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CHAPTER
4

Biodiversity of Aflatoxigenic *Aspergillus* section *Flavi* Species According to Food Matrices and Geographic Areas

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1. Introduction

Aflatoxins (AFs) are polyketide-derived metabolites produced by fungi on a wide range of crops (cereals, oilseeds, tree nuts, spices, dried fruits, etc.), both in the field and the post-harvest. As chemical stable molecules, resistant to conventional thermal or technological processes, they will pass through the whole food or feed supply chain to the final processed products (Kumar et al. 2017, Pankaj et al. 2018). There are more than 20 known AFs and derivatives, yet the most hazardous AFs include the four naturally-occurring AFB1, AFB2, AFG1 and AFG2, and the hydroxylated metabolites of AFB1 and AFB2, and AFM1 and AFM2, which are produced through biotransformation in the liver and excreted in the milk of humans and mammals (Kumar et al. 2017). AFs are known for their high acute and chronic toxicity to both humans and animals, and are considered among the most dangerous mycotoxins with carcinogenic,

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hepatotoxic, immunotoxic, teratogenic and mutagenic effects (Kowalska et al. 2017). AFB1 is the most prevalent and toxic aflatoxin, and is classified as a Group 1 human carcinogens (IARC 2012). The intake of high amounts of AFs can cause acute intoxication (aflatoxicosis) associated with jaundice, vomiting, hemorrhages, abdominal pain, acute liver failure, problems with absorption of nutrients, and can be lethal (IARC 2015). Reported outbreaks in western India (1974) and in Kenya (2004) caused the death of 106 and 125 people, respectively (Lewis et al. 2005, Azziz-Baumgartner et al. 2005). Chronic exposure to low levels of AFs is associated with high risk of hepatocellular carcinoma (HCC), immunosuppression, teratogenic and mutagenic effects, reduction of nutrient absorption, child stunting, detrimental effects in the endocrinal system, and liver failure (Stack and Carlson 2003, Turner et al. 2005, Bbosa et al. 2013). More than five billion people worldwide are at risk of chronic exposure to AFs through contaminated foods (Wu and Glucu 2012). Humans' exposure to AFs mainly occurs by direct intake of contaminated foods of vegetal or animal origin (Bhat et al. 2010, IARC 2015). Hence, the presence of AFs in foodstuff and feedstuff is a public health issue associated with detrimental effects in economy. In addition, commodities are generally contaminated by several mycotoxins, and this co-occurrence may result in a greater toxicity to humans caused by the possible additive or synergistic effects of these compounds (Grenier and Oswald 2011). The main aflatoxin-producing fungi belong to *Aspergillus* section *Flavi* of the *Circumdati* subgenus, and only five AF producers do not belong to this section, *A. ochraceoroseus, A. rambellii* (*A.* section *Ochraceorosei*), *A. astellatus, A. olivicola,* and *A. venezuelensis* (*A.* section *Nidulantes*) (Varga et al. 2015). The aim of the present chapter is to describe the characteristics of the aflatoxigenic *Aspergillus* section *Flavi* species isolated from food or feed, and to address the biodiversity according to food matrices and geographic areas.

2. Characteristics of the Aflatoxigenic *Aspergillus* section *Flavi* Species

The major producers of AFs worldwide are *Aspergillus flavus* and *A. parasiticus* and for a while they were recognized as the only AF producers, and later, diversity surveys pointed *A. nomius* as the third main AF producer for its frequency in spoiled food (Kurtzman et al. 1987, Perrone et al. 2014). However, the implementation of polyphasic species identification showed a more complex story. Over the last two decades, this approach demonstrated a high biodiversity and plasticity within the section *Flavi* (Varga et al. 2011, Soares et al. 2012, Taniwaki et al. 2012, Frisvad et al. 2019). Currently this section encloses 34 species, from which 19 are aflatoxigenic (Frisvad et al. 2019).

2.1 Morphological Characteristics

Macro- and micro-morphological characters of the 19 aflatoxigenic *Aspergillus* section *Flavi* species on Malt Extract Agar (MEA) and Czapek Yeast Agar

(CYA) after seven days of incubation, in the dark at 25°C are summarized in Table 1. These two media are recommended as standard for *Aspergillus* and commonly used in taxonomic studies on this genus (Samson et al. 2014). Most aflatoxigenic *Aspergillus* species grow well on MEA and CYA at 25°C attaining colony diameter of more than 50 mm after seven days; *A. austwickii* is the slowest growing species (colony diameter MEA: 45–47 mm, CYA: 4648 mm). Colony surface is mostly deep, floccose, rarely plane, velvety or powdery. Most species sporulate and produce sclerotia with the exception of *A. pipericola* (no sporulation) and *A. arachidicola*, *A. luteovirescens*, *A. novoparasiticus*, *A. pseudocaelatus* and *A. pseudonomius* (no sclerotia). Conidia are mainly in shades of (dark) yellow-green, but also in shades of brown. Conidial heads are uniseriate with smooth or rough conidia, biseriate with rough conidia, or uniseriate to biseriate with smooth or slightly rough, smooth to rough or rough conidia. Sclerotia size varies between large (400–2000 μm), intermediate (*A. sergii:* 513-551 μm) and small (< 400 μm). Sclerotia morphology can be globose to ellipsoidal, and they become dark brown or black with time (Varga et al. 2011, Frisvad et al. 2019). Morphological characters are useful to differentiate some aflatoxigenic species within section *Flavi,* but for closely related species a proper description based only on these characters is a challenge. For this reason, a polyphasic approach that includes the morphological, chemical (mycotoxins and other extrolite production) and molecular characteristics is necessary to identify and characterize the *Aspergillus* section *Flavi* species (Varga et al. 2011).

2.2 Mycotoxins and Other Extrolites

Aflatoxigenic species from section *Flavi* produce an ample spectrum of secondary metabolites, besides of AFs some important and emergent mycotoxins include cyclopiazonic acid (CPA), tenuazonic acid and aflatrems (Table 2). From the nineteen aflatoxigenic species, three produce only AFB (AFB1 and AFB2: *A. flavus, A. pseudotamarii*; AFB1: *A. togoensis*), the other species produce both AFB (B1, B2) and AFG (G1, G2). *A. flavus* is the main AFB1 producer across the world and therefore the best known species from *Flavi* section, its AF production potential varies from non-aflatoxigenic to aflatoxigenic strains, with a high incidence of non-aflatoxigenic strains (60–70%) (Varga et al. 2011). AF production potential is not associated with virulence or competitive ability during crop infection. This plasticity and the lack of production of AFG are driven by several genetic differences, including single polymorphisms and large deletions in the AF biosynthesis gene cluster (Ehrlich 2004, Chang and Ehrlich 2010). *A. flavus* L-morphotype generally presents a 0.8 kb deletion in the CypA/NorB (*AflU*/*AflF*) region of the aflatoxin biosynthetic gene cluster (BGC), whereas *A. flavus* S-morphotype present of 1.5 kb (Ehrlich and Yu 2010). The CYPA protein encoded by *AflU* is required for AFG production (Ehrlich et al. 2004). A third group, gathering the strains responsible of the lethal outbreak in Kenya, was highlighted with a 2.2 kb deletion (Probst et al. 2012). AF production by *A. flavus* L-morphotype isolates is variable, while *A. flavus* S-morphotype isolates produce high quantities

Table 1: Morphological characteristics of aflatoxigenic *Aspergillus* section *Flavi* species on MEA and CYA after seven days of incubation in the dark at 25°C

