Received: 17 January 2022 | Revised: 3 June 2022 | Accepted: 27 June 2022

DOI: 10.1111/1541-4337.13008

COMPREHENSIVE REVIEW

Comprehensive REVIEWS in Food Science and Food Safety WILEY

Occurrence of mycotoxins in pulses

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Abstract: Pulses, dry grains of the Fabaceae family used for food and feed, are particularly important agricultural products with increasing commercial and nutritional relevance. Similar to other plant commodities, pulses can be affected by fungi in the field and during postharvest. Some of these fungi produce mycotoxins, which can seriously threaten human and animal health by causing acute poisoning and chronic effects. In this review, information referring to the analysis and occurrence of these compounds in pulses is summarized. An overview of the aims pursued, and of the methodologies employed for mycotoxin analysis in the different reports is presented, followed by a comprehensive review of relevant articles on mycotoxins in pulses, categorized according to the geographical region, among other considerations. Moreover, special attention was given to the effect of climatic conditions on microorganism infestation and mycotoxin accumulation. Furthermore, the limited literature available was considered to look for possible correlations between the degree of fungal infection and the mycotoxin incidence in pulses. In addition, the potential effect of certain phenolic compounds on reducing fungi infestation and mycotoxin accumulation was reviewed with examples on beans. Emphasis was also given to a specific group of mycotoxins, the phomopsins, that mainly impact lupin. Finally, the negative consequences of mycotoxin accumulation on the physiology and development of contaminated seeds and seedlings are presented, focusing on the few reports available on pulses. Given the agricultural and nutritional potential that pulses offer for human well-being, their promotion should be accompanied by attention to food safety issues, and mycotoxins might be among the most serious threats.

KEYWORDS
food safety, food security, fungi, legumes, microbial growth, mycotoxins, pulses

Practical Application: According to the manuscript template available in the website, this section is for "JFS original research manuscripts ONLY; optional". Since we are publishing in CRFSFS this requirement will not be done.

1 | INTRODUCTION

Pulses are a group within the Fabaceae family that are used exclusively for dry grain production and that can be either utilized for food or feed (FAO, 1994; Sardana et al., 2010). This definition thus excludes those leguminous crops used for oil extraction or even common pulse species when they are consumed as fresh products. The Food and Agriculture Organization's (FAO) list for commodities lists 24 pulses, mainly of the genera *Phaseolus*, *Vigna*, and *Vicia*. The complete FAO list, supplemented with *Lathyrus sativus* and *Rhynchosia minima*, which also match the definition of pulse, can be found in Table 1.

In comparison to cereals, pulses have lower amounts of the amino acids methionine and tryptophan and of the oxidized dimer cystine but have higher contents of proteins containing the amino acid lysine (reviewed by N. Singh (2017) and Chibbar et al. (2010)). Consequently, a combination of pulses and cereals in the diet provides a balanced consumption of essential amino acids. Moreover, several compounds found in pulses may contribute to weight management in humans through different mechanisms, for example, achieving satiety, as reviewed by McCrory et al. (2010). Furthermore, their fiber content helps reduce energy density and provides a low glycemic index, making them good candidates for the development of novel food products (Rebello et al., 2014).

Despite their benefits, many people are reluctant to consume certain pulses because of their fermentation effect in the colon (Veenstra et al., 2010). Due to their low digestibility, some oligosaccharides pass undigested to the large intestine where fermentation by the colon microflora occurs, producing gases, mainly CO_2, hydrogen and methane, and short-chain fatty acids (Thompson, 2019; Tosh & Yada, 2010). Nonetheless, the demand for pulses has been increasing, especially in developed countries, where many people are changing to vegetarian or vegan diets (Sardana et al., 2010).

FAO declared 2016 as the International Year of the Pulses to raise awareness about the benefits of their consumption and to promote research to increase their production and productivity (Calles, 2016). According to FAOSTAT (FAO, 2019), for the period between 1999 and 2019, the production of beans, chickpeas, and peas increased by 61%, 50% and 29%, respectively. Despite this increase, in some regions, the production is still done in a rustic way with very low yield.

Contamination of grains and other dry agricultural products by molds may occur in the field, at harvest, and/or during transportation and storage. Some fungi are capable of producing mycotoxins, a group of secondary metabolites of low molecular weight that can seriously threaten human and animal health by causing acute poisoning and chronic effects (e.g., carcinogenesis and immune deficiency) (Barac, 2019; Bhat et al., 2010). The fungal genera *Fusarium, Alternaria, Aspergillus*, and *Penicillium* are the most prevalent in food and feed products (Berthiller et al., 2013). Improper postharvest handling is one of the factors that highly influences mycotoxin production, for

TABLE 1 Complete list of plants considered as pulses matching the FAO (1994) classification (adapted from Calles, 2016)

Scientific name	Common name(s)
Cajanus cajan (L.) Huth	Pigeon pea, arahar
Canavalia ensiformis (L.) DC	Jack bean
Cicer arietinum L.	Chickpea, Bengal gram, garbanzo
Cyamopsis tetragonoloba (L.) Taub	Guar bean
Lablab purpureus (L.) Sweet	Hyacinth bean, Indian bean, Lablab
Lathyrus sativus L.*	Khesari
Lens culinaris Medik	Lentil
Lupinus spp. L.	Lupin
Mucuna pruriens (L.) DC	Velvet bean
Phaseolus acutifolius A. Gray	Tepary bean
Phaseolus coccineus L.	Scarlet runner bean, runner bean
Phaseolus lunatus L.	Lima bean, butter bean
Phaseolus vulgaris L.	Common bean
Pisum sativum L.	Pea, garden pea, green pea
Psophocarpus tetragonolobus (L.) DC	Winged bean
Rhynchosia minima L.*	Jumby bean, least snout-bean, and burn-mouth-vine
Sphenostylis stenocarpa (Hochst ex A Rich) Harms	African yam bean
Vicia faba L.	Broad bean, faba bean
Vicia sativa L.	Common vetch
Vigna aconitifolia (Jacq) Maréchal	Moth bean
Vigna angularis (Willd) Ohwi & H Ohashi	Adzuki bean, red mung bean
Vigna mungo (L.) Hepper	Mungo bean, black gram, urad bean
Vigna radiata (L.) R Wilczek	Mung bean, mungbean, green gram
Vigna subterranea (L.) Verde	Bambara bean, Bambara groundnut
Vigna umbellata (Thunb) Ohwi & H Ohashi	Rice bean
Vigna unguiculata (L.) Walp	Cowpea, black-eyed peas/beans

*Not included in the FAO (1994) list but comply with the definition of pulse.

example, storing the produce at inadequate moisture contents allows molds to grow (FAO, 2001).

