likely ecological outcome, given that this possibility would be way quicker.

A key topic that must be addressed is how CC can stimulate toxin biosynthetic genes' expression. Medina et al. (2014) organized the first attempt to quantify the effects of interacting factors of water stress × temperature × elevated CO_2 on the growth of *A. flavus* and its biosynthetic gene expression and AFB1 production. This revealed how, under slightly elevated CO_2 conditions, AFB1 production was stimulated, especially under drought stress at 37°C and 650 or 1000 ppm CO_2 exposure. This was evident from results obtained at 0.92 and 0.95 $a_w \times 37°C$ and 650 or 1000 ppm CO_2, where a statistically significant increase in AFB1 was detected. Yet fungal growth was relatively unaffected by imposing 2× and 3× the existing CO_2 levels at 37°C under the different water stress treatments applied. The relatively greater expression of both the structural aflD and regulatory aflR genes suggests a significant impact on the biosynthetic genes involved in secondary metabolite production.

It is worth noting how some studies (e.g., Akbar et al., 2016; Magan & Medina, 2016) demonstrated how mycotoxin gene expression and mycotoxin biosynthesis were differentially expressed in relation to CC conditions by different fungal species and strains. For instance, in the study by Akbar et al. (2016), under CC-related stress conditions, *A. westerdijkiae*, *A. ochraceus*, and *A. steynii* exhibited an increase in OTA production, whereas *A. carbonarius* and *A. niger* displayed a reduction in it. Moreover, some intraspecific differences in T-2 production by subjecting different strains of *F. langsethiae* to interacting CC-related abiotic factors were recently highlighted (Verheecke-Vaessen et al., 2021).

Another point that warrants attention when considering the effects of interacting environmental factors on fungal growth, mycotoxin gene expression, and mycotoxin biosynthesis is that studies can obtain contrasting results. This happened with Cervini et al. (2021) and Akbar et al. (2016), whose results disagreed with respect to the growth of *A. carbonarius* under elevated CO_2 levels: According to Cervini et al. (2021), elevated CO_2 levels resulted in a general stimulation of growth and OTA production, whereas Akbar et al. (2016) found a reduction in OTA production. This is perhaps best explained by the different experimental conditions used, in which Akbar et al. (2016) excluded the effect of photoperiods and temperature cycling, as highlighted by Cervini et al. (2021). Moreover, the studies were conducted on different media substrates.

The evolution of plant pathogens due to CC could outpace host crops, leading to more efficient fungi and vulnerable crops. Changes like accelerated evolution, increased disease incidence, and mutations in fungi's aggressiveness are expected. Additionally, mycotoxigenic fungi's ability to mutate in response to environmental changes is crucial. Studies show how climate conditions influence fungal growth, mycotoxin production, and gene expression. Interactions of water stress, temperature, and CO_2 levels can stimulate toxin biosynthetic genes, impacting mycotoxin production. Different fungal species and strains may react differently to CC conditions, influencing mycotoxin production. Therefore, it is crucial to continue examining the possibility that CC may cause changes in mycotoxin prevalence within the same fungal species, leading to new predominant toxic compounds. Moreover, investigating whether higher temperatures coupled with other abiotic stresses can stimulate the expression of toxin biosynthetic genes in fungi, leading to an increase in the level of toxins produced, is of outmost importance.

3.6 | Modified mycotoxins

There is growing interest in the so-called "masked mycotoxins" or modified mycotoxins. These compounds can result from plants and fungi actions and have been linked to resistance and detoxification mechanisms. Although by themselves they often exert lower toxicity than their original form, some of them have been demonstrated to partially or totally cleaved under gastrointestinal conditions, resulting in similar toxic effects as their parent compound after ingestion (Dall'Asta & Battilani, 2016; Giorni et al., 2015; Medina et al., 2017). An example of modified mycotoxin concerns DON, which can be converted to DON-3-glucoside in cereal crops, yet other mycotoxins are also reportedly modified by plant defense mechanisms (Berthiller et al., 2013). Recently, "new" chemotypes have been identified in North America; Sumarah (2022) found that alterations in enzyme activity led to the production of a 3-acetyl NX (3ANX) toxin. This 3ANX is structurally similar to 3ADON and its interaction with the host plant results in deacetylation to form a NX toxin apparently more toxic than DON.