Aflatoxigenic Aspergillus species	*Medium*	*Colony diameter (mm)*	*Colony surface and conidial color*	*Sclerotia (μm)*	*Conidial head morphology and conidial surface*	*References*
*A. aflatoxiformans**	**MEA**	47–50	Colonies moderately deep, mycelium floccose and white Conidia yellow-green, moderately dense on MEA and sparse on CYA	100–250	Uniseriate Smooth	Frisvad et al. 2019
	CYA	50–51				
A. arachidicola	**MEA**	60–65	Colonies velvety Conidia olive to olive brown, abundant	Not observed	Uniseriate or biseriate Rough	Pildain et al. 2008
	CYA					
A. austwickii	**MEA**	45–47	Colonies moderately deep, mycelium floccose and white Conidia yellow-green, moderately dense on MEA and sparse on CYA	100–300	Uniseriate Smooth	Frisvad et al. 2019
	CYA	46–48				
A. flavus	**MEA**	50–70	Colonies similar to those on CYA although usually less dense Colonies plane, sparse to moderately dense, velutinous in marginal areas at least, often floccose centrally, rare deep; mycelium white Conidia greyish green, yellow green or olive yellow, sometimes yellow			
	CYA	60–70		< 400 (S-type) 400–800 (L-type) or not observed	Typically biseriate, rare uniseriate Finely rough, rarely smooth	Pitt and Hocking 2009, Frisvad et al. 2019
*A. korhogoensis**	**MEA**	37–60	Colonies deeply floccose with a dominant white aerial mycelium Conidia dull yellowish green	<400	Uniseriate or biseriate Smooth or slightly rough	Carvajal-Campos et al. 2017
	CYA	57–80				

(*Contd.*)

Table 1: (*Contd.*)

Aflatoxigenic Aspergillus species	*Medium*	*Colony diameter (mm)*	*Colony surface and conidial color*	*Sclerotia (μm)*	*Conidial head morphology and conidial surface*	*References*
*A. luteovirescens**	**MEA**	65	Colonies loose and deep, yellow-green becoming darker at maturity	Generally not observed, when present large	Mostly biseriate	Peterson et al. 2001, Frisvad et al. 2019
A. minisclerotigenes	**MEA**	60–70	Colonies floccose, white mycelium Conidia light-greyish green, sparse	150–300	Normally biseriate, rare uniseriate Smooth to rough	Pildain et al. 2008
	CYA		Colonies velvety Conidia light-greyish green			
A. mottae	**MEA**	>70	Colonies plane, mycelium white Conidia yellow-green, scarce	249–371	Normally biseriate, rare uniseriate Smooth to finely rough	Soares et al. 2012
	CYA					
A. nomius	**MEA**	40–70	Colonies mostly floccose. Conidia green	< 500	Mostly biseriate Rough	Kurtzman et al. 1987, Doster et al. 2009
	CYA	52–60	Colonies greyish green			
A. novoparasiticus	MEA **CYA**	56 – 60 58 – 63	Colonies powdery Greenish-yellow to olive	Not observed	Usually uniseriate, rarely biseriate	Gonçalves et al. 2012
A. parasiticus	**MEA**	50–65	Colonies similar to those on CYA but usually less dense	400–800	Mostly uniseriate Rough	Pitt and Hocking 2009
	CYA	50–70	Colonies plane, low, dense and velutinous, mycelium white Conidia dark yellowish green			

A. pipericola	**MEA** **CYA**	61–72 58–72	Colonies moderately deep, mycelium floccose and white Sporulation absent	75–250	Biseriate Rough	Frisvad et al. 2019
A. pseudocaelatus	**MEA** CYA	60–65	Colonies velvety Conidia olive to olive brown, abundant	Not observed	Uniseriate or biseriate Rough	Varga et al. 2011
A. pseudonomius	**MEA** **CYA**	60–65	Colonies floccose with dominant aerial mycelium Poor sporulation	Not observed	Uniseriate Rough	Varga et al. 2011
A. pseudotamarii	**MEA**	60–70	Colonies mostly floccose Conidia olive green	1000–2000	Biseriate Rough	Ito et al. 2001
A. sergii	**MEA** **CYA**	55	Colonies plane, velvety and dense. Conidia in a uniform, dense layer but sparse in the areas of sclerotium production, light green	513–551	Uniseriate Rough	Soares et al. 2012
A. texensis	**CYA**	71	Colonies velvety. mycelium white Conidia yellow-green, sparse	130–300	-	Singh et al. 2018
A. togoensis	**MEA** **CYA**	>50 >50	Conidia yellow-brown to orange-brown	Large sclerotia	Biseriate	Samson and Seifert 1985, Frisvad et al. 2019
A. transmontanensis	**MEA**	55–57	Colonies similar to growth on CYA with conidial heads more dense and floccose	458–609	Mostly uniseriate Rough	Soares et al. 2012
	CYA		Colonies dense and velutinous. Conidia in a uniform, dense layer but sparse in the areas of sclerotium production, dark yellow-green			

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* *A. parvisclerotigenus*, *A. bombycis* and *A. korhogoensis* synonimyzed as *A. aflatoxiformans*, *A. luteovirescens* and *A. cerealis*, respectively, by Frisvad et al. 2019.

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Table 2: Production of mycotoxins and other secondary metabolites by aflatoxigenic *Aspergillus* section *Flavi* species

Aflatoxigenic Aspergillus species	*Aflatoxins*	*Other mycotoxins*	*Other secondary metabolites*	*References*
A. aflatoxiformans	AFB1 AFB2 AFG1 AFG2	Aflatrems, cyclopiazonic acid, versicolorins	Aspergillic acid, aflavarins, aflavinines, aspirochlorin, kojic acid, paspaline, paspalinine, metabolite gfn	Frisvad et al. 2019
A. arachidicola		Versicolorins	Aspergillic acid, aspirochlorin, chrysogine, ditryptophenaline kojic acid, miyakimides, parasiticolide, "NO2" metabolite, parasitocolides	Pildain et al. 2008, Varga et al. 2011, Frisvad et al. 2019, Iamanaka et al. 2019
A. austwickii		Aflatrems, cyclopiazonic acid, versicolorins	Aflavarins, kojic acid, paspaline, paspalinine, metabolite gfn	Frisvad et al. 2019
A. korhogoensis		Aflatrems, cyclopiazonic acid, 3-O-methylsterigmatocystin, sterigmatocystin, versicolorins	Aspergillic acid, aflavarins, asparasones, asparasone A aflavinines, kojic acid, leporin B, norsolorinic acid, paspaline, paspalinine	Carvajal-Campos et al. 2017
A. luteovirescens		Tenuazonic acid (some strains)	Aspergillic acid, kojic acid For some strains: an altersolanol, chrysogine	Pildain et al. 2008, Varga et al. 2011, Frisvad et al. 2019
A. minisclerotigenes		Aflatrems, cyclopiazonic acid	Aspergillic acid, aflavarins, aflavinines, kojic acid, paspalinine, parasiticolides. For some strains: aflavazole	Pildain et al. 2008, Frisvad et al. 2019
A. mottae		Cyclopiazonic acid, 3-O-methylsterigmatocystin, versicolorins	Aspergillic acid, an aflavinin, kojic acid, parasiticol, paspalinine	Soares et al. 2012, Frisvad et al. 2019

A. nomius	3-O-methylsterigmatocystin tenuazonic acid, versicolorins	Aspergillic acid, anominine, aspernomine, kojic acid, a miyakamide, pseurotin, parasiticol, paspaline, paspalinine, pseurotin A	Kurtzman et al. 1987, Frisvad et al. 2019
A. novoparasiticus	Tenuazonic acid	Aspergillic acid, aspirochlorin, ditryptophenaline, kojic acid, miyakamides, parasiticolide, crysogine, a tetracyclic compound, ustilagoidin	Goncalvez et al. 2012, Frisvad et al. 2019, Iamanaka et al. 2019
A. parasiticus		Aspergillic acid, kojic acid, parasperone, parasiticol, parasiticolide A and B	Frisvad et al. 2019
A. pipericola	Aflatrem, cyclopiazonic acid	Aflavinins, aflavarins, paspaline, paspalinine	Frisvad et al. 2019
A. pseudocaelatus	Cyclopiazonic acid, tenuazonic acid	Aspirochlorin, dirtyptophenaline, kojic acid	Varga et al. 2011, Frisvad et al. 2019
A. pseudonomius	Tenuazonic acid	Aspergillic acid, chrysogine, kojic acid, a miyakamide	Varga et al. 2011, Frisvad et al. 2019
A. sergii	Aflatrem, cyclopiazonic acid, 3-O-methylsterigmatocystin, sterigmatocystin, versicolorins,	Aspergillic acid, aflavazole, an aflavarin, aflavinines, asperfuran, kojic acid, leporin B, paspalinine	Soares et al. 2012, Frisvad et al. 2019
A. texensis	Cyclopiazonic acid	Aspergillic acid	Singh et al. 2018

(*Contd.*)

Table 2: (*Contd.*)

