Mycotoxigenic *Fusarium* species associated with grain crops in South Africa – A review

AUTHORS:
Ilze Beukes[1]
Lindy J. Rose[1]
Gordon S. Shephard[2]
Bradley C. Flett[3]
Altus Viljoen[1]

AFFILIATIONS:
[1]Department of Plant Pathology, Stellenbosch University, Stellenbosch, South Africa
[2]Institute of Biomedical and Microbial Biotechnology, Cape Peninsula University of Technology, Cape Town, South Africa
[3]Grain Crops Institute, Agricultural Research Council, Potchefstroom, South Africa

CORRESPONDENCE TO:
Lindy Rose

EMAIL:
lindym@sun.ac.za

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Cereal grains include some of the most important crops grown in South Africa and play a major role in the local economy. Maize, wheat and sorghum are extensively consumed by humans and farm animals, and are also utilised in industrial processes. Grain crops that are grown commercially contribute up to 33% of the country's total gross agricultural production, whereas subsistence farmers grow grains mainly to sustain their families. In rural communities an average intake of maize grain of more than 300 g dry weight per person per day is not uncommon. The production of grains is often constrained by pests and diseases that may reduce their yields and quality. In South Africa, 33 mycotoxin-producing *Fusarium* species have been associated with grain crops. Mycotoxins, such as fumonisins and deoxynivalenol, have been found in levels exceeding the maximum levels imposed by the US Food and Drug Administration and the European Union and therefore pose a serious public health concern. We provide an extensive overview of mycotoxigenic *Fusarium* species associated with grain crops in South Africa, with particular reference to maize, wheat and sorghum.

Significance:

- Mycotoxigenic *Fusarium* species negatively affect the most important staple food crops grown in South Africa.
- Mycotoxin contamination has a direct impact on food safety and security.
- The genus *Fusarium* includes some of the most important mycotoxin-producing species.

Introduction

Grain crops grown in South Africa contribute between 25% and 33% of South Africa's total gross agricultural production.[1,2] The most commonly cultivated grain crops include maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), sorghum (*Sorghum bicolor* L.), oats (*Avena sativa* L.), millet (*Pennisetum glaucum* L.) and rye (*Secale cereal* L.). Of these, maize is considered the most important and wheat the second most important.[2,3] The grains are utilised for food and livestock feed and, to a lesser extent, for malting purposes and bioethanol production.[1,2] Grains constitute the major portion of the total calorie intake of South Africans, across all age groups. The average consumption of maize by people older than 10 years varies from 762 g to 848 g cooked weight per person per day.[4]

The production of grain crops in South Africa is constrained by various abiotic and biotic stresses. Drought, nutrient deficiency, insect damage and diseases all cause a reduction in yield and grain quality.[5,6] One of the more important biotic stresses affecting maize, wheat and sorghum grain in the country involves the fungal genus *Fusarium*. The *Fusarium* sp. most commonly associated with these three grain crops is *F. graminearum* sensu lato (s.l.) Schwabe, also referred to as the *Fusarium graminearum* species complex.[7-10] Other *Fusarium* species affecting maize grain in South Africa include *F. verticillioides* (Sacc.) Nirenberg (syn. *F. moniliforme* Sheldon) and *F. subglutinans* (Wollenweber & Reinking) Nelson, Toussoun & Marasas, with *F. proliferatum* (Matsushima) Nirenberg occurring less frequently.[8,11,12] *Fusarium verticillioides* is also associated with grain mould of sorghum in South Africa.[9,13] Additional *Fusarium* species associated with sorghum include *F. thapsinum* Klittich, Leslie, Nelson & Marasas; *F. andiyazi* Marasas, Rheeder, Lamprecht, Zeller & Leslie; *F. nygamai* Burgess & Trimboli; and *F. pseudonygamai* O'Donnell & Nirenberg.[13] Fusarium head blight of wheat is associated with several species including *F. culmorum* (W.G. Smith) Sacc., *F. cerealis* (Cooke) Sacc. (syn. *F. crookwellense* Burgess, Nelson & Toussoun) and *F. avenaceum* (Fries) Saccardo.[10]

Infection of grain by *Fusarium* spp. does not only result in reduced yield and grain quality, but could lead to food safety concerns. Most *Fusarium* species produce one or more toxic secondary metabolites, commonly known as mycotoxins, in the grain.[14] *F. graminearum* s.l. produces type B trichothecenes (TCT-B) such as deoxynivalenol (DON) and nivalenol (NIV). Another important group of mycotoxins, the fumonisins (FUM), are produced by several *Fusarium* species (Table 1). Both *F. verticillioides* and *F. proliferatum* have been associated with the production of fumonisins in maize and sorghum grains in the country.[8,12,13]

The discovery of fumonisins in South African maize grain by Bezuidenhout et al.[15] sparked a significant interest in *Fusarium*-associated mycotoxins in the country and also worldwide. The objective of the current review is to give an overview of the information available on mycotoxigenic *Fusarium* species associated with grain crops in South Africa. We furthermore provide an outline on the production of the three most important grain food crops in South Africa: maize, wheat and sorghum.