Under CC conditions, the complexity of fungus–plant interactions and consequent mycotoxin modification is more complicated because of the dual effects on both actors in the system. According to Medina et al. (2017), no research has yet examined how different environmental conditions, in particular CC, will affect the production of modified mycotoxins. Nevertheless, it is often stated that CC will lead to changes in plant physiology and thereby also alter the interaction between a pathogen and its host plant. Therefore, studies addressing how these changes will lead to modifications of plant protection mechanisms are needed (Medina et al., 2017).

There is a rising interest in modified mycotoxins derived from plant and fungi interactions. New chemotypes like 3ANX toxin have been discovered. Anyways, under changing climate conditions, the complexity of fungus–plant interactions and mycotoxin modifications increases. Therefore, research on how CC leads to changes in plant physiology that may alter the interaction between a pathogen and its host plant, thereby modifying the production of modified mycotoxins, is needed.

3.7 | Effects on postharvest

Mycotoxin contamination occurs when crops are growing, but it can continue from crop maturation until consumption under suitable conditions for fungi activity. The mature crop may be exposed to warm, moist conditions during its transportation and storage (Paterson & Lima, 2010). According to Paterson and Lima (2011), the currently cool regions, like North America, will experience worsening storage conditions as the temperature increase to those compatible with greater fungal growth. Conversely, the new hot and dry conditions that will ensue in some regions (e.g., Africa) will lead to good storage conditions, a potential advantage of CC. This is because hot and dry conditions will assist in maintaining the crop in a dry environment that could well be unsuitable for fungal growth and mycotoxin production. In general, regarding cereal crops, spoilage should not happen if grains are stored at a moisture content lower than 0.70 a_W; CC can help to reach this level, especially in the tropics. Additionally, those farms able to afford keeping their silos within safe ranges may experience higher costs from an increased need for energy (Paterson & Lima, 2010, 2011). Storage will be difficult in cases where CC results in high moisture levels, leading to problems with ensuring the drying of crops. High humidity (>85%), high temperatures (>25°C), insect and rodent activity, improper drying of crops, and water infiltration in the storage structure can promote the growth of *A. flavus* and hasten AF accumulation (Paterson & Lima, 2011). Accordingly, changes in storage procedures are required in both developing and developed countries. The former via technological progress sponsored by institutions and national authorities; the latter through adaptation and proper control of storage room conditions. This objective should be neither complex nor hard to achieve in light of the investments, technical progress, and continuous advancement in those regions.

Mycotoxin contamination in crops can occur during growth and persist through transportation and storage, impacting regions differently based on temperature changes. Hot and dry conditions in some areas may reduce fungal growth, whereas cool regions like North America may face worsening storage conditions. Proper storage moisture levels below 0.70 a_W are crucial to prevent spoilage. Changes in storage practices are necessary globally, requiring technological advancements in developing countries and better control of storage conditions in developed regions.

3.8 | Mitigation measures

Several technologies have been recommended for reducing mycotoxin accumulation in crops and subsequent human and animal exposure. These include cultural practices, biological control, monitoring and crop destruction, grain drying, sorting, proper storage, postharvest processing, and dietary interventions. However, most of these are quite resource-consuming efforts (in terms of time, labor, and money), and some are out of reach for developing countries. Biological control strategies, breeding crops for enhanced resistance traits, and support actions from institutions and national authorities are deemed essential elements to counteract mycotoxin contamination in developing and developed countries alike.