Aflatoxigenic Aspergillus species	*Aflatoxins*	*Other mycotoxins*	*Other secondary metabolites*	*References*
A. transmontanesis			Aspirochlorin, kojic acid, a miyakamide	Soares et al. 2012, Frisvad et al. 2019
A. flavus	AFB1 AFB2	Aflatrems (only in sclerotium producers), cyclopiazonic acid	Aspergillic acid, asperfuran, aspirochlorin, citreoisocoumarin, ditryptophenaline, flavimin, kojic acid, miyakamides, ustilaginoidin C, ustiloxin B. Only in sclerotium producers: aflavarins, aflavinines, paspaline and paspalinine	Amaike and Keller 2011, Umemura et al. 2013, Arroyo-Manzanares et al. 2015, Cary et al. 2015a,b, Frisvad et al. 2019
A. pseudotamarii		Cyclopiazonic acid, tenuazonic acid	Aflavinines, kojic acid, For some strains: an altersolanol, aspirochlorin, paspaline and paspalinine	Ito et al. 1999, Varga et al. 2011, 2015, Frisvad et al. 2019
A. togoensis	AFB1	Sterigmatocystin	A bisiderin, paspaline, paspalinine. For some strains: paxilline	Frisvad et al. 2019

AQ : or Kjærbølling as in references?

of AFs (Ehrlich 2004). Recently *A. pseudotamarii* genome was sequenced and BGC analysis showed it lacks the first 600 base pairs in the *AflU* gene encoding for CYPA protein (Kjaerbolling et al. 2020). *A. parasiticus*, the second main AF producer, also shows AF production plasticity, 3 to 6% of strains are considered non-aflatoxigenic (Chang et al. 2007). For the other AFBG species, the production seems to occur in all isolates.

Besides of AFs, some of their biosynthetic intermediates, like versicolorins, 3-O-methylsterigmatocystin and sterigmatocystin, are considered to be potentially toxic and reported in several aflatoxigenic species (Table 2). Though, these species are weak producers, as the intermediates are mainly transformed into AFs. Sterigmatocystin is considered an emerging mycotoxin and classified as 2B carcinogen for its potentially carcinogenic, mutagenic and teratogenic effects (IARC 2012, Bertuzzi et al. 2017). It is reported to be produced by *A. korhogoensis*, *A. sergii* and *A. togoensis*. The latter species is the only species from *Flavi* section capable to storage sterigmatocystin (Varga et al. 2015). Versicolorin A was shown as cytotoxic and genotoxic for lungs (Jakšić et al. 2012), renal and hepatic cells (Theumer et al. 2018). Recently, versicolorin A was reported as more cytotoxic than AFB1 for human intestinal cells. The toxic effects of 3-O-methylsterigmatocystin are less acute than AFs, sterigmatocystin and versicolorin A (Jakšić et al. 2012).

Cyclopiazonic acid is an important mycotoxin from section *Flavi* that has a synergetic effect with AFs. It might play a role in niche adaptation, providing an advantage in fungal fitness under specific environmental conditions (Georgianna et al. 2010). It is produced by *A. flavus* and closely related species, as well as *A. pseudocaelatus* and *A. pseudotamarii* (Table 2). Some species from section *Flavi* unable to produce CPA are believed to have deletions of the biosynthetic pathway silencing its production, such as *A. parasiticus, A. nomius* and their closely related species (Moore et al. 2016). Tenuazonic acid is a non-mutagenic mycotoxin that causes tremors, diarrhea, vomiting and hemorrhages. In section *Flavi,* it is reported in the clades *A. nomius* and *A. tamarii* (Table 3) and some strains of *A. novoparasiticus*. Aflatrem is another emergent mycotoxin, classified as a potent tremorgenic compound that causes neurological disorders. It seems that it might interfere with the release of neurotransmitters by receptors in the central and peripheral nervous systems (Zhang et al. 2004).

Two common extrolites produced by several aflatoxigenic species in section *Flavi* are kojic acid and aspergillic acid; the first organic acid is used in various industrial applications, especially in cosmetic and health care industries (Mohamad et al. 2010). Kojic acid is only not produced by *A. togoensis* and *A. pipericola*, whereas aspergillic acid is not produced by *A. austwickii*, *A. pipericola*, *A. pseudocaelatus*, *A. transmontanesis*, *A. pseudotamarii* and *A. togoensis* (Table 2). The lack of aspergillic acid production is characteristic of *A. tamarii* clade (Varga et al. 2011, Frisvad et al. 2019). Leporins are also found in several *Flavi* section species and are proven to have anti-insectan activity (Cary et al. 2015 a, b). Sclerotia extrolites include some mycelium extrolites and some unique extrolites; among them some reported in aflatoxigenic species are AFs and aflatrems (already mentioned above), aflavazole, aflavinines, aflavarins, anominine, aspernomine, and paspalines (Table 2) (Cary et al. 2015b, Frisvad et al. 2019). Aflavinines and aflavarins are frequently reported, especially in species closely related with *A. flavus.* They have anti-insectan activity (Gloer et al. 1988), and are suggested to have key ecological roles in species survival (TePaske and Gloer 1992, Cary et al. 2015b).

2.3 Molecular Markers and Phylogenetic Analyses

The inclusion of molecular markers for species identification in *Aspergillus* section *Flavi* is proven to be advantageous, especially for cryptic species identification. It helped not only to unmask diversity but also to understand the relationships within *Aspergillus* section *Flavi*. Genes tested with fruitful results include *benA*, *cmdA* and *RPB2*. These markers are advantageous because they have conserved and variable regions and are widely described in literature (primers and sequences) (Varga et al. 2011, Frisvad et al. 2019). Phylogenetic studies showed that most aflatoxigenic species are derived species. A recent study performed by Frisvad et al. (2019) showed that aflatoxigenic species are grouped in three main clusters: *A. flavus*-clade, *A. tamarii*-clade and *A. nomius*-clade (Table 3). *A. togoensis* is a basal species and is not considered as a food contaminant.

Species from *A. flavus*-clade can be sub-divided in two main clusters, one that includes species with *A. flavus* overlapping traits and the other that includes species with *A. parasiticus* overlapping traits, and *A. mottae* as its basal species (Table 3). *A. flavus* sub-clade species number has increased dramatically over the last decade, and as aforementioned, it is composed of cryptic species (overlapping morphological, genetic and chemotype traits) (Frisvad et al. 2005, 2019, Varga et al. 2011). Within this sub-group four clusters are formed: (1) *A. flavus*, (2) *A. minisclerotigenes* and *A. texensis*, (3) *A. pipericola* and (4) a cluster including *A. aflatoxiformans*, *A. korhogoensis* and *A. austwickii* (Varga et al. 2011, Carvajal-Campos et al. 2017, Singh et al. 2018, Frisvad et al. 2019). *A. oryzae*, considered as a domesticated variant of *A. flavus* for a long time, forms a subgroup based on the three above-mentioned genes. The origin of *A. oryzae* is controversial. A recent study based on 200 monocore genes supports an earlier hypothesis that it is closer to *A. aflatoxiformans* and *A. minisclerotigenes* (Kjaerbolling et al. 2020), thus, another study based on 82 genomes of *A. oryzae* strains used in the manufacture of Asian fermented foods confirmed that it formed a monophyletic cluster nested in *A. flavus* clade (Watarai et al. 2019). AFBG strains with small sclerotia are commonly misclassified as *A. flavus* S_{BG} morphotype; however phylogenetic surveys revealed that this classification includes several cryptic species related to *A. flavus*: *A. minisclerotigenes, A. texensis, A. aflatoxiformans, A. korhogoensis, A. pipericola* and *A. austwickii* (Pildain et al. 2008, Frisvad et al. 2005, 2019, Varga et al. 2011, Soares et al. 2012, Perrone et al. 2014, Carvajal-Campos et al. 2017, Singh et al. 2018, Singh and Cotty 2019). *A. parasiticus* sub-clade species are AFBG producers. Their phylogenetic relationships are more complicated to explain as they present slight differences depending on the molecular markers used. Anyhow, *A.*

Table 3: Main clades of aflatoxigenic ***Aspergillus*** section ***Flavi***

Clade	*Sub-clade*	*Species*
A. flavus-clade	Group of species closely related to *A. flavus sensu stricto*	*A. flavus, A. aflatoxiformans, A. austwickii, A. korhogoensis, A. minisclerotigenes, A. pipericola, A. texensis*
	Group of species closely related to *A. parasiticus*	*A. parasiticus, A. arachidicola, A. novoparasiticus, A. sergii, A. transmontanensis*
	Basal species to the *A. flavus* and *A. parasiticus* groups	*A. mottae*
A. tamarii-clade	-	*A. tamarii, A. caelatus, A. pseudocaelatus, A. pseudotamarii*
A. nomius-clade	-	*A. nomius, A. luteovirensces, A. pseudonomius*

parasiticus and *A. sojae* (domesticated species) cluster together. Both species are closely related to *A. arachidicola* and *A. novoparasiticus,* the latter being morphologically similar to *A. parasiticus. A. sergii* and *A. transmontanensis* are the basal species of this sub-clade. Finally, *A. mottae* sets as the basal species of the *A. flavus* and *A. parasiticus* sub-clades, though it resembles the species from the *A. parasiticus* sub-clade, sharing morphological, genetic and chemical traits (Varga et al. 2011, Soares et al. 2012, Carvajal-Campos et al. 2017, Frisvad et al. 2019).