Table 1: Mycotoxigenic *Fusarium* species associated with South African grain crops

Species	South African grain host	References	Mycotoxins associated with fungal species	References
Fusarium acuminatum	Barley, oats, sorghum, wheat	25,140,141	BEA, DON, HT-2, MON, T-2	14,140–143
F. andiyazi	Sorghum	13,33	FUM	11
F. anthophilum	Rice	144	BEA, FUM, MON	45,145
F. avenaceum	Barley, oats, sorghum, wheat	7,10,52,146	BEA, FusaC, MON	14,147,148
F. brachygibbosum	Wheat	10	Unconfirmed	149
F. cerealis (syn: *F. crookwellense*)	Wheat	10	DON, NIV, Fx, ZEA	14,150
F. chlamydosporum	Amaranth, maize, sorghum, wheat	10,49,52,151	HT-2, MON, T-2	45,152
F. culmorum	Barley, wheat	7,10	AcDON, DON, Fx, MON, NIV, T-2, ZEA	14,148,153–155
F. dimerum	Maize	49		
F. fujikuroi	Wheat	10	BEA, FUM, MON	11,26,156
F. globosum	Maize	157	BEA, FUM	158,159
F. incarnatum-equiseti species complex	Amaranth, maize, sorghum, wheat	10,48,52,151	BEA, DON, MON, NIV, ZEA	14,45,140,143,160
F. merismoides	Sorghum	52	ENN	161
F. napiforme	Millet, sorghum	32	FUM, MON	156,162
F. nygamai	Millet, sorghum	13,53	BEA, FUM, MON	45,156,163
F. oxysporum	Barley, maize, sorghum, wheat	10,140,164	BEA, FA, FUM, MON, ZEA	142,165,166
F. poae	Barley, maize, wheat	7,10,35,49	BEA, Fx, HT-2, NIV, T-2	14,27,45,148
F. proliferatum	Maize	12	BEA, FUM, MON	167–169
F. pseudograminearum	Ryegrass, wheat	10,103	AcDON, DON, Fx, NIV, ZEA	170,171
F. pseudonygamai	Sorghum	13	FUM, MON	11,13,172
F. semitectum	Sorghum	52	BEA, DON, MON, NIV, ZEA	46,140,173
F. solani species complex	Maize, sorghum, wheat	10,49,52	DON, FUM, T-2, ZEA	47,51 (unconfirmed)
F. subglutinans	Maize, sorghum	8,52	BEA, FA, FUM, MON	14,173–177
F. thapsinum	Sorghum	13	FA, FUM, MON	178,179
F. temperatum	Maize	180	BEA, FUM, MON	181
F. tricinctum species complex	Wheat	10	BEA, T-2, ENN, MON	14,27,148,182
F. verticillioides (syn: *F. moniliforme*)	Maize, rice, sorghum	8,13,146	BEA, FusaC, FUM, MON	80,183,184
F. graminearum species complex:	Amaranth	151	AcDON,DON, Fx, NIV, T-2, ZEA	45,50
F. acaciae-mearnsii	Wheat, sorghum	7, 9	3-ADON, NIV	185
F. boothii	Barley, maize, wheat	7	15-ADON	185
F. brasilicum	Wheat	7	3-ADON, NIV	185
F. cortaderiae	Wheat, sorghum	7, 9	3-ADON, NIV	185
F. graminearum	Barley, maize (roots), wheat	7,21	3-ADON, 15-ADON, NIV	185
F. meridionale	Maize (roots), sorghum, wheat	7,9,21	NIV	185

BEA, beauvericin; DON, deoxynivalenol; HT-2, HT-2 toxin; MON, moniliformin; T-2, T-2 toxin; FUM, fumonisins; FusaC, fusarin C; NIV, nivalenol; Fx, fusarenon-X; ZEA, zearalenone; AcDON, acetyldeoxynivalenol; ENN, enniatins; FA, fusaric acid; 15-ADON, 15-acetyldeoxynivalenol; 3-ADON, 3-acetyldeoxynivalenol