3.8.1 | Biological control

Regarding biological control, one successful application exploits non-aflatoxigenic strains of *Aspergillus* spp., which could prevent AF contamination. Their use is based on competition for space and substrate, the potential production of inhibitory metabolites, and on their inability to recombine with native toxigenic strains (Wambui et al., 2016). This technology was pioneered in the USA, where two atoxigenic genotypes are currently registered with the US Environmental Protection Agency for prevention of AF contamination, namely, *A. flavus* AF36 and Afla-Guard (Cotty et al., 2007; Dorner & Lamb, 2006). The success of biocontrol products as biopesticides in the USA has encouraged researchers at the International Institute of Tropical Agriculture and USDA-ARS to develop, adapt, and improve the biocontrol approach for African agroecosystems. The result of this collaboration is the development of several biocontrol products, under the trade name "Aflasafe," that consist of four non-aflatoxigenic genetic groups (vegetative compatibility groups [VCGs]) developed to provide stable, long-term, and additive beneficial effects in diverse environments. Since the first use applications, they were able to deliver a successful control of *A. flavus* contamination in areas where AF contamination posed a major hurdle to farmers (in Burkina Faso, Burundi, Gambia, Ghana, Kenya, Malawi, Mozambique, Nigeria, Rwanda, Senegal, Tanzania, Uganda, and Zambia) (Bandyopadhyay et al., 2016; Pickova et al., 2021). Due to the high efficacy of this mitigation method, its application in other geographical areas has been strongly encouraged.

In Italy, research started in 2003 and an AF biocontrol product under the commercial name AF-X1 was successfully developed (Jallow et al., 2021; Mauro et al., 2018). In Pakistan, AflaPak, a product based on native non-aflatoxigenic strains, is under development for the control of AF in maize, whereas in Serbia Mytoolbox Af01 was developed with the same aim (Ajmal et al., 2022; Pickova et al., 2021; Savić et al., 2020).

Nevertheless, the efficacy of *A. flavus* non-aflatoxigenic strains, and more broadly the biological control approach, has been questioned under CC conditions. A recurring concern is that non-aflatoxigenic strains may be unable to sporulate on carrier grains under low humidity and severe drought conditions. But as Cotty et al. (2007) and Doster et al. (2014) demonstrated, using the non-aflatoxigenic biopesticide *A. flavus* AF36 in Arizona's desert valleys, for drought-prone maize production in Texas, and for pistachio production in California has enabled those crops produce yields with low AF concentrations irrespective of AF-conducive environmental conditions. Native non-aflatoxigenic strains are being used for AF biocontrol because of their adaptation to target agroecosystems (Bandyopadhyay et al., 2016). Actually, the active ingredient of AF36 is native to them and adapted to hot, dry conditions; hence, its use has effective results under those conditions (Bandyopadhyay et al., 2016). Further, because native strains of the same fungal species are selected for each biocontrol product, a similar behavior and outcome is expected even under extreme weather conditions; in fact, AF reduction is commonly reported as being more successful in high-risk years (Ouadhene et al., under revision).

Another concern is the possibility of genetic recombination among the non-aflatoxigenic *A. flavus* strains used and the role that CC could play in that process. Recently, sexual reproduction in *A. flavus* has been reported (Wambui et al., 2016). Yet, after about a decade of commercial use of non-aflatoxigenic *A. flavus* strains for biocontrol in Italy as well as Africa and for more than 30 years in the USA, dangerous recombinants have not been observed, demonstrating that non-aflatoxigenic phenotypes have high genetic stability across vast geographical areas (Bandyopadhyay et al., 2016; Cotty, 2006; Cotty et al., 2007; Ouadhene et al., under revision). As Moral et al. (2020) pointed out, isolates used in biocontrol formulations belong to ancient, highly stable non-aflatoxigenic VCGs selected through carefully designed and elaborate microbiological, chemical, molecular, and field studies. Members of non-aflatoxigenic VCG do not exchange genetic material with members of other VCGs (either toxigenic or atoxigenic), despite plenty of opportunities to do so in both treated and non-treated areas. Clonality is the predominant mode of *A. flavus* reproduction (Moral et al., 2020; Ouadhene et al., under revision). Moreover, recombination events between members of aflatoxigenic and non-aflatoxigenic VCGs are typically rare or not occurring in nature, having occurred only in laboratory settings and in certain field studies under specific conditions. Therefore, the risk for recombination and generation of aflatoxigenic variants when applying non-aflatoxigenic isolates in the field is currently deemed minimal (Moral et al., 2020).