A. tamarii-clade species produce AFBG with the exception of *A. tamarii* and *A. caelatus.* Mature colonies of *A. pseudotamarii* resemble morphologically to the *A. tamarii* and *A. pseudocaelatus* overlap traits with its sister taxon, *A. caelatus* (Varga et al. 2011).

A. nomius-clade is composed only by AFBG species. *A. pseudonomius* (Varga et al. 2011) is the sibling species of *A. nomius*, and both overlap traits, risking misidentification (Peterson et al. 2001, Moore et al. 2016). *A. luteovirescens* also share traits with species from its cluster (Peterson et al. 2001). Although *A. luteovirescens* produces AFBG, it is not considered as a pathogen for humans or animals as it occurs less frequently in food and feedstuff (Varga et al. 2015, Moore et al. 2016). *A. nomius, A. pseudonomius,* and *A. luteovirescens* lack production of CPA, which has been suggested as a fixed trait in the cluster (Varga et al. 2011, Frisvad et al. 2015).

3. Aflatoxigenic *Aspergillus* section *Flavi* Biodiversity According to Food Matrices, Production Chain Stage and Geographical Areas

The presence of aflatoxigenic *Aspergillus* section *Flavi* species in various foodstuff (cereals, dried fruits, legumes, oilseeds, roots and tubers, spices, tree nuts, etc.) and on all continents (Africa, Asia, Oceania, Europe and America) are highlighted by several studies (Table 4). Species distribution is not homogenous, a higher diversity is found in tropical and subtropical regions, as environmental conditions enhance their development (Schatzmayr and Streit 2013), *Aspergillus* section *Flavi* species physiological requirements of moisture are around 0.85 to 0.99 $a_{w,}$ while optimal temperatures are between 28 and 42°C (Medina et al. 2015, Yogendrarajah et al. 2016). Aflatoxigenic species of section *Flavi* are mainly saprophytic and inhabit numerous ecological niches, like soil, decaying vegetation, hay and seeds, agricultural fields, and stored products. Fungal contamination of staples occurs during pre-harvest steps (crops and recollect) and/or in post-harvest steps (mainly storage and manufacturing production processes) (Rodrigues et al. 2012).

3.1 Biodiversity According to Food Matrices and Geographical Areas

The aflatoxigenic *Aspergillus* section *Flavi* species reported worldwide in the main food matrices are listed in Table 4. Species in this section were also reported in other food crops like *A. flavus* from acha in Nigeria, canola in Serbia, mustard seeds and chilgoza pine nuts in India (Tomar-Balhara et al. 2006, Sharma et al. 2013, Škrinjar et al. 2013, Ezekiel et al. 2014). In sugarcane, besides of *A. flavus*, *A. novoparasiticus* was reported in Egypt, Brazil, Japan and USA while *A. parasiticus* and *A. arachidicola* only in Asian countries and Brazil, respectively (Takahashi et al. 2004, Kumeda et al. 2004, Ahmed et al. 2010, Garber and Cotty 2014, Iamanaka et al. 2019, Abdallah et al. 2020). *A. flavus*, *A. parasiticus* and *A. nomius* were isolated from cocoa beans in Brazil (Copetti et al. 2011) and *A. aflatoxiformans* from edible mushrooms in Nigeria (Ezekiel et al. 2013a).

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3.2 Cereals

3.2.1 Maize

Worldwide, *A. flavus* is reported as the most common species from section *Flavi* through the maize production chain (field, storage, derived products) (Table 4), including aflatoxigenic and non-aflatoxigenic isolates (Probst et al. 2014, Kachapulula et al. 2017). Maize plants are sensitive to drought and temperature, by consequence prone to fungal infection under plant stress conditions. *A. flavus* is considered to have a commensal relationship with this crop (Kornher 2018, Taniwaki et al. 2018); nevertheless, it is not the only species from section *Flavi* contaminating maize, *A. parasiticus* is the second most important contaminant, and occasionally some other species are reported (Table 4). In Africa, the presence of aflatoxigenic species on maize are mainly reported at post-harvest steps, with *A. flavus*, *A. parasiticus* and S_{BG} isolates as the most important contaminates. *A. flavus* L-morphotype strains are more common, including aflatoxigenic and non-aflatoxigenic strains (Probst et al. 2014, Kachapulula et al. 2017). S_{BG} isolates in the region are more probably *A. aflatoxiformans* and *A. minisclerotigenes* (in this order). *A. minisclerotigenes*

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Table 4: Aflatoxigenic *Aspergillus* section *Flavi* species according to food matrices, production chain stage and geographical areas

Crops	*Production chain step*	*Geographic zone*		*Aflatoxigenic* Aspergillus *species*	*References*
Cereals					
Barley	**Post-harvest:** Grains**	Asia	Pakistan	*A. flavus*	Fakhrunnisa et al. 2006
		Europe	Spain	*A. flavus* *A. parasiticus*	Mateo et al. 2011
Maize	**Post-harvest:** kernels from storage or market	Africa	Nigeria, South Africa	*A. flavus*	Atehnkeng et al. 2008, Chilaka et al. 2012, Ekwomadu et al. 2017
			Egypt, Kenya	*A. flavus**	El-Shanshoury et al. 2014, Gachara et al. 2018, Abbas et al. 2020
			Cameroon	*A. flavus* *A. parasiticus*	Njobeh et al. 2009
			Kenya	*A. flavus* *A. minisclerotigenes* *A. parasiticus*	Okoth et al. 2018
			Ghana	*A. flavus* *A. parasiticus* S_{BG} isolates	Agbetiameh et al. 2018
			Nigeria	*A. korhogoensis*	Frisvad et al. 2019
	Non-specified step: at harvest and kernels from market		Cameroon, Ghana, Mali, Rwanda, Sierra Leona, Tanzania, Uganda	*A. flavus*	Probst et al. 2014

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Table 4: (*Contd.*)

Crops	*Production chain step*	*Geographic zone*		*Aflatoxigenic* Aspergillus *species*	*References*
			Malawi, Zambia	*A. flavus* *A. parasiticus*	Probst et al. 2014, Kachapulula et al. 2017
			Burkina Faso, Ethiopia, Senegal	*A. flavus* S_{BG} isolates	Diedhiou et al. 2011, Probst et al. 2014
			Congo, Kenya, Nigeria	*A. flavus* *A. minisclerotigenes* S_{BG} isolates	Probst et al. 2014
			Mozambique, Zambia, Zimbawe	*A. flavus* *A. parasiticus* S_{BG} isolates	Probst et al. 2014
			Somalia	*A. minisclerotigenes*	Probst et al. 2014
	Pre-harvest: at harvest	Asia	China, Pakistan	*A. flavus*	Saleem et al. 2012, Mamo et al. 2018
	Post- harvest: fresh kernels, corn meal		South Korea	*A. flavus*	Frisvad et al. 2019
			China, Vietnam	*A. flavus**	Gao et al. 2007, Trung et al. 2008, Tran-Dinh et al. 2009
			Pakistan, Philippines	*A. flavus* *A. parasiticus*	Ibrahim et al. 2016, Balendres et al. 2019
	Non-specified step		China	*A. flavus* *A. arachidicola* *A. novoparasiticus* *A. pseudonomius*	Rasheed et al. 2019