Grain crops in South Africa

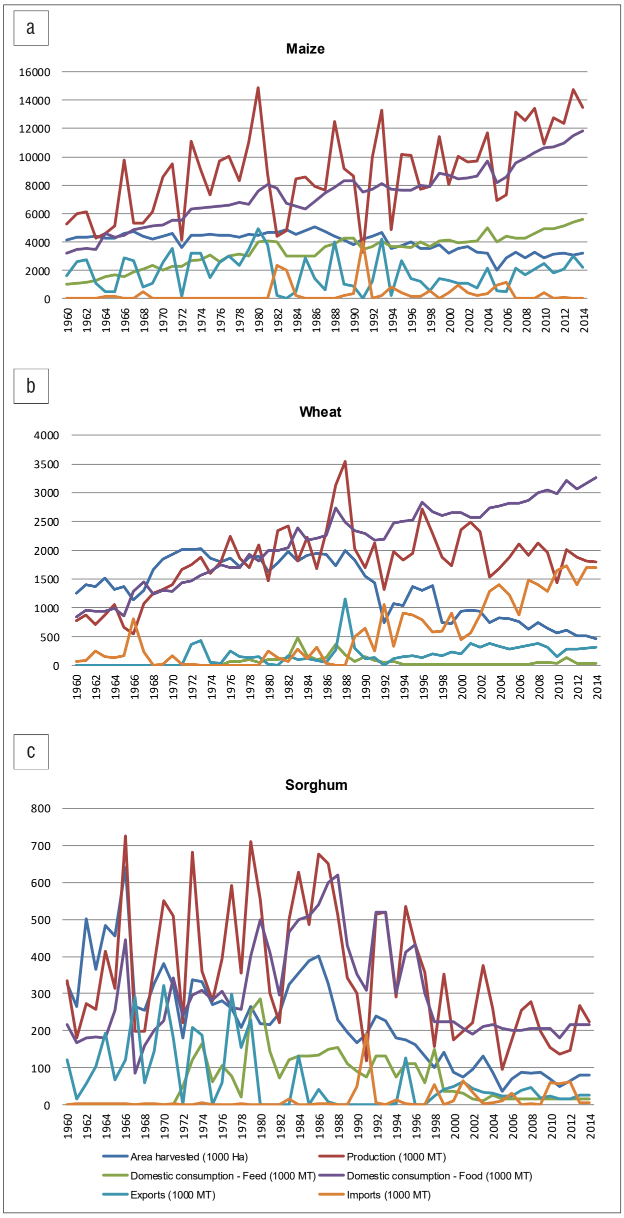
Maize

Maize forms the main staple food for the majority of South Africans, and constitutes a major component of animal feed. In 2014/2015, approximately 56% of the total area under maize cultivation (2 656 500 ha) comprised white maize, mainly used for human consumption, and 44% yellow maize, mostly used for animal feed.[2] The maize industry, therefore, is an important contributor to the economy of South Africa, both as an employer and generator of income.[1] In addition to its use as food and feed, maize is utilised in the manufacturing of paper, paint, textiles, adhesives, biodiesel, medicine and food.

Advances in maize cultivation practices – such as improved cultivars, effective crop rotation and enhancements in fertilisation and pesticide programmes – have steadily improved the yield per hectare. Whereas the total area harvested in South Africa has decreased from 4 118 000 ha in 1960 to 2 656 500 ha in 2014, yield has increased by 8 225 000 metric tons (Figure 1a).[2,16] The increase in production has ensured that the importation of maize has been minimised, and any surplus can be exported (Figure 1a), thus contributing towards generating foreign currency. The Free State (43%), North West (20%) and Mpumalanga (19.5%) Provinces of South Africa were the main production areas during the 2013/2014 production season for total white and yellow maize harvested.[2] Maize in South Africa is cultivated during the summer months with ideal planting times in November and December.

Maize production systems in South Africa can vary from resource-poor subsistence farming to small-scale and intensive commercial farming.[12,17] Chambers and Ghildyal[18] defined a resource-poor farm family as 'one whose resources of land, water, labour and capital do not permit a decent and secure family livelihood'. The Merriam-Webster online dictionary[19] defines subsistence farming as: 'Farming or a system of farming that provides all or almost all the goods required by the farm family usually without any significant surplus for sale.' The average yield per hectare recorded from 2008 to 2012 for non-commercial farmers was a meagre 1.3 tons/ha, while commercial farmers produced an average of 4.6 tons/ha.[2]