Gasperini et al. (2019) examined the preharvest and postharvest resilience of non-aflatoxigenic strains of *A. flavus* for the control of AFB1 contamination of maize, including nongenetically modified (GM) and isogenic GM cultivars with herbicide/pesticide resistant traits. The non-aflatoxigenic biocontrol strains were tested for their resilience to temperature fluxes and their ability to tolerate a range of water availability conditions to ensure that competitiveness is maintained at both pre and postharvest phases. This study found that AFB1 control was more effective at the milky ripe and dough stages of maize cobs at preharvest whereas at the dent stage it was less effective. The applied non-aflatoxigenic strains were less resilient in non-GM stored maize cultivars; the use of the GM cultivar led to better results in terms of relative biocontrol under abiotic stress (0.95 a_w) and an increased CO_2 level.

Besides the use of non-aflatoxigenic strains of *A. flavus*, there are other promising biocontrol agents. Dovenyi-Nagy et al. (2020) mentioned that crops treated with antagonistic strains of *Pseudomonas*, *Bacillus*, and *Trichoderma* spp. incurred lower *A. flavus* infection levels on groundnuts (Anjaiah et al., 2007). The potentiality of bacterial species is also emphasized by the work of Jallow et al. (2021), it finding that *Bacillus* spp., *Streptomyces* spp., and *Pseudomonas* spp. exert inhibitory effects against AF producers. Nevertheless, Gasperini et al. (2019) stated how choosing fungal species as biocontrol agents could be more effective under CC conditions, as fungi are more resilient under critical abiotic conditions than, for example, bacterial species. Bacteria require almost freely available water (>0.98–0.99 a_w) for their growth and have significantly less resilience to water stress than many mycotoxigenic fungi, which instead are either xerotolerant or xerophilic.

3.8.2 | Breeding for resistance

Breeding of fungus-resistant cultivars is another promising strategy for the control of fungi. Yet this is not always an easy task to accomplish. With respect to wheat and barley, there are no cultivars sufficiently resistant to FHB. Nevertheless, scientific research is focusing on the development of new genetic and biotechnological approaches to controlling mycotoxigenic fungi (Hameed et al., 2022). The need for viable, accessible, and affordable drought-resistant seeds is among the top priorities for adaptation to CC (Wambui et al., 2016). Therefore, it is imperative to increase efforts to breed for robust resistance against pathogens like *A. flavus* and FHB-causing fungi (West et al., 2012). Yet CC can render the host crop susceptible to fungal enemies, so breeding is a possible strategy, for example, in trying to control the a_w of grain, a key parameter for the colonization and infection by *A. flavus* and other fungi (Dovenyi-Nagy et al., 2020). In addition, as evinced by Gasperini et al. (2019), the use of GM-maize crops seems promising as they are resistant to pests, minimizing host tissue damage that provides entry points for *A. flavus*, which preserves the efficacy of biocontrol strategies (Gilbert et al., 2018).

3.8.3 | Adaptation of farming practices

In a given CC scenario, those areas where crops are bioclimatically suitable for cultivation could get modified environmentally, so farming practices ought to be tailored to these changed growing conditions. In Spain, for example, the temperature during summer months may become too high to grow tomatoes, and thus the harvesting period can be pushed back to span earlier months (Perre et al., 2015). Irrigation requirements and rotations can be affected too; however, the use of pesticides and fertilizers should be considered carefully because the former's efficacy when applied preharvest may be substantially modified by CC factors and, in some cases, control of mycotoxigenic pathogens and toxin contamination could be less effective (Magan et al., 2011; Medina, Jiménez, et al., 2007; Medina, Mateo, et al., 2007). The introduction of new cultivars should be deliberated as well in this context (Moretti et al., 2019). For example, investment in new grapevine varieties whose wine flavor is similar but their climate tolerance is changed may be crucial, especially in major wine-producing regions facing a likely reduction of 19%–73% by 2050 in their suitable area for viticulture (Paterson et al., 2018).