	Pre-harvest: at harvest	Central and South America	Mexico, Venezuela	*A. flavus*	Mazzani et al. 2008, Ortega-Beltran et al. 2015
			Argentina	*A. flavus* *A. parasiticus*	Etcheverry et al. 1999, Nesci and Etcheverry 2002
	Post-harvest: fresh kernels, corn meal		Colombia	*A. flavus*	Acuña et al. 2005
			Argentina, Ecuador	*A. flavus* *A. parasiticus*	Etcheverry et al. 1999, Pacin et al. 2003
			Argentina	*A. flavus* *A. parasiticus* S_{BG} isolates	Camiletti et al. 2017
	Pre-harvest: at harvest	Europe	France	*A. flavus* *A. parasiticus*	Bailly et al. 2018
	Post-harvest: kernels from storage and market		Hungary, Italy, Serbia	*A. flavus*	Giorni et al. 2007, Dobolyi et al. 2013, Mauro et al. 2013, Baranyi et al. 2015a
			France, Hungary	*A. flavus* *A. parasiticus*	Sebők et al. 2014, Bailly et al. 2018
			Portugal	*A. flavus* *A. mottae*	Soares et al. 2012
			Serbia	*A. pseudonomius*	Jakić-Dimić et al. 2009
	Pre-harvest: at harvest	North America	USA	*A. flavus*	Probst et al. 2014
				A. flavus, *A. parasiticus*	Jaime-Garcia and Cotty 2004, 2010

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Table 4: (*Contd.*)

Crops	*Production chain step*	*Geographic zone*		*Aflatoxigenic* Aspergillus *species*	*References*
	Post-harvest: kernels**			*A. flavus*	Frisvad et al. 2019
	Non-specified step: kernels			*A. texensis*	Singh et al. 2018
	Post-harvest: kernels**	Oceania	Australia	*A. flavus*	Egmond and Jonker 2004
Millet	**Post-harvest:** grains from storage or markets	Africa	Nigeria	*A. flavus*	Osamwonyi and Wakil 2012, Ezekiel et al. 2014
Rice	**Post-harvest:** grains from market	Africa	Egypt	*A. flavus**	El-Shanshoury et al. 2014
		Asia	Nigeria	*A. aflatoxiformans* *A. austwickii* *A. korhogoensis*	Frisvad et al. 2019
	Pre-harvest: field		China	*A. flavus*	Mamo et al. 2018
	Post-harvest: grains from market		Cambodia, India, Indonesia, Malaysia, Saudi Arabia, Thailand	*A. flavus*	Jayaraman and Kalyanasundaram 1990, Reddy et al. 2010, Al-Husnan et al. 2019
			South Korea, Pakistan	*A. flavus* *A. parasiticus*	Park et al. 2005, Ibrahim et al. 2016
	Non-specified step		Thailand	*A. flavus*	Frisvad et al. 2019
			Philippines	*A. flavus* *A. parasiticus*	Sales and Takumi 2005
	Pre-harvest: fields	South America	Brazil	*A. flavus* *A. arachidicola* *A. novoparasiticus* *A. pseudocaelatus*	Katsurayama et al. 2018

	Post-harvest: grains from market			*A. flavus*	Katsurayama et al. 2018
Sorghum	**Post-harvest:** stored grains	Africa	Ethiopia	*A. flavus* *A. parasiticus*	Weledesemayat et al. 2016
	Non-specified step: seeds	Asia	Turkey, India, Pakistan,	*A. flavus*	Fakhrunnisa et al. 2006, Turgay and Ünal 2009, Divakara et al. 2014
	Post-harvest: stored grains	Europe	Serbia	*A. flavus*	Jakić-Dimić et al. 2009
Wheat	**Pre-harvest:** kernels**	Africa	Algeria	*A. flavus*	Riba et al. 2008, 2010
	Post-harvest: stored grains, grains and flour from market		Algeria, Egypt, Morocco	*A. flavus*	Riba et al. 2008, 2010, Dahab et al. 2016, Ennouari et al. 2018
			Egypt	*A. flavus**	El-Shanshoury et al. 2014
	Pre-harvest: grains**	Asia	Pakistan	*A. flavus*	Fakhrunnisa et al. 2006, Hussain et al. 2013
	Post-harvest: stored grains, grains and flour from market		India, Iran, Saudi Arabia, Turkey	*A. flavus*	Sinha and Sinha 1990, Saberi-Riseh et al. 2004, Doolotkeldieva 2010, Al-Wadai et al. 2013, Joshaghani et al. 2013
			Iran, Pakistan	*A. flavus* *A. parasiticus*	Kachuei et al. 2009, Ibrahim et al. 2016

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Table 4: (*Contd.*)

Crops	*Production chain step*	*Geographic zone*		*Aflatoxigenic* Aspergillus *species*	*References*
	Pre-harvest: grains**	South America	Argentina, Brazil	*A. flavus*	González et al. 2008, Savi et al. 2014
	Post-harvest: stored grains	Europe	Serbia	*A. flavus*	Jakić-Dimić et al. 2009
			Slovakia	*A. parasiticus*	Dovičičová et al. 2012
		North America	Canada	*A. flavus*	Wallace and Sinha 1962
Dried Fruits					
Apricot	**Post-harvest:** dried fruit from market	Africa	Egypt	*A. flavus*	Zohri and Abdel-Gawad 1993
Figs		Asia	Iraq	*A. flavus* *A. parasiticus*	Saadulah and Abdullah 2015
		Africa	Egypt	*A. flavus*	Zohri and Abdel-Gawad 1993
			Algeria	*A. flavus*, *A. parasiticus*	Ait Mimoune et al. 2018
		Asia	Iran, Turkey	*A. flavus*	Şenyuva et al. 2008, Javanmard 2010
			Iraq	*A. flavus* *A. parasiticus*	Saadulah and Abdullah 2015
Plum		Africa	Egypt	*A. flavus*	Zohri and Abdel-Gawad 1993

		Asia	Iraq	*A. flavus* *A. parasiticus*	Saadulah and Abdullah 2015
Raisins		Africa	Egypt	*A. flavus*	Zohri and Abdel-Gawad 1993
		Asia	Iraq	*A. flavus* *A. parasiticus*	Saadulah and Abdullah 2015
Legumes					
Beans	**Post-harvest:** dried grains from market	Africa	Cameroon	*A. flavus* *A. parasiticus*	Njobeh et al. 2009
		South America	Brazil	*A. flavus* *A. parasiticus*	Costa and Scussel 2002
Soybeans		Africa	Cameroon	*A. flavus* *A. parasiticus*	Njobeh et al. 2009
Oilseeds					
Cotton	**Pre-harvest:** fields	North America	USA	*A. flavus*	Cotty 1997
	Post-harvest: cotton balls				Klich et al. 1986
	Post-harvest: cotton seeds, cake and meal	Asia	India	*A. flavus*	Mazen et al. 1990, Tomar et al. 2012
Peanuts	**Pre-harvest:** at harvest	Africa	Egypt	*A. flavus*	Embaby and Abdel-Galel 2014
			Ethiopia, Nigeria	*A. flavus* *A. parasiticus*	Mohamed and Chala 2014, Guchi 2015, Wartu et al. 2015

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Table 4: (*Contd.*)

Crops	*Production chain step*	*Geographic zone*		*Aflatoxigenic* Aspergillus *species*	*References*
	Post-harvest: dried peanuts, peanuts from storage; peanuts, butter or cake from markets		Côte d'Ivoire	*A. aflatoxiformans* *A. korhogoensis*	Carvajal-Campos et al. 2017, Manizan 2019
			Algeria, Benin, Cameroon, Congo, Côte d'Ivoire, Egypt, Ethiopia, Nigeria, South Africa	*A. flavus* *A. parasiticus*	Njobeh et al. 2009, Sultan and Magan 2010, Adjou et al. 2012, Boli et al. 2014, Kamika et al. 2014, Mohamed and Chala 2014, Wartu et al. 2015, Ait Mimoune et al. 2018
			Botswana, Ghana, Nigeria	*A. flavus* *A. parasiticus* S_{BG} isolates	Mphande et al. 2004, Ezekiel et al. 2013b, Agbetiameh et al. 2018,
			Ethiopia	*A. flavus* *A. parasiticus* *A. nomius*	Guchi 2015
			Nigeria	*A. aflatoxiformans*	Frisvad et al. 2019
	Pre-harvest: fields	Asia	China, Indonesia, Vietnam	*A. flavus*	Tran-Dinh et al. 2009, Mamo et al. 2018, Frisvad et al. 2019
	Post-harvest: stored peanuts and peanut-based products		Malaysia	*A. flavus* *A. nomius*	Norlia et al. 2018