Diseases caused by fungal pathogens – aggravated by the use of inferior seed, monoculture and retaining crop residues – lead to reduced yields and lower grain quality.[12] A survey by Ncube et al.[12] during two production seasons determined that *F. verticillioides* was the most common *Fusarium* species associated with maize grain produced in a subsistence farming system, followed by *F. subglutinans* and *F. proliferatum*. Maize grain infected with these species was also contaminated with FUM, often at levels much higher than the maximum levels set by the US Food and Drug Administration (FDA) and the European Union (EU). A maize crop quality survey of commercially produced maize is performed annually by the Southern African Grain Laboratory (SAGL) with the financial support of The Maize Trust. Despite the general good quality of commercial maize, high levels of some mycotoxins can be found when weather or other conditions are favourable for fungal infection. Subsequently, mycotoxin contamination levels, in excess of the maximum levels allowed by the EU for maize intended for direct human consumption, have been found in commercially produced maize.[8,17,20] A 2-year survey of two susceptible maize cultivars, collected at 14 localities across South Africa, found a maximum total FUM level of 16 717 μg/kg, with an average of 2542 μg/kg and DON levels as high as 4731 μg/kg (average of 1031 μg/kg). Beauvericin (BEA) was recorded at a maximum level of 1507 μg/kg (average of 506 μg/kg) and moniliformin (MON) at a maximum of 1530 μg/kg and an average of 604 μg/kg.[8] Zearalenone (ZEA) has also been sporadically detected in South African maize. During the 2011/2012 season, only two samples analysed by SAGL tested positive. However, with an average of 249 μg/kg, they exceeded the maximum level of 100 μg/kg allowed by the EU.[20] The occurrence of these mycotoxins could be attributed to the presence of *F. verticillioides*, *F. graminearum* s.l. and *F. subglutinans*. The presence of high mycotoxin levels in commercial maize could possibly be attributed to the fact that commercial farmers still consider yield, not disease resistance, the number one criteria when deciding on a hybrid to plant. *Fusarium* spp. do not only cause ear rot, but can furthermore cause root, crown and stalk rot of maize, thereby causing additional yield losses.[21]



Values used to generate these graphs were obtained from: GrainSA[2] and the US Department of Agriculture[16]

Figure 1: Cultivation, usage and trade in South Africa between 1960 and 2014 of (a) maize, (b) wheat and (c) sorghum.

Wheat

Wheat is the second most important grain crop produced in South Africa and is also regarded as an important staple food. It serves as the second main provider of energy in the national diet after maize meal, even though more money is spent on bread annually (ZAR6.7 billion in 2000) than on maize food products (ZAR6.2 billion in 2000).[22] The majority of wheat cultivated in South Africa is bread wheat, with minor quantities of durum wheat produced for the production of pasta. Wheat is primarily used for human consumption (bread, biscuits, breakfast cereals, rusks), while the balance is used as seed for re-planting. Poorer quality wheat is marketed as animal feed and other non-food industrial uses such as the production of alcohol for ethanol, absorbing agents for disposable diapers, adhesives and starch on coatings.[23] Approximately 3900 commercial wheat farmers provide job opportunities to almost 28 000 people.[24]

Wheat production in South Africa can be divided into two different cultivation systems, each with their own adapted wheat varieties. In summer-rainfall areas, wheat is mostly cultivated under irrigation, and planted between mid-May to the end of July (Northern Cape, Free State, KwaZulu-Natal). In the Western Cape, a winter-rainfall area, wheat is mostly planted under dryland conditions between mid-April and mid-June. About 600 mm water per year is required for wheat cultivation and, in dry areas where zero tillage or minimum tillage are practised, stubble mulching is recommended for moisture conservation.[23]

The main wheat production areas in South Africa during the 2013/2014 season were the Western Cape (50%), Northern Cape (16%) and Free State (15%). Wheat is predominantly produced by commercial farmers with negligible amounts produced by small-scale and subsistence farmers, mainly because of high input costs and low yields, which results in smaller profit margins. Although the yield per hectare of wheat has shown a steady increase over the past 10 years (2.02 tons/ha in 2004 to 3.73 tons/ha in 2014)[2], the area harvested has decreased at a higher rate than the increase in yield could support, resulting in an overall reduction in production (Figure 1b). Lower production has led to an increase in the importation of wheat into South Africa to accommodate the drastic increase in domestic consumption (Figure 1b). Production of wheat in South Africa is constrained by several factors. Input costs have increased because of substantial increases in the cost of fertilisers and fuel, competitive international wheat prices and poor climatic conditions, amongst others.[23] Fertiliser costs in the Swartland wheat-producing area of the Western Cape can be as much as 30% of the total input cost and weeds may limit grain yields by approximately 20% annually.