Cropping strategies that could be applied to control mycotoxigenic fungi range from establishing a disease-suppressive environment by applying soil solarization and agronomic practices like intercropping, mixed cropping, and crop rotation to using pathogen-free seeds, field sanitation by removal of plant debris, and cultivation of resistant cultivars and seed treatments with biocontrol agents (Desai et al., 2020). However, a recent study on mycotoxin hazard analysis revealed land preparation (tillage, crop rotation, and cover cropping), planting and intercropping, application of botanical extracts, and fungal biocontrol agents as the most important preharvest practices that can influence/control mycotoxin production (Hamad et al., 2023; Nada et al., 2022). Arguably what is generally required in this situation is an adequate proactive policy and sensitization actions structured in a way to raise awareness among farmers on how to farm effectively in newly found environmental conditions.

Various technologies have been suggested to decrease mycotoxin build-up in crops, reducing the risk of exposure to humans and animals. To contrast mycotoxin contamination effectively, essential measures include biological control strategies, breeding crops with improved resistance traits, and support from institutions and national authorities in both developed and developing countries. For the future, the identification of new crop varieties with characteristics similar to those currently used but resilient to CC conditions can result as an effective approach. Moreover, promoting research and application of biocontrol agents, such as non-aflatoxigenic strains of A. flavus, in new geographical areas that may become more vulnerable to AF contamination, as well as promoting research into drought-resistant varieties, are crucial steps to decrease mycotoxin contamination in crops.

3.9 | Predictive models

Mycotoxin models able to predict contamination offer a key tool for addressing the impact of CC on plant–pathogen interactions. Using such models, it is possible to quantify the future impact of CC in a particular area. This, in turn, will foster the development of improved management procedures, better allocation of monitoring efforts, adjustment of practices, and support the development of proactive strategies in anticipation of CC effects. Preferably, such models should consider all meaningful interactions among the climate, plant development, fungal populations, and mycotoxin formation (Paterson & Lima, 2010; Wambui et al., 2016). Several predictive models now exist; these have been developed worldwide for predicting the risk of mycotoxin contamination.

DONcast, developed by Hooker et al. (2002), is an empirical model based on weather conditions just prior to and during wheat head emergence. It includes the input of local or regional weather data, number of rainy days preceding anthesis, and later, during ripening, as well as maximum, minimum, and mean temperatures. Validation has shown that, provided the information is up to date, risks from DON contamination can be very accurately predicted, and this tool can be used for the timing of sustainable fungicide applications based on the relative level of risk. However, this model did require recalibration for its regional applications in South America and in Europe, where additional factors had to be incorporated (Magan et al., 2011). Lately, predictive models have moved from an empirical basis to employing a mechanistic approach. They have begun to consider the impact of CC on different pathosystems by trying to define distinct future scenarios and how epidemics can develop in the near and far term.

3.9.1 | DON contamination in northwest Europe

Fels-Klerx et al. published throughout 2012 several studies with the aim of estimating the CC impact on DON contamination of wheat cultivated in northwestern Europe through 2040, by using a modeling approach. First, two empirical models were developed: One to estimate the phenology of wheat crops grown in northwestern Europe and one to estimate their levels of DON contamination (van der Fels-Klerx et al., 2012, 2013). The wheat phenology model estimates the various stages of crop development, in particular flowering and full maturation, using climate data. Both models were developed using a series of observed historical data. The model to predict DON contamination likewise used climate data in addition to wheat phenology data as inputs to estimate the DON concentrations in wheat grown in northwestern Europe (van der Fels-Klerx et al., 2016). Their results showed CC was expected to result in an earlier date of flowering and of full maturation of winter wheat, advancing each by 1–2 weeks and ranging up to ca. 26 days. Both *F. graminearum* and *F. culmorum* were the dominant DON-producing *Fusarium* spp., and the DON contamination of winter wheat was, in general, likely to increase across most of the study area by a factor of two, yet up to a factor of four in some grid cells. For spring wheat, even more severe impacts were discernable. However, the variation between runs and between regions was large, and in some grids, a decrease in DON levels was predicted. A similar study for the Netherlands region predicted high spatial and annual variability of DON contamination in wheat in future climates (van der Fels-Klerx et al., 2013, 2016).