One of the main problems with mycotoxins is their high stability to physical and chemical treatments and, therefore, the absence of reliable methods to decontaminate raw material and processed food and feed. The efficacy of several procedures involving physical and mechanical decontamination is reviewed elsewhere (Stoev, 2013). Alternative biological degradation of these toxins has also been tested and has shown some promising results when microorganisms and particular microbial-derived enzymes have been used (Ji et al., 2016).

There are several review articles on the incidence of mycotoxins in cereals. However, there is a lack of similar works dealing with this issue in pulses. Kunz et al. (2020) probably provide the closest attempt to compile information on mycotoxins in pulses. Nonetheless, since the latter is an experimental study, it neither aimed at presenting a comprehensive list of reports nor focused on pulses, since it also refers to other leguminous grains, like soybean. Therefore, the present review aims to describe published information about the occurrence of mycotoxins in pulses, complemented with information about the potential effect of climatic conditions on fungi colonization and mycotoxin accumulation. In addition, the association between the degree of infection and the subsequent concentration of mycotoxins, together with mechanisms involving accumulation of phenolics that some pulses naturally have to defend themselves against the synthesis of mycotoxins, will be addressed. The importance of a specific group of mycotoxins found in pulses, the phomopsins, will be discussed. Finally, the physiological effects of mycotoxins in seeds and seedlings, with emphasis on pulses, will be discussed.

2 | METHODOLOGY

An extensive literature search was performed using the Scopus and Google Scholar databases. Because this review aims to list all scientifically reliable literature related to mycotoxins in pulses, a specific time frame was not selected. The keywords used to perform the searches were "pulses" OR each of the names of the individual pulses listed in Table 1 AND "mycotoxins". In addition, references within the reviewed articles that did not appear in the database search were also revised and included when relevant. Theses and dissertations, as well as manuscripts that exclusively studied the mycoflora without any reference to mycotoxin production/occurrence, were not considered for this review.

Considering that several pulses listed in this review are relevant for local consumption and that results may have been published in regional journals, each article was revised individually to assess the relevance of the research to avoid discarding references based solely on the publication source. As a relevant quality parameter, the existence of a detailed description of adequate and reliable analytical methods in the report was considered. The complete list of all manuscripts reviewed can be found in the Excel sheet available as Supporting Information 1.

For further analysis, data were extracted from the references and categorized as follows: continent, country/region where the studies were carried out or samples were collected, income of the country, pulse(s) studied, mycotoxin(s) and mycoflora (if mentioned), research aim (explained in detail in Section 3.1), and detection technique employed. Moreover, beyond just listing detection methodologies, it was in our interest to analyze whether the techniques employed in the detection of mycotoxins in pulses had gone through a validation process prior to their use. We considered a methodology tested or validated when at least one reference method was cited. In some cases, the cited reference method may have developed its methodology for another commodity (e.g., cereals). Additionally, the quality parameters used for validation should have been described thoroughly. All references used to generate the summarized numbers presented in this review, which are not directly cited in this document, are included in Table S1.

Furthermore, the relationship between the country's income and the research aim was analyzed. For income classification, countries were grouped into four categories according to the classification of The World Bank: low, lower-middle, upper-middle, and high income (The World Bank Group, 2022). Regarding the research aim, the studies were grouped into nine broad topics: plant resistance against mycotoxin accumulation, associated fungi and mycotoxin accumulation, development of analytical method, mycotoxin reduction/decontamination, storage-related physiological effect on plants, toxigenicity determination of fungal isolates on the studied pulse(s), market sampling (defined as the monitoring of mycotoxin status in a particular country or region, including other commodities), and specific survey in pulses (which is a dedicated monitoring of the mycotoxin status on a specific country but focused specifically on pulses). Relationships between income and aim were determined through a correspondence analysis with R version 4.1.3 software (R Core Team, 2022) using the FactoMineR package (Le et al., 2008).

3 | REPORTS ON FUNGI AND MYCOTOXIN INCIDENCE IN PULSES

Studies characterizing the capacity of fungi to grow on pulses and to synthesize mycotoxins started more than 50 years ago, when some of the negative health

consequences of mycotoxin intake were already known (Alpert et al., 1971; Enomoto & Satto, 1972; Wilson, 1978). In a pioneer work, Beuchat and Lechowich (1970) studied how temperature and water activity affect the production of mycotoxins in different bean varieties and found that the aflatoxin production rate was higher in navy beans compared to kidney and pinto beans. In addition, it was observed that the maximum production of the toxin in the navy bean occurred after 1 week, while for the other two, it occurred after 3 weeks. Little to no mold growth was found when the beans were dried to 20% moisture content, and consequently, very few or no toxins were detected. Some years later, Mislivec et al. (1975) isolated the fungi present in diverse types of dried beans and found that 54.4% of the isolates synthesized at least one mycotoxin, as analyzed by thin-layer chromatography (TLC). They also proved that mycotoxins were not present in noninfected beans, confirming that they are not metabolites of beans but compounds produced by fungi growing on them instead. A brief section on the occurrence of mycotoxins in legumes (including an even shorter report on dry beans) was published shortly afterward as part of a more general review on the subject (Stoloff, 1976).

Successive reports on the analysis of pulses regarding infection with mycotoxigenic fungi and mycotoxin accumulation(s) have continued to be published since the 1980s but at a much lower frequency than for other contaminated sources, mainly cereals and processed products. This is noticeable in the review article of Rahmani et al. (2009) that referenced only four pulse-related articles among 226 reports from 1975 to 2009 describing mycotoxin detection in different raw and processed matrixes and the total absence of mentioning pulses in the review article of V. Kumar et al. (2008). It is only for chickpea that a specific review article on mycotoxigenic fungi and mycotoxins was recently published (Ramirez et al., 2018). In addition, although not specifically for pulse crops, Weidenbörner (2018) structured a very comprehensive list on the mycotoxin contamination of plants and plant products different from cereals and derived products.