Wheat is susceptible to a range of insect pests and diseases caused by plant pathogenic viruses, bacteria and fungi.[5-7,10] Several *Fusarium* species are associated with root rot, crown rot and head blight of wheat in South Africa, including *F. avenaceum*, *F*. *brachygibbosum* Padwick, *F. cerealis*, *F. chlamydosporum* Wollenweber & Reinking, *F. culmorum*, *F. graminearum* s.l., *F. incarnatum-equiseti* (syn. *F. equiseti* (Corda) Saccardo), *F. lunulosporum* Gerlach, *F. oxysporum* Schlechtendahl emend. Snyder & Hansen, *F. poae* (Peck) Wollenweber, *F. pseudograminearum* Aoki & O'Donnell, *F. solani* (Martius) Appel & Wollenweber emend. Snyder & Hansen and *F*. *tricinctum* (Corda) Saccardo.[7,10,25] The presence of some of these species may result in the contamination of the infected grain with mycotoxins such as DON, ZEA, BEA and MON.[14,26,27]

Sorghum

Sorghum is the fourth most important grain crop produced in South Africa after maize, wheat and barley, and the third most important food grain crop.[2,28] Barley is mostly used for malting purposes in the production of beer, and is not considered a major food crop in South Africa. Sorghum is indigenous to Africa and is considered a staple food in many rural communities in South Africa. Approximately 90% of commercially grown grain sorghum is used for human consumption in the form of beverages and food (e.g. malt and sorghum meal), while the remainder is used as animal feed.[28,29] Industrial uses of sorghum include wallboards, biodegradable packaging materials and the production of ethanol. The brewing industry is the main consumer of sorghum, and about 55% of the total domestic produce is used for the manufacturing of traditional African sorghum beer. Sorghum flour competes directly with maize meal as a breakfast cereal or as soured porridge, known as 'mabele'.[28] However, mabele has been found to have better nutritional value (9.7% protein, 1.6% fat) when compared to super maize meal (7.4% protein, 1.0% fat). In South Africa, sorghum cultivars are divided into three classes: Class GM includes sweet sorghum with a low tannin content, which is especially suitable for malting and milling purposes; Class GL includes sweet sorghum with a low tannin content, which is especially suitable for milling and animal feed purposes; and Class GH includes bitter sorghum with a high tannin content (bird resistant), which is used for industrial malting.[28]

The area under sorghum cultivation and the total production of sorghum in South Africa has been on a decline since 1986 (Figure 1c).[2,16] While maize and wheat increased in yield per hectare (Figure 1a,b), the same was not observed for sorghum (Figure 1c), for which the yield per hectare has remained mostly unchanged since 1995, fluctuating only with climatic changes.[2] This observation could be explained by the limited amount of research and development funds available to the sorghum industry, which is relatively small when compared to other major grain crops. A total of only 903 000 tons sorghum was produced in the 5 years from 2009 to 2014, in comparison to 8.9 million tons of wheat and 61 million tons of maize produced during the same period.[2]

Sorghum is planted from mid-October to mid-December in South Africa.[29] The Limpopo Province is the main sorghum-producing province, with limited production in other provinces such as Mpumalanga, North West, Northern Cape, Eastern Cape, KwaZulu-Natal and the Free State.[30] As with maize, sorghum farming systems vary from subsistence to intensive commercial farming, depending on farm sizes, production and marketing methods.[30] Subsistence farmers consume most of their products without measuring the area under production and yield. The average sorghum yield on smallholder farms is estimated to be 0.8 tons/ha[30], significantly lower than the 2.4 tons/ha produced on commercial farms[2]. The lower yield per hectare for subsistence farmers can be attributed to insufficient fertiliser and pest control programmes as well as soil cultivation and crop rotation practices, amongst others. These factors furthermore favour disease development by fungal pathogens, thus increasing the possibility of mycotoxin contamination.

Fusarium grain mould is a very important biological constraint to sorghum production worldwide, while Fusarium stalk and root rot may result in lodging, causing decreased yields.[13,31-33] Several mycotoxin-producing *Fusarium* species have been isolated from sorghum grain in South Africa. *F. andiyazi*, *F. nygamai*, *F. thapsinum* and *F. verticillioides*[13] are known FUM producers, while species within *F. graminearum* s.l. are TCT-B and ZEA producers[9].