3.9.2 | AF contamination in Europe

Battilani et al. (2012, 2013, 2016) developed a project whose aim was to understand the evolution of AF contamination in cereals grown in Europe. Three different IPCC-based CC scenarios were used: the present, +2°C, and +5°C scenarios. Weather outputs were generated for 100 runs, for the 2000–2100 period, on a 50 × 50-km^2 grid. These data served as inputs for crop phenology's estimation and for the AF prediction model for AFLA-maize, the latter being mechanistic model for predicting *Aspergillus* spp. infection and AF accumulation. The outputs of this model, conveyed as an AF risk index, were linked to AF contamination observed in field studies. A European database providing mean daily temperatures during maize emergence, flowering, and harvesting was used to estimate, utilizing weather data, the shifts in maize flowering and harvesting in the three different climate scenarios. The results showed a contraction in the growing season length and earlier flowering and harvest dates. This would lead to an enlarged area in Europe, toward its northern area, deemed suitable for maize cultivation. Weather data and estimated shifts in maize phenology were then fed into the AFLA-maize model, which revealed an expected increase in the AF contamination of maize, mainly under the +2°C scenario. In this scenario, a particular increase in expected AFB1 contamination was seen in the southern European countries, namely, in the center and south of Spain and of Italy and also in the Balkans. Under the +5°C scenario, the area in Europe predicted to incur maize contamination was much wider than that under the +2°C scenario. However, estimated AFB1 contaminations were lower under +5°C than +2°C scenario. Further, considerable variability throughout Europe was predicted between simulated years (Battilani et al., 2016).

3.9.3 | AF contamination in Georgia, USA, and Malawi

Kerry et al. (2021) investigated the future contamination risk of AFs to maize in southern GA, USA. That study shows the main maize growing counties are increasingly at risk of AF contamination, exceeding two weather risk factors (June T Max >30°C and June RF < 50 mm) in a greater proportion of years. The modeling approach used June T Max and RF, the two most important factors linked to AFs' concentrations in the 1977–2004 survey. Several other factors could influence AFs' concentrations, such as soil type warmer temperatures earlier and later in the growing season, but this model assumes that these factors will continue to exercise less influence in the future. A general increase in the number of counties at risk of high levels of AF contamination over the next 80 years is expected. Moreover, a shift in the spatial patterns of the highest risk counties toward those that currently grow the most maize is projected. More recently, Yu et al. (2022) investigated the AF's presence in USA's maize fields, concluding that over 89.5% of corn-growing counties in 15 states, including those of the Corn Belt, will face increased AF contamination in 2031–2040 compared with 2011–2020.

Warnatzsch et al. (2020) described how CC could influence AFB1 contamination of maize in Malawi. That research used regional climate models to determine the climatic conditions in Malawi's three regions (northern, central, and southern) in 2035 and 2055 as compared to the baseline climate of 1971–2000. The data was used as input for AFLA-maize. It was found that Malawi's climate is projected to get warmer and drier in all three regions, although some uncertainty remains around the changes in precipitation levels. Moreover, shortening of the growing season for maize is projected, advancing the harvest date by 10–25 days for the short-season variety and by 25 and 65 days for the long-season variety. Therefore, the preharvest conditions for Malawian maize are more favorable for AFB1 contamination. Dangerous levels of AFB1 will also be reached in regions of the country that have never historically faced this challenge (Warnatzsch et al., 2020).

3.9.4 | *Alternaria* spp. contamination in Spain and Poland

The mechanistic model of Perre et al. (2015) quantifies the effect of CC on mold growth and mycotoxin production in tomato, as function of changing temperature. This quantification has been done for the present, near future (2031–2050), and far future (2081–2100). Four representative concentration pathways (RCP) scenarios—RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5—were used in two tomato-producing regions (Badajoz, Spain and Krobia, Poland). Daily minimum and maximum temperature data were gathered from the closest and most representative weather stations for the years 1981–2000. The results uncovered impacts that were region specific. For Spain, the temperatures in RCP 6.0 and 8.5 were projected to be too high (18.2–38.2°C) for *Alternaria* spp. to grow, thus the diameter of mold was calculated as being lower in the far future than now. For Poland, the projected temperatures got closer to the optimal temperature (14.2–28.4°C) for *Alternaria* spp. growth. According to this study, the situation in Poland in the far future (2081–2100) is projected to resemble that in Spain in the present time frame (1981–2000).