3.1 | Overview of the research conducted to date in pulses

Targeting at being as comprehensive as possible and because of the absence of a specific review on mycotoxins in pulses as a group, a general characterization of the research aim of every referred study was made. Additionally, the aim of each study was associated with the respective country's income through a correspondence analysis to detect trends in the different regions of the world. Figure 1 shows a clear separation in dimension 1 between high- and lower-income countries. The categories related to mycotoxin management and how it affects plant seedlings (i.e., plant resistance against mycotoxin development, associated fungi and mycotoxin accumulation, storage-related, and physiological effects on plants) relate more to the lower-income and low-income countries associated with the African continent. Among these categories, research in "plant resistance against mycotoxin accumulation" is a variable with a high contribution to the correspondence analysis. This research has been conducted mainly in Egypt (El-Kady et al., 1996, 1991; Saber, 1992) and Tanzania (Seenappa et al., 1983).

In contrast, high-income countries, mainly Germany (Schloß et al., 2015), the Netherlands (de Nijs et al., 2013; Kunz et al., 2020), Switzerland (Reinhard et al., 2006), and Taiwan (Yu et al., 2013, 2011), are the leading developers of detection methods. It is necessary to clarify that even though the correspondence analysis (Figure 1) shows Oceania associated with this classification, it is mainly because all the studies found belong to Australia, classified as a high-income country. However, later in this section, we will expand on the type of studies conducted on this continent.

Additionally, Figure 1 shows a high contribution degree of the category "toxigenicity determination of fungal isolates" associated with high-income and upper-middle-income countries. The countries that conducted this investigation were the United States (Beuchat & Lechowich, 1970; Mislivec et al., 1975), Brazil (dos Cordeiro et al., 1995; Freitas-Costa & Scussel, 2002; Santos-Ciscon et al., 2019), Argentina (Castillo et al., 2002), Japan (Hitokoto et al., 1981), Poland (Waskiewicz et al., 2013), and Canada (Sanchis et al., 1988).

Moreover, the category named "specific survey in pulses" (which is the monitoring of a mycotoxin status specifically in pulses and does not involve other commodities) is related to lower-middle-income countries, perhaps because in these places, these products are widely consumed. All income categories are represented on the Asian continent, so its range of research covers almost all research aims. For market sampling, whose emphasis was to monitor the mycotoxin status in a particular country/region, it can be seen that all income groups carried out this type of research. Finally, something similar occurs with research on "mycotoxin reduction/contamination," where all regions have studies on this topic.

Regarding the total reports per continent, considering where the study and sampling were conducted, Africa has the most publications (33), followed by Europe (22), Asia (21), the Americas (20), and finally Oceania (3). In terms of countries, Egypt is the country in Africa, with most reports (11) investigating lentils, broad beans, beans, cowpeas, and peas. For the American continent, Brazil is the leading

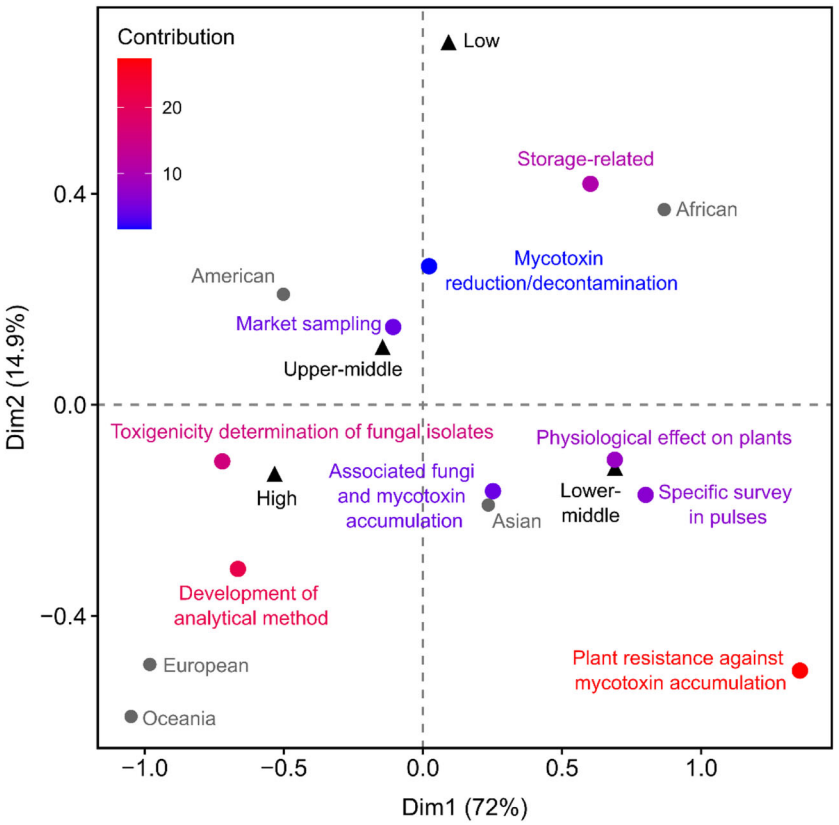

FIGURE 1 Correspondence analysis between the research aims and their association with the country's income level from where the samples or the study originated. Colors blue to red indicate the level of contribution of the research aim to the variability, with red representing the highest. Continents in gray are supplementary variables associated with the country's income. Countries were categorized according to The World Bank income classification. "Market sampling" is defined as monitoring the mycotoxin status in a particular country or region, including other commodities, and "specific survey in pulses" is dedicated monitoring of the mycotoxin status in a specific country, specifically in pulses

country, with nine publications, where research focuses solely on beans. In Asia, India and Iran are the countries with the largest number of reports (four publications each) investigating a great diversity of pulses. In India, the most investigated pulses were mung beans, chickpeas, cowpeas, green gram, Indian beans, black gram, arahar, Bengal gram, khesari, peas, lentils, and beans, while in Iran, they were beans, green gram, chickpeas, lentils, and peas. For Europe, Germany has most reports (5) on a wide variety of pulses (beans, lupin, peas, lentils, chickpeas, mung beans, urad beans, black-eyed beans, adzuki beans, lima beans, hyacinth beans, and pigeon peas). Finally, in Oceania, Australia is the only country listed with reports (3) focusing on lupin and lentils.