The high consumption levels of up to 500 g/person/day[34] of inferior quality maize and sorghum by subsistence farmers pose a considerable threat to human health. Case studies have shown that the incidence of oesophageal cancer in areas where grain with high levels of FUM contamination is consumed is much higher than in other populations where FUM-contaminated food is not a staple.[35,36]

Mycotoxigenic *Fusarium* species affecting South African grains

The mycotoxin-producing *Fusarium* species first described from grain in South Africa was *F. culmorum*, which was isolated from the stems and roots of wheat grown near Stellenbosch, Western Cape, in the 1930s.[37] By the end of 1985, a total of 27 *Fusarium* species, either toxigenic or non-toxigenic, had been reported from a broad range of hosts in South Africa.[32,38] To date, 33 mycotoxigenic *Fusarium* species have been associated with local grain crops (Table 1). These species include *F. verticillioides, F. proliferatum* and *F. subglutinans*, which are commonly associated with Fusarium ear rot (FER) of maize, and *F. graminearum* s.l. that causes Gibberella ear rot of maize, Fusarium head blight (FHB) of wheat and barley and grain mould of sorghum (Table 1). Certain *Fusarium* species are associated with FER, FHB and Fusarium crown rot under specific climatic conditions. For instance, FHB of wheat is caused by *F. avenaceum*, *F. culmorum* and *F. poae* in the cooler regions, whereas *F. graminearum* is predominant in the warmer regions worldwide.[39] In South African maize, the FER pathogen *F. verticillioides* predominates in the warmer dry areas, while *F. subglutinans* is abundant in cooler areas. The Gibberella ear rot pathogen, *F. graminearum* s.l., is most prevalent in intermediate climate areas.[40] Mycotoxin-producing species such as *F. polyphialidicum* Marasas, Nelson, Toussoun & van Wyk and *F. sacchari* (E. J. Butler) W. Gams are known to occur on grain crops elsewhere in the world, but have, to date, not been found on South African grains. These two species have, however, been found in soil debris and sugarcane, respectively, in South Africa.[41,42]

FUM-producing *Fusarium* species, such as *F. verticillioides* and *F. proliferatum*, are often associated with maize and sorghum in South Africa (Table 1). Maize samples collected from 2001 until 2013 tested positive for FUM, sometimes at levels in excess of the maximum levels allowed by the EU.[20] More FUM and FUM-producing *Fusarium* species were found in maize grain produced commercially in warmer production areas of the Northern Cape, North West and Free State Provinces[17] than in the cooler production regions. Although FUM contamination of small grain cereals has been reported[43], this mycotoxin has not been found in wheat and barley in South Africa when employing a multi-mycotoxin screening method using ultra-performance liquid chromatography mass-mass spectrometry[44]. ZEA and TCT-Bs, however, have been found in both maize and wheat in the country,[20,44] but at higher levels and more frequently in maize than in wheat. The TCT-Bs and ZEA are primarily produced by *Fusarium* species within *F. graminearum* s.l.[45,46], and are commonly associated with Gibberella ear rot of maize, FHB of wheat and grain mould of sorghum[7-10].

The highly toxic mycotoxin, T-2 toxin, has until recently not been recorded in South Africa. T-2 toxin is most commonly produced by *F. sporotrichioides*, a fungus well-adapted to survive in colder countries.[47] Some T-2-producing *Fusarium* species, such as *F. poae* and *F. chlamydosporum* (Table 1), have periodically been isolated from wheat with FHB and maize with FER symptoms in South Africa.[35,48,49] The presence of T-2 toxin in local maize grain, recently reported by the SAGL[20], as well as its association with *F. verticillioides* and *F. graminearum*[50,51], requires further investigation.

Information on mycotoxin contamination of oats, sorghum and millet in South Africa is limited. Sorghum is affected by *Fusarium* species[32,33,52,53] that produce BEA, FUM, MON, TCT-B and ZEA, such as *F. avenaceum*, *F. chlamydosporum*, *F. nygamai* and the *F. solani* species complex (Table 1). Some of the same *Fusarium* species have also been associated with oats, millet or other less important grains such as amaranth. *F. verticillioides*, a common producer of FUM, also produces mycotoxins of lesser importance such as BEA, Fusarin C and MON (Table 1). The lower toxicity of these mycotoxins, and the relative complexity of multi-mycotoxin analysis,[54] limits the amount of data available on their occurrence in South African grains.