In the development of predictive models, and particularly those that consider the impact of CC, uncertainties must be incorporated (van der Fels-Klerx et al., 2016). Obtaining a clear picture of climate's influence on overall crop contamination, especially under the effects of CC, is a complex and often difficult task. Different years can impact mycotoxin contamination in very distinct ways (Battilani et al., 2016). As an example, Schaafsma et al. (2010) found that the variable "year" accounted for 48% of variability in DON contamination in the 4 years tested in that study.

Research gaps in predictive model development can be highlighted as well, including validations limited to one/few countries and focusing on a few selected mycotoxin-crop combinations (van der Fels-Klerx et al., 2016; Battilani, 2016; Leggieri et al., 2013). Modeling of mycotoxin contamination needs to be done separately for each pathosystem (plant × fungus system). There is still a limited availability of predictive models for combinations of non-cereal crops and mycotoxins (van der Fels-Klerx et al., 2016), and long-term georeferenced datasets on mycotoxin occurrence in crops are scarce. Having long-term datasets is a paramount prerequisite for uncovering fingerprints of interannual climatic variation in mycotoxin contamination, and likewise for robust predictive model validations.

Lastly, more data is required to enable a better understanding of fungal and plant ecophysiology and pathogen/host interactions, especially in cropping systems, to develop and validate predictive models (Leggieri et al., 2021; Magan & Medina, 2016).

4 | CONCLUSION

The results of this timely review show how CC has become an increasingly paramount topic in relation to plant pathology and mycotoxin contamination of foodstuff. In the last 20 years, CC has started to show its adverse effects in both developing and developed countries, resulting in situations that were often tough to predict and even more challenging to counteract. This demonstrates how continuous research and scientific efforts are indispensable tools for better understanding the complexity of a phenomenon such as global CC, not only to figure out how the situation could evolve in the future around the world but also to define realistic strategies to prevent and mitigate the potential harmful effects that could occur in the agrifood systems.

Global agriculture is facing a convergence of pressures, such as a rapidly growing population, land availability reduction and degradation, and loss of biodiversity. In this context, CC could potentially interrupt the progress toward a world without hunger, and it is likely that this phenomenon will accentuate food insecurity in areas already vulnerable.

As agriculture continues to face challenges related to CC, there are several topics that require further exploration. This includes investigating the relationship between abiotic stresses and vulnerability to fungal diseases, mycotoxin production, prevalence among fungal species and their co-occurrence, studying and implementing biocontrol agents, as well as drought-resistant crop varieties. Additionally, there is a need for predictive models focusing on combinations of crops beyond the most considered cereals and mycotoxins, so as the extension of model use to more countries. All these research endeavors should add value to existing knowledge and contribute to supporting farmers in overcoming CC challenges.

It is evident how investments in adaptation and mitigation actions are needed to counteract the impacts of CC on global food security.

Sound policies, sensitization actions, and education activities structured in a way to raise awareness on how to face new environmental conditions are recommended actions. National authorities and policymakers should facilitate the technological transfer and the access to solutions for those developing countries that will be most affected by CC impacts. More data is needed to clarify and support the assumptions that have been made throughout the years. In the end, an update of international regulations is strongly warranted to protect consumer health in these newly arisen and challenging environmental scenarios.

AUTHOR CONTRIBUTIONS

Alessia Casu: Writing—original draft; writing—review and editing; data curation; formal analysis; conceptualization; methodology. **Marco Camardo Leggieri**: Writing—review and editing; conceptualization; methodology; data curation. **Piero Toscano**: Writing—review and editing; data curation; formal analysis; conceptualization; methodology. **Paola Battilani**: Conceptualization; methodology; supervision; writing—original draft; writing—review and editing.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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