From the reports analyzed, Figure 2 describes the frequency at which individual pulses with mycotoxins and mycotoxins in pulses have been studied. As shown in Figure 2a, common bean is by far the most frequently studied commodity (79 studies). This could be related to its higher economic importance and wider distribution. In this sense, and according to FAOSTAT (FAO, 2019), from all pulses, common beans had the highest production worldwide (between 2014 and 2019), followed by lentils and chickpeas. The column referring to "others" in Figure 2a comprises those pulses that have been reported in less than six articles and can be classified into two subgroups: those mentioned in 2–6 studies (pigeon peas, black gram, hyacinth, and lima bean) and those mentioned in only one study (jumby bean and khesari [sic]). For detailed information, see Table S1.

Regarding the number of mentions of the individual mycotoxins in the analyzed articles, Figure 2b shows that aflatoxins are the most commonly studied (65 studies mentioned them), followed by ochratoxins, fumonisins, and zearalenone with 37, 20, and 19, respectively. Those mycotoxins that have been mentioned in fewer than five studies fall within the category "others" in Figure 2b and can be divided into three groups: those mentioned in four studies (penicillic acid, patulin, trichothecenes, alternariol, nivalenol, and beauvericin), those mentioned in two studies (altenuene and fusarenon-X), and those mentioned only once (griseofulvin, tenuazonic acid, ergosterol, enniantins, and moniliformin). It is important to note that some of the articles in this review also studied the metabolized forms of some of these mycotoxins. These are described in more detail in Supporting Information 1 and are not listed in this general characterization. The frequent mention of particular mycotoxins might be related to their health and agro-economical relevance. The five most frequently mentioned groups coincide with the top five in terms of incidence and severity found in recent reviews dealing with the prevalence of mycotoxin contamination in food crops (Eskola et al., 2020; Omotayo et al., 2019). It must be noted that mentioning a particular mycotoxin

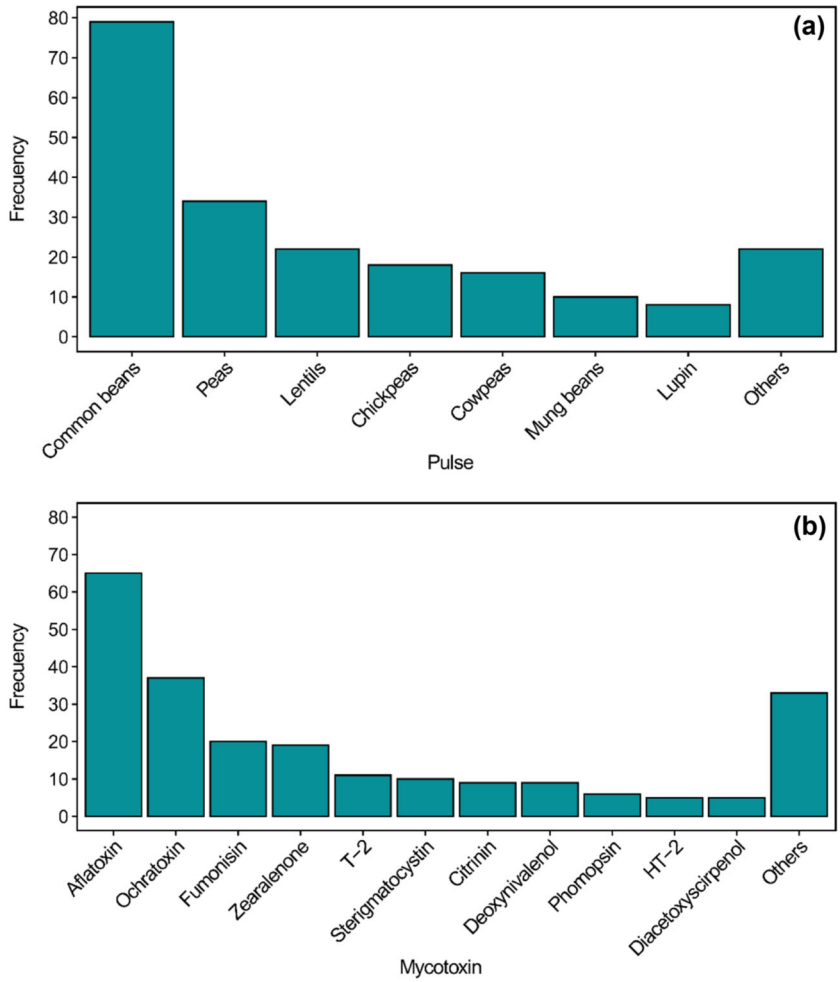

FIGURE 2 Frequency of mentions of the different (a) pulses and (b) mycotoxins in the studies cited in Table S1

in an article does not necessarily mean that the toxin was detected in a certain foodstuff. It might also be the case that, although there was an interest in looking at the particular compound, this could not be detected, or its level was below the regulatory limits. A possible explanation for this is included in Section 6 of this review.

3.2 | Techniques used for the detection of mycotoxins in pulses

Several techniques are available for detecting mycotoxins in different matrixes (J. Singh & Mehta, 2020). Thin-layer chromatography (TLC) is the pioneering technique for detecting these compounds. Currently, more sensitive chromatographic techniques [e.g., liquid chromatography (LC) or gas chromatography (GC)] are available, which allow more precise quantification of mycotoxins. Among these, LC coupled with mass spectrometry is the leading detection method because of its sensitivity and selectivity (De Girolamo et al., 2022). For this reason, and due to the reliability of the results obtained, modern chromatographic techniques are considered the current reference methods. On the other hand, rapid detection methods have been developed in response to the need to simplify the laboratory process and obtain faster results, even on site in the field, in industry or in storage facilities.

In mycotoxin studies related to pulses, we found the use of both rapid and traditional techniques. Modern chromatography methods have taken advantage of the availability of several detectors. For GC, the detectors mentioned for mycotoxin analysis in pulses comprise mass spectrometry (MS), flame ionization detection, and electron capture detection, while those for high-performance liquid chromatography (HPLC) are fluorescence detection, diode array detection, ultraviolet, refractive index, and MS or tandem MS (MS/MS). For more detailed information, see Table S1.