Role of mycotoxins in plant disease development

The role of mycotoxins in the interaction of fungi with plants is not always clearly understood. Some have, however, been shown to benefit the fungus.[55,56] The TCT-Bs, for instance, are phytotoxic and act as virulence factors on sensitive hosts, allowing the fungus to progress in plant tissue.[57] This effect was demonstrated by non-TCT-producing *F. graminearum* mutants that were pathogenic, yet caused less disease in maize than did wild-type TCT-producing isolates.[58,59] The virulence of *F. graminearum* and *F. culmorum* was also closely correlated with their DON and NIV deposition in wheat grain.[56] Adams and Hart[60], in contrast, reported that DON was not a virulence or pathogenicity factor for *F. graminearum* on maize, following virulence trials with non-toxic protoplast fusion *F. graminearum* strains.

FUM has been shown to be phytotoxic to maize seedlings, but its role in phytotoxicity, virulence and pathogenicity is unclear. The phytotoxicity of FUM was demonstrated by Williams et al.[61] and Arias et al.[62] who reported that FUM had a direct inhibitory effect on root growth, root hair development and other functions within the plant, whereas van Asch et al.[63] reported the mycotoxin to be phytotoxic to maize callus in culture. Symptoms were further induced when seedlings were watered with high concentrations of FUM in the absence of the pathogen.[62] Glenn et al.[64] demonstrated that FUM production by *F. verticillioides* is necessary for the development of foliar disease symptoms on maize seedlings. Desjardins et al.[65] acknowledged that FUM could play a role in virulence, but argued that it is not essential for pathogenicity to maize seedlings. These authors compared the offspring of a *fum*1^+ field strain of *F. verticillioides* with a high degree of virulence and that of a *fum*1^- field strain. They found that progeny with high levels of virulence were associated with FUM production, while highly virulent FUM-non-producing progeny were not observed. However, a highly virulent FUM-non-producing wild-type isolate was also identified, indicating FUM is not required for virulence. FUM non-producing mutants of *F. verticillioides*, generated by the disruption of the *FUM5* gene, have been as virulent on maize ears as their wild-type predecessor strains.[59]

Mycotoxins could also be involved in reproduction, fungal development and the colonisation of plant tissue. Disruption of a cyclin-like (C-type) gene, *FCC1*, resulted in reduced FUM B_1 synthesis and sporulation.[66] FUM is also believed to provide a competitive advantage to the fungus as it inhibits the mycelial growth of other fungal species in vitro.[67] The oestrogenic mycotoxin ZEA enhances perithecial production in *F. graminearum*, therefore the sexual development of the fungus is suppressed when ZEA synthesis is inhibited.[55]

Impact of mycotoxins on human and animal health

The mycotoxins most commonly found in South African grains include DON, FUM and ZEA.[8,12,20] DON, also known as vomitoxin because of its strong emetic effects after consumption, is one of the most widely distributed TCTs found in grain. When consumed by livestock, DON can lead to food refusal, vomiting, decreased weight gain and less effective feed utilisation.[68-70] These disorders then cause anorexia in pigs and other monogastric animals. Ruminants and poultry appear to be resistant to DON.[71] In humans, ingestion of DON-contaminated food has been associated with nausea, vomiting and diarrhoea.[72] Outbreaks of acute DON-associated gastrointestinal illness in humans have been reported in China in 1984/1985 and in India in 1987.[73] The ingestion of NIV, which is considered more toxigenic than DON, has resulted in decreased feed consumption, lower feed conversion efficacy and decreased liver weights when fed to chickens.[74,75] NIV and NIV-producing *F. graminearum* s.l. species have, however, been less frequently associated with South African grains.[7,8]

High levels of FUM in maize grain has been associated with leukoencephalomalacia. Leukoencephalomalacia is a fatal condition that causes the softening of brain tissue as a result of vascular insufficiency or degenerative changes in horses and rabbits.[76-78] FUM has also resulted in fatal pulmonary oedema in pigs and high tumour formation incidences in rats.[79-81] FUM was discovered following the association of *F. verticillioides*-contaminated maize grain with a high incidence of oesophageal cancer in the Transkei region (Eastern Cape Province) of South Africa.[35,80,82,83] Since then, the mycotoxin has also been associated with human oesophageal cancer in China and Italy and with prenatal birth defects and higher HIV transmission rates.[84,85]

ZEA is one of the most widely distributed *Fusarium* mycotoxins globally. Despite its relatively low acute toxicity, ZEA is biologically potent[86] and may cause reproductive disorders in farm animals[45,86,87]. ZEA-containing feed and fungal cultures fed to chickens and turkeys have resulted in significantly reduced egg production.[88,89] In humans, ZEA has been linked to hypoestrogenic syndromes and is believed to be an eliciting factor for advanced puberty development in girls.[90,91] The potential of ZEA to stimulate the growth of human breast cancer cells has also been demonstrated in vitro.[92]

The EU and FDA established maximum allowable levels for certain food contaminants, including mycotoxins, with the aim to reduce their presence in foodstuffs to the lowest levels reasonably achievable by means of good manufacturing or agricultural practices.[73,93] In addition to the USA and countries within the EU, more than 100 other countries have established mycotoxin regulations for at least aflatoxin B_1, mostly produced by *Aspergillus* spp., to aid in minimising food safety concerns.[94] Fewer countries regulate *Fusarium* mycotoxins, and in South Africa no restrictions for maximum allowable levels of any of the *Fusarium*-related mycotoxins in food and feed are governed by legislation.