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	Pre-harvest: plants and grains from field	South America	Argentina, Brazil	*A. flavus* *A. arachidicola* *A. minsclerotigenes* *A. parasiticus*	Vaamonde et al. 2003, Barros et al. 2003, Pildain et al. 2008, Martins et al. 2017
	Post-harvest: drying processes and storage		Argentina	*A. flavus*	Vaamonde et al. 2003, Barros et al. 2003, Pildain et al. 2008
	Pre-harvest: fields	North America	USA	*A. flavus* *A. parasiticus*	Jaime-Garcia and Cotty 2004, 2010
	Post-harvest: drying processes and storage				Horn 2007
	Pre-harvest: fields	Oceania	Australia	*A. flavus* *A. minisclerotigenes* *A. parasiticus*	Pitt and Hocking 2006, Frisvad et al. 2019
	Post-harvest: drying and storage				Pitt and Hocking 2006, Frisvad et al. 2019
Sesame	**Post-harvest:** grains from storage and market	Africa	Nigeria	*A. flavus* *A. aflatoxiformans*	Ezekiel et al. 2014
			Nigeria	*A. aflatoxiformans* *A. austwickii*	Frisvad et al. 2019
			Senegal	*A. flavus* S_{BG} isolates	Diedhiou et al. 2011
	Post-harvest: Grains**	Central America	Mexico	*A. aflatoxiformans*	Frisvad et al. 2019
Roots and Tubers					
Cassava	**Post-harvest:** chips	Africa	Benin	*A. flavus*	Gnonlonfin et al. 2008

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Table 4: (*Contd.*)

Crops	*Production chain step*	*Geographic zone*		*Aflatoxigenic* Aspergillus *species*	*References*
			Benin	*A. flavus* *A. aflatoxiformans* *A. novoparasiticus*	Adjovi et al. 2014
			Cameroon	*A. flavus* *A. parasiticus* *A. nomius*	Onana et al. 2013
Yam		Africa	Benin, Nigeria	*A. flavus*	Bankole and Mabekoje 2004, Gnonlonfin et al. 2008
Spices					
Chili peppers	**Post-harvest:** market	Africa	Benin, Mali, Nigeria, Togo	*A. flavus*	Hell et al. 2009, Ezekiel et al. 2019
			Morocco	*A. flavus* *A. minisclerotigenes*	El Mahgubi et al. 2013
			Nigeria	*A. flavus* *A. aflatoxiformans* *A. minisclerotigenes A. parasiticus*	Singh and Cotty 2019
		Asia	Pakistan	*A. flavus* *A. parasiticus*	Ibrahim et al. 2016
			India, Lebanon	*A. flavus*	Sharfun-Nahar et al. 2004, Makhlouf et al. 2019
Cumin	**Post-harvest:** market	Africa	Morocco	*A. flavus* *A. minisclerotigenes*	El Mahgubi et al. 2013

Curry	**Post-harvest:** market	Asia	Lebanon	*A. flavus*	Makhlouf et al. 2019
Pepper	**Post-harvest:** market	Africa	Morocco	*A. flavus* *A. minisclerotigenes*	El Mahgubi et al. 2013
	Post-harvest: market	Asia	Lebanon, Turkey	*A. flavus*	Probst et al. 2014, Makhlouf et al. 2019
	Post-harvest: market	South America	Brazil	*A. flavus*	Freire et al. 2000
Tree Nuts					
Almonds	**Post-harvest:** storage and market	Africa	Algeria	*A. flavus* *A. parasiticus*	Ait Mimoune et al. 2018
	Pre-harvest: orchards and at harvest	Europe	Portugal	*A. flavus* *A. minisclerotigenes A. parasitcus* *A. sergii*	Rodrigues et al. 2009, 2012, Soares et al. 2012
	Post-harvest: drying, storage			*A. flavus* *A. minisclerotigenes A. parasitcus* *A. sergii* *A. transmontanensis*	Rodrigues et al. 2009, 2012, Soares et al. 2012
	Pre-harvest: orchards and at harvest	North America	USA	*A. flavus* *A. parasiticus*	Purcell et al. 1980, Bayman et al. 2002, Doster et al. 2014
	Post-harvest: drying, storage				Bayman et al. 2002, Doster et al. 2014

(*Contd.*)

Table 4: (*Contd.*)

Crops	*Production chain step*	*Geographic zone*		*Aflatoxigenic* Aspergillus *species*	*References*
Brazil nuts	**Pre-harvest:** at harvest	South America	Peru	*A. flavus*	Taniwaki et al. 2017
			Brazil	*A. flavus* *A. nomius*	Taniwaki et al. 2017
	Post-harvest: drying, storage		Brazil	*A. flavus* *A. arachidicola* *A. luteovirescens* *A. nomius* *A. parasiticus* *A. pseudocaelatus* *A. pseudonomius* *A. pseudotamarii*	Freire et al. 2000, Pacheco et al. 2010, Freitas-Silva et al. 2011, Reis et al. 2012, Andersson 2012, Baquião et al. 2013, Calderari et al. 2013, Massi et al. 2014, Taniwaki et al. 2017
Hazelnuts	**Pre-harvest:** orchards and at harvest	Europe	Italy	*A. flavus* *A. parasiticus*	Rodrigues et al. 2012, Prencipe et al. 2018
	Post-harvest: drying process, storage				
Nuts	Post-harvest	Europe	Croatia, Hungary	*A. flavus*	Baranyi et al. 2015a
Pistachios	**Pre-harvest**: orchards	Asia	Turkey	*A. flavus*	Heperkan et al. 1994, Kabirian et al. 2011
			Iran	*A. flavus** *A. parasiticus*	Rahimi et al. 2007

	Post-harvest: drying, storage		Turkey	*A. flavus*	Heperkan et al. 1994, Kabirian et al. 2011
	Pre-harvest: orchards	North America	USA	*A. flavus*	Bayman et al. 2002
	Post-harvest: market				Bayman et al. 2002

* The survey results may include other species closely related to *A. flavus*

S_{BG} isolates correspond to *A. flavus* closely related species that produce AFBG and have small sclerotia (*A minisclerotigenes*, *A. aflatoxiformans*, *A. korhogoensis* or an unknown non-characterized species) and were generally identified as *A. flavus.*

** Step not specified

AQ : missing in References

was properly identified in Kenya, Congo, Nigeria and Somalia, whereas *A. korhogoensis* was reported in Nigeria (Table 4).