To identify which techniques are most commonly used in studies conducted in different parts of the world, they were grouped according to the continent (Figure 3). This figure shows that in the case of Africa, Asia, and the Americas, TLC and rapid tests were prevalent compared to Europe. This could be because it is easier to use this type of techniques that do not require highly trained personnel, and the equipment needed is more affordable than

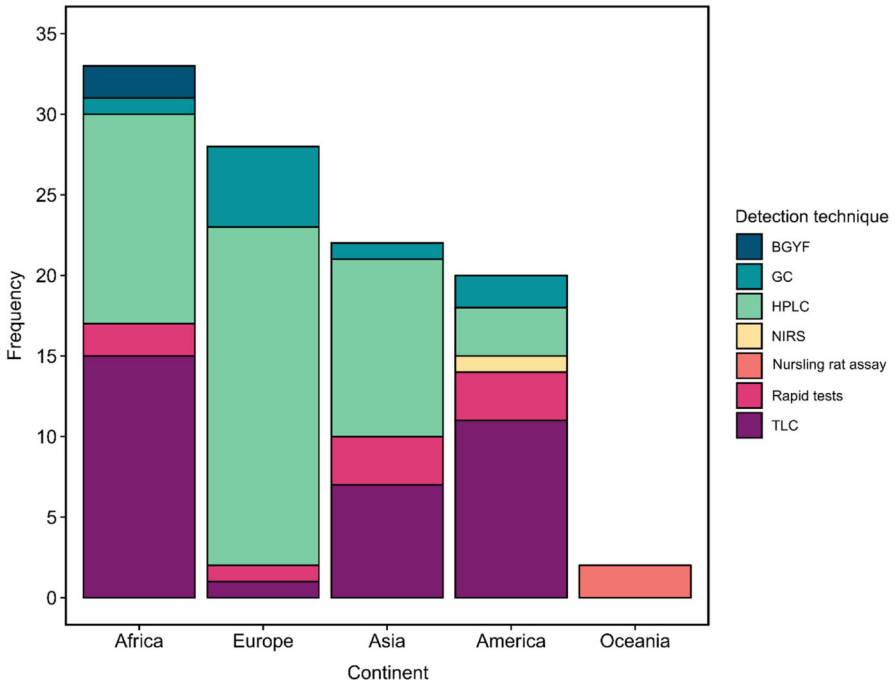

FIGURE 3 Detection techniques used to determine mycotoxins in pulses grouped by continent. Rapid tests include enzyme-linked immunosorbent assay (ELISA), indirect competitive assay, lateral flow immunochromatographic assay, and AflaTest. Abbreviations: BGYF, bright greenish-yellow fluorescence; GC, gas chromatography; HPLC, high-performance liquid chromatography; NIRS, near-infrared spectrometry; TLC, thin layer chromatography

high-performance chromatographers. Moreover, some rapid tests have the benefit that they can be performed in situ, which represents an advantage for mycotoxin monitoring. In contrast, in Europe, GC and HPLC predominate. As explained in Section 3.1, most countries belonging to the high-income classification are from Europe, which facilitates access to more sophisticated equipment. As discussed above, this continent is where the development of detection methodologies is most frequent. Although most African countries were classified as low- and lower-middle-income, the use of HPLC almost equals that of TLC and rapid detection techniques in their research, unlike in the Americas, where chromatographic techniques are not commonly used for these studies (Figure 3). As mentioned before, the African continent has the largest number of publications on mycotoxins in various pulses. Consequently, this greater interest may have led to more effort in implementing more sophisticated and accurate detection technologies. In contrast, the American continent has lagged in this research area, according to the number of publications, the type of detection technologies employed, and the limited variety of pulses investigated (as mentioned above, it is mainly dedicated to common beans). This situation opens an opportunity for collaboration between countries belonging to the global south (Africa and the Americas) and between Europe and the Americas, which would help diversify the type of pulses consumed in the Americas and modernize detection techniques of mycotoxins in pulses.

In the case of Oceania, the reports found are from the 1980s (Petterson et al., 1985; Wood et al., 1987), which explains the use of this unusual bioassay called the "nursling rat assay." It was initially developed as an alternative detection technique to detect phomopsins in lupin but quickly lost importance due to the difficulties of performing the assay and because it is a nonquantitative technique. In the case of the most recent report from this continent (Davidson et al., 2012), the authors mentioned the protocol used for the National Residue Survey, but this could not be found for the assessment. For this reason, this was left out from the survey of detection techniques.

The methodology involving the use of bright greenish-yellow fluorescence (BGYF) is used widely by the corn-milling industry for aflatoxin detection (Moreno et al., 2009). These authors mentioned that BGYF is not a quantitative technique and that evaluation can be subjective; therefore, it may produce misleading results. Thus, it is necessary to confirm the toxin's presence by a second detection technique. Perhaps because of this, in the two pulse reports where BGYF was employed, it was used only as a screening method, and the mycotoxin content was determined through TLC (El-Nagerabi & Elshafie, 2001; Qutet et al., 1983).

Figure 3 also shows near-infrared spectroscopy (NIRS) as an incipient detection methodology for mycotoxins in pulses. NIRS is classified as an optical detection method among the rapid detection techniques. Optical methodologies for detecting mycotoxins in cereals and other commodities have been extensively investigated, as shown by reviews on this topic (Jia et al., 2020; Fox & Manley, 2013; Mishra et al., 2021; Tao et al., 2018). These reviews indicate an interest in further developing this type of technology to be applied at the industrial level for real-time monitoring (e.g., online detection). The single report on pulses in this area (Acuña-Gutiérrez et al., 2021) points out a research opportunity for this commodity group.

Regarding the validation or testing of the detection techniques prior to their use in a pulse matrix, five out of 99 studies were excluded from this analysis because a mycotoxin was added at a known concentration instead of quantified. In addition, from 94 studies analyzed, 10 did not indicate any type of validation, while 84 were further considered because they used a previously validated methodology. From the latter, 33 studies validated the pulse matrix studied, while 51 did not mention a reference test. Therefore, mycotoxin detection is frequently conducted without considering the pulse matrix's effect on the results. In addition, and considering that Figure 3 shows the great need for rapid tests in many countries, it is crucial to develop rapid tests for the industry, including pulses in their validation matrixes.

4 | EFFECT OF CLIMATIC CONDITIONS ON MYCOFLORA DEVELOPMENT AND ITS RELATIONSHIP TO MYCOTOXIN PRODUCTION IN PULSES

Colonization and growth of toxigenic fungi and subsequent production of mycotoxins are highly related to environmental conditions (i.e., high humidity and elevated temperature), both during cultivation and throughout postharvest and storage (Garcia-Cela et al., 2018; Nesic et al., 2015; Patriarca & Fernández Pinto, 2017; Perincherry et al., 2019). Such a positive correlation has been established for many crop plants, including cereals, vegetables, and fruits (Cotty & Jaime-Garcia, 2007; Ferrigo et al., 2016; Medina et al., 2017; Scala et al., 2016; Vaquera et al., 2016), but less information is available for pulses. In an early work, de Campos and Olszyna-Marzys (1979) evaluated aflatoxin contamination in different food products in various regions of Guatemala with contrasting climatic conditions and found the highest contamination rate in samples coming from hot and humid regions (26%) compared to the hot and dry and the cold/temperate (highlands) regions. However, although they considered beans in their analysis, the number of samples taken did not allow conclusive results. In another report, evaluating the evolution of climatic conditions throughout the year for a single site, aflatoxin accumulation was higher in chickpea seeds during August and September, coinciding with extremely high temperatures and relative humidity in Bihar (India) (Ahmad & Singh, 1991). More recently, the potential effects of location, agricultural management, and climatic conditions on fungi growth and mycotoxin production were evaluated by Tseng et al. (1995) in dry beans produced in Ontario and Taiwan. In the samples from Ontario, the more frequently isolated genera were *Alternaria, Fusarium, Rhizoctonia, Penicillium, Rhizopus, Sclerotinia, Gliocladium*, and *Mucor*. In the Taiwanese samples, the most common were *Aspergillus, Penicillium, Eurotium, Rhizopus*, and *Curvularia*. They found that the Taiwanese samples showed higher levels of contamination with seed-borne fungi than those from Ontario. The authors explained that the conditions in Taiwan are more suitable for fungi development (subtropical climate vs. temperate). *Fusarium* toxins were only detected in samples from Ontario, while aflatoxins were only detected in samples from Taiwan. In a further study, in Poland, colonization of faba beans by *Fusarium* was augmented with increased field temperature and precipitation; however, mycotoxins were not analyzed to establish a further correlation (Pszczółkowska et al., 2019).

5 | (ABSENCE OF) ASSOCIATION BETWEEN INFECTION GRADE AND ACCUMULATION OF MYCOTOXINS

As mentioned in Section 4, hot and humid climatic conditions favor fungal growth. However, a direct correlation between the presence of a fungus and mycotoxin accumulation does not always occur. An additional limitation for the establishment of such correlations is that not all studies characterized the associated mycoflora to the individual mycotoxin contamination. This could be related to the aim of the particular study, which could be focused on just detecting mycotoxin contamination from a public health perspective without looking for association with causal agents, or because artificial contamination with specific mycotoxins was conducted for specific studies, such as evaluating decontamination strategies. In those works, in which the pulse-associated mycoflora is mentioned, it can be seen that the most predominant are the genera *Aspergillus, Penicillium, Fusarium*, and *Alternaria* (with 27, 22, 22, and 13 mentions, respectively). This is consistent with the fact that these are the most studied genera in relation to mycotoxin production since the toxins they generate are of greater health concern to human and animal health (Moretti et al., 2017).

In addition to considering the existence of constitutively and genetically determined toxigenic and nonmycotoxigenic strains in the same fungal species, there are toxigenic strains that, under particular growing conditions, modify their toxigenicity, as initially reported by Cotty (1997) in a survey conducted in several cotton-producing areas in the United States. Such reports are not very frequent for pulses. However, this was observed by Freitas-Costa and Scussel (2002), who isolated fungal strains in black and colored Brazilian varieties of *Phaseolus vulgaris* to determine their toxigenic potential, initially by means of fluorescence. TLC further confirmed positive cases. However, not all contaminated samples contained mycotoxins. The authors postulate that, since all isolates were grown under the same conditions, this is related to the different reactions of diverse strains to particular environments. This is an issue that needs to be explored further to better understand fungal reactions to specific climatic conditions during growth in the field and during transport and storage of goods to avoid or reduce mycotoxin contamination.

Atoxigenic strains are now seen as a biocontrol option for mycotoxin management due to the competitive exclusion of toxigenic strains, probably resulting from competition for space and nutrients (Agbetiameh et al., 2019; Kagot et al., 2019). In the particular case of *Aspergillus*, it is known that atoxigenic strains have deletions in the gene cluster involved in toxin production (Rao et al. (2020) and references therein), a feature that can be easily used for strain differentiation by molecular methods (Hua et al., 2018; Norlia et al., 2019). In a specific study on pulses, dos Santos-Ciscon et al. (2019) molecularly analyzed different *Aspergillus* species and strains isolated from dry bean samples in Brazil to find the presence of genes involved in the biosynthesis of aflatoxins, ochratoxins, and fumonisins. Among the main results found for the *Aspergillus* species, only *Aspergillus flavus* contained all the genes for aflatoxin production. In addition, *Aspergillus niger* was the only species that had the whole gene cluster for the biosynthesis of fumonisins, thus demonstrating that *Fusarium* is not the only species that can produce this toxin. However, this work fails to demonstrate the actual synthesis of mycotoxins because their presence and contents were not determined.