In Asia, *A. flavus* is the main contaminant but not all strains are AF producers; other species reported less frequently include *A. parasiticus, A. arachidicola, A. novoparasiticus* and *A. pseudonomius* (Table 4). Surveys in China and Vietnam may unmask diversity, as *A. flavus* isolates have been reported with atypical chemotypes and morphological traits (Gao et al. 2008, Trung et al. 2008, Tran-Dinh et al. 2009). Rasheed et al. (2019) showed that diversity in the region is sub-estimated by reporting *A. arachidicola, A. novoparasiticus* and *A. pseudonomius*; whereas in Philippines, Balendres et al. (2019) reported *A. flavus* and *A. parasiticus* from maize and soil field samples. Similarly, in Pakistan, surveys from maize samples reported *A. flavus* and *A. parasiticus* (Table 4), while in Iran samples from maize soil fields showed *A. flavus* as the most frequent species, followed by *A. parasiticus* and *A. nomius* (Razzaghi-Abyaneh et al. 2006). In Central and South America, *A. flavus* and *A. parasiticus* are pointed as the major aflatoxigenic species infecting maize (Table 4). Ortega-Beltran et al. (2015) reported *A. flavus* S- and L-morphotypes and a S_{BG} strain from maize soil in Sonora (Mexico). In Argentinean crops, *A. flavus* L-morphotype was frequent in pre-harvest steps, whereas *A. parasiticus* aflatoxigenic strains in pre-planted crops (soil with plant debris). Camiletti et al. (2017) suggested that infection by aflatoxigenic *Aspergillus* section *Flavi* species increases while the flowering period is hot in some Argentinean regions. It is highly possible that the S_{BG} isolate reported in Argentina corresponds to *A. minisclerotigenes* because it has been isolated from the same region in other staples. In Europe, over the last decade, maize contamination by aflatoxigenic species from section *Flavi* has become an increasing issue. Climate change in Europe has a seasonal impact, as seasons are becoming hotter and drier, especially in the Southern, Central and Eastern regions, increasing the chances of *A. Flavi* species colonization (EFSA 2013, Battilani et al. 2016, Moretti et al. 2019). Despite the fact that *Fusarium* spp. such as *F. verticillioides* and *F. graminearum* are still the main contaminants of maize in Europe, the reports of AFs are rising (Giorni et al. 2007, Covarelli et al. 2011, Gallo et al. 2012, Mauro et al. 2013, Dobolyi et al. 2013, Baranyi et al. 2015a, Bailly et al. 2018, Kos et al. 2018). In European maize, *A. flavus* and *A. parasiticus* are the most frequent species (Table 4), yet *A. parasiticus* infection may be favored as cooler temperature suits its physiological requirements better (Horn 2007, Bailly et al. 2018). Also, *Aspergillus* section *Flavi* diversity seems to rise in storage conditions, at present *A. flavus* (non-aflatoxigenic and aflatoxigenic strains) and *A. parasiticus* (mainly aflatoxigenic strains) have been reported in fields and at harvesting steps while *A. flavus* (non-aflatoxigenic and aflatoxigenic strains), *A. parasiticus, A. pseudonomius* and *A. mottae* in silos and storage samples (Table 4). In the USA, *A. flavus* is the main species recovered from maize fields (soil, debris and ears) and stored maize kernels, followed by *A. parasiticus* and less frequent *A. texensis. A. flavus* diversity in the region includes S- and L-morphotypes, and aflatoxigenic and non-aflatoxigenic strains (Bayman et al. 2002, Jaime-Garcia and Cotty 2004, 2010), being the S-morphotype more frequent and generally aflatoxigenic. In Australia, *Fusarium* spp. are prone to contaminate maize as environmental conditions favors its development, yet *A. flavus* has been reported to occur in soil and kernels (Egmond and Jonker 2004).

3.2.2 Rice

Globally, rice is the second most produced and consumed cereal after maize, and *A. flavus* the most frequent contaminant species from the section *Flavi*. In Asia, *A. flavus* is the most common species reported, followed by *A. parasiticus* (Table 4), yet its identification has been based principally in morphological characteristics. In Africa, Frisvad et al. (2019) reported the presence of *A. aflatoxiformans* and two rare species from Nigerian markets, *A. korhogoensis* and *A. austwickii*; while in South America, Katsurayama et al. (2018) reported *A. novoparasiticus*, *A. arachidicola*, *A. pseudocaelatus* and *A. flavus* from rice and rice plantation soil in Brazil (Table 4). The proportion of aflatoxigenic *A. flavus* strains reported was low (1.5% of the isolated *A. flavus*), yet most of the strains produced CPA (Katsurayama et al. 2018). In Europe, rice is produced in some southern regions, like Spain and France, and even though surveys targeting *Aspergillus* section *Flavi* diversity in this staple do not exist to our knowledge. A study by Suárez-Bonnet et al. (2013) isolated the four AFs B and G from Spanish rice samples and traces of AFGs from French rice samples, suggesting a contamination caused by other species than *A. flavus.*

3.2.3 Wheat and Barley

Wheat and barley are the third and fourth cereals more produced and consumed around the world. Both cereals are more prone to be infected by *Fusarium* spp. hence most studies target these species; despite some reports based on morphology include *A. flavus* and *A. parasiticus* (Table 4).

3.2.4 Millet and Sorghum

Millet and sorghum are better adapted to harsh environments than other cereals and are common crops in Asia and Africa (FAO 1995). The main aflatoxigenic species from section *Flavi* reported to occur in these staples is *A. flavus* and *A. parasiticus* was identified only in stored sorghum grains from Ethiopia (Table 4), but reports of AFBG occurrence in grains and byproducts suggest species misidentification.

3.3 Dried Fruits and Legumes

Contamination of these food matrices by aflatoxigenic species from *Flavi* section was reported from market samples. Based on morphological description, *A. flavus* is the most common identified species in dried apricot, figs, raisins and plums collected in North Africa and Asia, followed by *A. parasiticus.* Both *A. flavus* and *A. parasiticus* were reported in all dried beans and soybeans samples from Cameroon and Brazil (Table 4).

3.4 Oilseeds

3.4.1 Peanuts

A. parasiticus and *A. flavus* are commonly reported in peanuts through the production chain (Table 4), both reported as commensal species of peanut plant (Pitt et al. 2012). The presence of fungal propagules in soil increases infection risk, notably if peanut crop suffers drought stress or related factors, raising the risk of high levels of AF production before harvest. Depending on the region, other species were also isolated in high frequencies (Table 4). In addition, the methods used for identification might fall to underestimate cryptic species and interesting populations, like S_{BG} species (Table 4). In Africa, many studies indicated the presence of *A. flavus* and *A. parasiticus* in peanuts during pre- and post-harvest stages including manufactured products such as cake and butter. Other species reported to infect peanuts during post-harvest include *A. aflatoxiformans*, *A. korhogoensis* and *A. nomius* (Table 4). Slow drying and poor storage conditions are a serious issue in the humid tropics, as moisture absorption might favor aflatoxigenic fungal infection after harvest (Pitt et al. 2012, Taniwaki et al. 2018). In Asia, *A. flavus* was found to be the most common species isolated from peanuts along the production chain and the most common mycotoxigenic component from the mycobiota (Table 4). In Malaysia, *A. nomius* and an atypical *A. flavus* L-morphotype were isolated in post-harvest steps (Table 4). In South America, studies are scarce though peanuts are widely consumed. In Argentina, the principal infectious species during pre-harvest from *Aspergillus* section *Flavi* were *A. flavus* (aflatoxigenic and non-aflatoxigenic strains) and *A. parasiticus*. Yet, *A. arachidicola* and *A. minisclerotigenes* were also present, whereas only *A. flavus* was identified during post-harvest (Table 4). In Brazil, throughout the peanut production chain, *A. flavus* was the most frequent species from section *Flavi,* followed by *A. parasiticus* (Martins et al. 2017). Nevertheless, species prevalence varied among the production chain stages. *A. flavus* prevalence was higher at sorting stage (78.3%), followed by drying (63.2%), threshing (54.5%), blanching (47.6%), field (40.7%) and ready-to-eat products (31.3%), while *A. parasiticus* was reported at drying (12.5%) and in ready-to-eat (1.3%) samples. This study also tested the aflatoxigenic potential of *A. flavus* strains, around 50% of samples were aflatoxigenic, and were isolated more frequently from fields than from processing plants (83% and 31%, respectively) (Martins et al. 2017). In northern USA, *A. flavus* and *A. parasiticus* were reported as the main peanut contaminants, both occurring in fields and after harvest (Table 4). *A. flavus* follows the same trend observed for other crops in USA, being S-morphotype more common. In Australia, studies on peanuts have reported the presence of *A. flavus, A. parasiticus* and *A. minisclerotigenes* (the latter especially in soil samples), during pre- and post-harvest steps (Pitt and Hocking 2006).

3.4.2 Cotton and Sesame

Reports from these staples are poor, probably the best know from them is cotton from USA. Cotton is contaminated by *A. flavus* (Table 4), mainly by

A. flavus S-morphotype isolates (Cotty 1997). Sesame contamination during post-harvest steps in Africa are caused by *A. flavus* and S_{BG} isolates (*A. aflatoxiformans* and the newly described species *A. austwickii*) (Table 4).

3.5 Roots and Tubers

Cassava and yam are important staples in Africa. Cassava is ranked as the third most important food crop in tropical regions after rice and maize. The conditions of production and storage of cassava, yam, and their traditional derivatives favor contamination and development of fungi (Adjovi et al. 2014). *A. flavus* is the most frequent species isolated, though *A. aflatoxiformans, A. novaparasiticus, A. nomius* and *A. parasiticus* were also reported from cassava chips (Table 4).