In addition, there is a marked effect of the host on the colonization (establishment) of the fungus and the subsequent production of mycotoxins. This preference can be seen at the species level but also between genotypes within the same species (Boutigny et al., 2011; Campbell & White, 1995). In the case of pulses, Seenappa et al. (1983) found differential accumulation of aflatoxins in 22 cowpea lines/cultivars inoculated with *Aspergillus parasiticus*, postulating partial (but not total) resistance to aflatoxin production in some of the samples. Since they did not measure the infection rate, a correlation between fungal contamination and mycotoxin accumulation could not be established. In addition, El-Kady et al. (1991) observed reduced fungal invasion in seeds of 20 *Vicia faba* lines and cultivars out of 100 they inoculated with *Aspergillus flavus*. The degree of fungal contamination correlated with the accumulation of aflatoxins. Similarly, Saber (1992) identified two highly resistant and two partially resistant cultivars out of nine *V. faba* cultivars in terms of *A. flavus* establishment and aflatoxin accumulation. They also looked for a potential relationship between the degree of susceptibility and the mineral composition of the seeds and found some differences in Ca, P, K, Mg, Zn, and Na contents. Additional evidence on the differences in aflatoxin production in individual cultivars was subsequently published for *Vigna unguiculata* and *Pisum sativum* by the same research group (El-Kady et al., 1996).

Particular characteristics of the host seeds have been suggested to regulate the infection rate and subsequent accumulation of mycotoxins. Makun et al. (2010) related the thick and hard coat of the bean seed, which might deter invasion of the seed by fungi, as an obstacle for higher contamination rates in this crop. Králová et al. (2006) postulated that pisumin, an antifungal protein found in some *P. sativum* varieties, could have been the reason for consistently not detecting *Alternaria* toxins in pea samples that were growing in the same locality with flax and linseeds that tested positive. Further investigation into pulse-specific proteins (e.g., pisumin) and other potential compounds is still needed to develop strategies for mycotoxin reduction. An example of one group of these potential compounds is detailed in the following section.

6 | POTENTIAL EFFECT OF PHENOLIC COMPOUNDS ON MYCOTOXIN PRODUCTION IN PULSES

Pulses tend to accumulate low amounts of mycotoxins when compared to other commodities exposed to similar conditions. This can be exemplified in the study of Castillo et al. (2002), where rice and black bean samples were inoculated with *Fusarium semitectum*, *Fusarium graminearum*, and *Fusarium equiseti*. Black bean samples accumulated lower amounts of zearalenone and trichothecenes than rice samples. Furthermore, Davidson et al. (2012) found that lentils harvested during the rainy season did not contain mycotoxins, although this climatic condition favors fungal growth. These are examples among 38 other reports, further characterized in Table S1, with similar results. Because of the relevance and potential practical applications of understanding the mechanisms behind these findings, further research might be of interest.

The relatively higher phenolic content in pulses could be a mechanism by which they tend to accumulate fewer mycotoxins. Phenols are plant secondary metabolites that have also been related to the defense against phytopathogenic fungal attacks by reducing spore germination and/or mycelial growth (Martínez et al., 2017; Zabka & Pavela, 2013) with a positive effect on reducing mycotoxin accumulation (Atanasova-Penichon et al., 2016; Gauthier et al., 2016; Righetti et al., 2019; Suárez-Quiroz et al., 2013). The predominant phenolic compounds in pulses include tannins, phenolic acids, and flavonoids, and higher contents usually coincide with darker kernel colors (B. Singh et al., 2017; Campos-Vega et al., 2010; Gao et al., 2017; Mecha et al., 2020).

Ahmed et al. (2022) recently presented the state-of-the-art on the use of phenols as antimycotoxigenic agents. Their review summarizes several in vitro studies where phenolic plant extracts from fruits, cereals, microalgae, and others (e.g., mint) were used to reduce mycotoxin contents. Consequently, as there are no citations of studies using phenols from pulses, it is evident that the potential of their extracts has been overlooked.

For the characterization of phenolic compounds in pulses, the composition of beans is known. Strong colored beans are especially rich in flavonoids (catechin, proanthocyanidins, and anthocyanins) (Chen et al., 2015). Higher contents of these particular secondary metabolites have not only been related to potential direct health benefits to consumers because these compounds act as antioxidants and radical scavengers (Campos-Vega et al., 2010) but also have a positive impact on reducing fungal contamination, as previously mentioned (Ramirez et al., 2018).

On the other hand, only two investigations were found where extracts of pulses, particularly of beans, were used in an attempt to explain the mechanism of inhibition in the production of mycotoxins. The first one analyzed free, conjugated, and bound phenolics in 10 bean varieties to study the potential defense mechanisms against fungal contamination (Telles et al., 2017). The most abundant phenol in the free and conjugated phenolic extracts was chlorogenic acid, which has been reported to have antifungal activity (Martínez et al., 2017). Subsequently, the authors prepared phenolic extracts from two out of 10 varieties and found an inhibitory effect on the activity of fungal α-amylase, which was not associated with the occurrence of aflatoxins in the samples.

The second study proposed a different mechanism by which bean phenols can protect against aflatoxin B_1 accumulation (Cardador-Martínez et al., 2002). In this case, they performed a microsuspension assay where they cultivated *Salmonella typhimurium* strains (TA98 and TA100) with either phenolic bean extract, aflatoxin B_1 or a combination of both. The best inhibition, evidenced by a lower mutagenicity in *Salmonella*, occurred when both substances were present during incubation. Since the molar quantities of the phenolic extract are not comparable with the molar quantities of aflatoxin B_1, the authors suggest that the inhibition mechanism is due to a complex that forms between the phenolic extract and the aflatoxin B_1, which in the end would reduce the toxin bioavailability. Further research showed that the biological activity of the phenolic compounds diminishes with storage time (Aparicio Fernández et al., 2005).

7 | PHOMOPSINS—AN UNDER-STUDIED MYCOTOXIN THAT PRIMARILY AFFECTS PULSES

As mentioned above, of the 300–400 compounds acknowledged as mycotoxins, recurrent attention has been directed mainly to the most prevalent and health-threatening compounds (Bennett & Klich, 2003). Within the group of mycotoxins that are not regularly studied but that are of relevance for pulses, phomopsins are probably the most significant. This mycotoxin group, which mainly affects lupin, is composed of five different metabolites (phomopsin A being the one with the highest toxicity) and is produced by the fungus *Phomopsis leptostromiformis* (anamorph of *Diaporthe toxica*). Animal feed contaminated with this mycotoxin can cause a disease known as lupinosis, which affects the liver of sheep and cattle (Abraham et al., 2019; Weidenbörner, 2018; Williamson et al., 1994). Although lupin seeds are mainly used for animal feed due to their alkaloid contents, there is an increasing trend to utilize them to prepare various products and to extract proteins for human consumption (Abraham et al., 2019; Lo et al., 2021; Shrestha et al., 2021). This represents a latent risk of introducing this toxin directly into the human diet (Reinhard et al., 2006). Only Australia and New Zealand have legislation to regulate the limit of phomopsins, which has been set at 5 μg kg^{-1} (Battilani et al., 2011). Although lupin has been described as the main host for this fungus, it may also grow on peas and beans (Schloß et al., 2015). For this reason, it is important to conduct further studies and monitor the occurrence of phomopsins in other hosts and look for potential strategies to reduce infection and toxin accumulation, for example, resistance to fungal infection (Cowley et al., 2014; Ksiazkiewicz et al., 2020). Reports on the development of sensitive tests, including the use of enzyme-linked immunosorbent assay and HPLC-MS/MS, for the detection of phomopsins in pulses have been published by Swiss, Dutch, and German groups (de Nijs et al., 2013; Reinhard et al., 2006; Schloß et al., 2015).

8 | PHYSIOLOGICAL EFFECTS OF (MYCO)TOXINS ON PULSE SEEDS AND SEEDLINGS

Mycotoxins not only affect vertebrate health, which is by far the main concern, but can also have a negative influence on seed (and seedling) physiology (germination, color, viability, etc.). It is important to separate direct effects caused by the toxins from other consequences related to fungal growth and damage to the seeds, which are reviewed elsewhere (Javaid et al., 2005; Pedrozo & Little, 2017; R. Kumar & Gupta, 2020). When evaluating the effects of mycotoxins on plants, other types of secondary metabolites must also be considered, such as phytotoxins, which may also have adverse effects (Graniti, 1991; Strange, 2007; Xu et al., 2021). These compounds promote the pathogenicity process of fungi through different mechanisms of action (Möbius & Hertweck, 2009). A recent literature review compiled information associated with this topic, with a section dedicated to legumes (including soybean) (Evidente et al., 2019). However, the fungi mentioned in the section are mainly phytopathogenic (i.e., *Ascochyta pisi*, *Ascochyta pinodes*, *Ascochyta fabae*, and *Phoma putaminum*) and cause diseases such as anthracnose in beans and peas. No additional information about pulses and the primary mycotoxigenic fungi was mentioned in that review article.

In general, information about the direct effect of mycotoxins on plant physiological parameters is scarce, and only a few examples can be found in the literature (Agar et al., 2006; Divakara et al., 2017; Prasad, 1997), with even fewer reports on pulses. In an early work, Sinha and Kumari (1989) soaked mung bean seeds in different concentrations of ochratoxin A and found a direct correlation between the color change (from bright greenish to yellowish green) caused by a reduction in the chlorophyll contents concomitant with increasing toxin concentrations. A parallel reduction in protein, DNA and RNA concentrations was also observed. Alkahtani et al. (2011) studied the influence of several mycotoxins (aflatoxins, alternariol, and zearalenone) on particular quality characteristics of bean seeds, such as discoloration, deterioration, and reduction of viability. A direct correlation between the degree of discoloration and mycotoxin concentration could be established, which also impacted germination. The highest germination percentage (96.4%) was observed in the nondiscolored seeds, followed by the golden-brown seeds (70.5%) and, finally, the dark brown seeds with the lowest (42.2%). Likewise, increasing doses of fumonisin B_1 applied to cowpea seeds correlated with a reduction in germination, and the highest concentrations (50 and 100 mg L^{-1}) inhibited root and shoot elongation (Kritzinger et al., 2006), while lower doses (5-40 mg L^{-1}) reduced the percentage of germination and seedling length (Kotze et al., 2017). In addition to the direct influence on plant physiology, there is a report on the negative effects of mycotoxins on the physiology and function of nodule bacteria by decreasing nodule number, fresh weight, and total nitrogenase activity associated with contaminated *V. faba* (Mahmoud & Abd-Alla, 1994).

9 | CONCLUSION AND FUTURE PERSPECTIVES

Pulses are highly nutritious food products, and their consumption is becoming increasingly popular. Nonetheless, they are a good substrate for fungal growth and, if the right conditions exist, for the consequent synthesis of mycotoxins. Reports from different parts of the world show that, depending on the region and the legume species and variety, different mycoflora compositions can be found. Considering the health relevance of these toxins, it is important to carry out characterizations, such as those mentioned in the reports above, to identify the main fungi affecting a specific geographical region and particular crop under certain growing/storage conditions and the subsequent synthesis and accumulation of mycotoxins. Attention should be drawn to phomopsins because they have been neglected to a certain extent, probably because they seem to be limited to a few pulses. As mentioned before, only Australia and New Zealand have regulatory thresholds to monitor this mycotoxin. Due to the increased interest in using lupin as a soybean substitute in processed products, it is of particular interest that other regions of the world begin to establish thresholds for phomopsin contamination. Even though there is evidence about a positive effect of phenolic compounds in pulses against fungal attacks and mycotoxin accumulation, further research to explain the involved mechanisms needs to be conducted. Additional research should also focus on the physiological effects of mycotoxin accumulation in infected seeds and seedlings, considering agronomical implications. Moreover, this review shows an excellent opportunity for collaboration between the global south-south and global north-south countries to develop detection techniques tailored to pulses and mechanisms to mitigate mycotoxin accumulation. This collaboration should keep in mind the development of rapid detection technologies to bring this particular food group to the same level of research as in cereals.

ACKNOWLEDGMENTS

The authors would like to thank Mrs. Sabine Nugent for her help in the language proofing and editing and M.Sc. Andrés Hernández-Pridybailo for advice on the statistical analysis. Catalina Acuña-Gutiérrez thanks the German

Academic Exchange Service (DAAD) for financial support in the form of a scholarship and the University of Costa Rica for academic support.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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How to cite this article: Acuña-Gutiérrez, C., Jiménez, V. M., & Müller, J. (2022). Occurrence of mycotoxins in pulses. *Comprehensive Reviews in Food Science and Food Safety*, 1–16. https://doi.org/10.1111/1541-4337.13008