3.6 Spices

Post-harvest practices and environmental conditions during growth make spices susceptible to *Aspergillus* section *Flavi* fungal infection, principally by *A. flavus* and S_{BG} species (Table 4). In Asia and South America (based on morphological identification), *A. flavus* is the only spice contaminant (pepper and curry); in Central America, *A. pipericola* was isolated from a Mexican pepper sample (Frisvad et al. 2019) whereas in Africa, besides this species, *A. minisclerotigenes* has been identified (pepper and cumin) (Table 4). Chili peppers (paprika and chili) are frequently reported to present AFs, among the aflatoxigenic species *A. flavus* is most reported, followed by *A. minisclerotigenes, A. parasiticus* and *A. aflatoxiformans* (Table 4). Singh and Cotty (2019) reported that the majority of aflatoxigenic fungi isolated from chili peppers in Nigeria were *A. flavus* L-morphotype (76.7%), followed by *A. aflatoxiformans* (8.3%), *A. minisclerotigenes* (8.0%), and a non-identified S_{BG} lineage (2.8%).

3.7 Tree Nuts

3.7.1 Brazil Nuts

Brazil nuts are produced in the Amazon rainforest in Brazil, Bolivia and Peru and are vulnerable to the contamination of several aflatoxigenic, *i.e. A. flavus, A. nomius*, *A. pseudonomius*, *A. parasiticus*, *A. luteovirescens*, *A. arachidicola*, *A. pseudocaelatus* and *A. pseudotamarii* (Table 4). Incidence of Brazil nut contamination by these species can reach 100% (Calderari et al. 2013, Taniwaki et al. 2017). *A. flavus* and *A. nomius* are suggested to contaminate Brazil nuts before they are collected in dry seasons, while other *Flavi* species contaminate them during rainy season, drying processes, storage and markets (Taniwaki et al. 2017).

3.7.2 Pistachios, Almonds, Hazelnuts and Nuts

The most common aflatoxigenic species identified in pistachios during pre- and post-harvest is *A. flavus*, both in Asia and USA. Only in the survey from Iran, besides *A. flavus, A. parasiticus*, and an unknown AFBG strain were isolated (Table 4). *Aspergillus* section *Flavi* surveys on almonds showed higher diversity. In Europe (Portugal), the species reported are *A. flavus, A. minisclerotigenes, A. parasiticus, A. sergii* and *A. transmontanensis*; from these, *A. transmontanesis* was isolated only from plant processor environments (Table 4), while in USA and Algeria *A. flavus* and *A. parasiticus* have been identified in this crop (orchards and post-harvest steps). Hazelnuts in Europe (Italy) were contaminated by *A. flavus,* mostly non-aflatoxigenic strains, followed by *A. parasiticus* whereas *A. flavus* is the only section *Flavi* species reported from nuts in Europe (Table 4). Surveys showed differences between orchards and raw products in market outlets, the latter presented higher ratios of contamination, while considering the matrices pistachios are more sensitive, followed by walnuts and almonds (Bayman et al. 2002, Doster et al. 2014).

3.8 Biodiversity According to Food Production Chain Stages

In crops and pre-harvest stages, fungal infection is favored under humid and hot environmental conditions. In addition, cropping system may increase the incidence of fungal propagules in soil, if plant debris is left or incorporated into soil it becomes a source of infection and favors spore inoculation into the next planting cycle. The increase of fungal propagule number from year to year is reported for section *Flavi* species (Nesci and Etcheverry 2002, Jaime-Garcia and Cotty 2004, 2010). Insects also facilitate fungal infection by dispersing spores and wounding kernels and plants (Rychlik et al. 2014, Aiko and Mehta 2015). The main aflatoxigenic *Aspergillus* section *Flavi* species reported in the pre-harvest stages of the food production chain are *A. flavus* and *A. parasiticus*, which seem to have commensal relationships with certain crops (maize and peanuts) (Taniwaki et al. 2018). Some other species identified in these stages were *A. arachidicola, A. minisclerotigenes, A. nomius, A. novoparasiticus, A. pseudocaelatus* and *A. sergii* (Table 4).

In post-harvest a key step is the drying process, if the raw material is not properly dried, mold can easily develop. Moisture enhances *Aspergillus* section *Flavi* development, so its control is a delicate step in the food production chain to prevent AFs presence in final products. This control is easiest to be achieved in developed countries than in developing countries, especially for small producers (Marin et al. 2012, Gowda et al. 2013, Baranyi 2015b). The diversity of *Flavi* species is higher in post-harvest and first storage steps: *A. flavus, A. parasiticus, A. minisclerotigenes, A. aflatoxiformans, A. korhogoensis, A. austwickii, A. transmontanensis, A. sergii, A. luteovirescens, A. mottae, A. nomius, A. pipericola, A. pseudonomius, A. arachidicola, A. pseudocaelatus*, and *A. pseudotamarii* (Table 4).

A. flavus and *A. parasiticus* are the most frequent species found in commodities along the production chain, *i.e.* in pre- and post-harvest, and in a less extent *A. nomius* in Brazil nuts, *A. minisclerotigenes* in peanuts and almonds and *A. sergii* in almonds (Table 4).

4. Biodiversity of Aflatoxigenic *Aspergillus* section *Flavi* Species and Climate Change

Food security has become a very important issue across the globe and the potential effects of climate change on production and quality of food crops, including mycotoxins, is under scope, especially from a risk assessment perspective (Magan et al. 2011). Crop growth and its interaction with beneficiary and pathogenic and/or toxigenic microorganisms vary from year to year, mainly depending on local weather, making the agricultural sector particularly exposed to climate change (Moore and Lobell 2015). Climate change is a driver for distribution shifts in *Aspergillus* section *Flavi*, as it modifies the environmental conditions, resulting in new suitable niches favoring species development and also facilitating their colonization into temperate regions (Perrone et al. 2014); hence, climate change is an emerging issue worldwide for food and feed safety (Battilani et al. 2016). Projections of climate change suggest that in Africa and Oceania the suitable areas for agriculture will decrease, whereas some areas in Asia and Latin America tropical forest will become savanna (Paterson and Lima 2011). The possible change in patterns of AFs occurrence in crops due to climate change is a matter of concern that may require anticipatory actions, as these phenomena can lead to more health risk in affected areas (Battilani et al. 2016). However, it is difficult to create accurate projections as the knowledge of *Aspergillus* section *Flavi* diversity is poor (distribution, frequency and poor information of the life history and ecology). Although some species are found rarely, their total AF production is high and they produce other mycotoxins, like CPA that has additive effects. For instance, in Africa under climatic changing conditions there is a possibility that *A. minisclerotigenes*, *A. aflatoxiformans* and *A. korhogoensis* could expand their home ranges, as the scenarios of climate change suggest drier and warmer conditions, which may favor their frequency. The case of Africa is interesting, over the last three decades several studies performed in the region have increased the comprehension of the effects of AFs in human populations, unmasked species diversity of *Aspergillus* section *Flavi*, and helped to identify sensitive steps of production chain prone to mold contamination. These studies have shown a rapid diversification of species closely related to *A. flavus* (*A. minisclerotigenes, A. aflatoxiformans, A. korhogoensis* and *A. austwickii*). *A. flavus*, *A. minisclerotigenes* and *A. aflatoxiformans* contaminate staples in field, during harvesting and storage; whereas, *A. korhogoensis* and *A. austwickii* at storage steps (Cotty and Cardwell 1999, Carvajal-Campos et al. 2017, Frisvad et al. 2019). Rapid radiation in Africa may be a unique phenomenon linked with environmental conditions and evolutive pressures; or it can be just an artifact caused by the diversity underestimation in other world regions, originated by the reduced number of diversity surveys in Asia, Oceania (Pacific Islands) and Central and South America. Lack of studies is caused mainly by two factors: (1) diversity surveys are costly, time consuming and need special skills; (2) several studies are performed with the *a priori* that the only aflatoxigenic species are *A. flavus* and *A. parasiticus.* Likewise, several species identification surveys are based only on morphology and AF production, so misidentification of species occurs; as *A. nomius* in Brazil, which was considered to be the main contaminant of Brazil nuts, and later corrected by *A. pseudonomius* (Baquião et al. 2014, Massi et al. 2014).

Author: To maintain consistency throughout the book, we have standardized the reference section of all the chapters by listing up to six names followed by et al.

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