Management of mycotoxigenic *Fusarium* species

Good Agricultural Practice is a collective set of international codes of practice which forms part of the Codex Code of General Principles on Food Hygiene.[95] These codes are concerned with all aspects of primary food production, including environmental protection and sustainability, economics, food safety, food quality and health security. It also complements the Hazard Analysis Critical Control Point food management system designed to limit food safety concerns, including food poisoning by mycotoxins.[95,96] The Good Agricultural Practice codes recommend practices for primary production of foodstuffs including fruits, vegetables, grains and legumes. Adherence to these codes of good practice does not only impact on food safety locally, but also influences international trade. Great attention should thus be given to these codes when deciding on an integrated disease management strategy to control *Fusarium* species and their associated mycotoxins in different grains produced in South Africa.

Pre-harvest control

Field preparation and cultivation practices play a central role in the management of *Fusarium* diseases and their associated mycotoxins.[95] The burial of residue plant material from a previous planting season by deep ploughing can reduce the primary inoculum that causes infections.[97] This is especially important when crops are affected by the same *Fusarium* species, such as *F. graminearum* s.l. on maize, wheat and sorghum grown in rotation. While minimum tillage has significantly decreased stalk rot and increased grain yield of sorghum in South Africa[31], it also has increased inoculum build-up of mycotoxigenic fungi in maize cropping systems[95]. Crop rotation with legumes, brassicas and potato could also significantly reduce *F. graminearum* s.l. levels.[98] Limiting plant stress to increase plant vigour by adhering to optimum plant dates, preventing drought stress and the optimal use of fertilisers have reduced *Fusarium* infection in a number of grain crops.[99-101] Control of alternative hosts for *Fusarium* species, which include grasses and weeds, can also reduce unwanted inoculum build-up.[95,102,103]

No fungicides are registered for the control of *Fusarium* grain diseases on maize, wheat or sorghum in South Africa.[104] Triazole fungicides such as metconazole and tebuconazole, however, have been shown to control FHB and DON contamination in wheat.[105] Control of mycotoxigenic *Fusarium* species in maize with fungicides, however, is difficult as ears are covered by tight husks which prevent contact with ear rot pathogens. Field trials in South Africa have reported no significant differences in the colonisation of maize grain by *F. verticillioides* or FUM contamination after application of protective fungicides such as the strobilurins, triazoles and benzimidazoles.[106] Chemical elicitors also failed to reduce FER and FUM contamination in maize.[107] As strict regulations on chemical pesticides and fungicide use are implemented to reduce human exposure and prevent environmental pollution, biological control has become more popular.[108] Non-pathogenic fungal antagonists such as *Phoma betae* A.B. Frank and *Trichoderma* spp*.* Persoon have reduced FHB and DON contamination under greenhouse conditions, but field results were variable and often failed.[99,109,110] In Ethiopia, 100% disease suppression of Fusarium root and crown rot of sorghum was reported after application of *Bacillus* spp. under greenhouse conditions.[111]

Disease resistance is the most proficient and environmentally safe management practice to reduce *Fusarium* diseases in grain crops. Several quantitative trait loci (QTLs) that underlie resistance to FHB have been mapped in wheat, and can be used for marker-assisted selection.[112-114] In South Africa, commercial wheat cultivars and breeding lines containing resistance QTLs derived from Sumai 3 lines with low levels of FHB and DON content were identified under field conditions.[115] The resistance of maize cultivars grown in South Africa to FER and FUM contamination are uncharacterised but resistant maize inbred lines were identified.[116] These inbred lines could be used as sources of resistance within maize breeding programmes. Mapping studies have previously identified QTLs associated with resistance to FER and FUM contamination in maize.[117,118] However, studies to identify possible QTLs for resistance to grain mould in sorghum were less frequent, but have shown some success.[119-121]

Unconventional methods to control plant diseases are becoming more common. Maize hybrids genetically modified with crystal (*Cry*) genes from the bacterium *Bacillus thuringiensis*, known as *Bt*-maize, reduced the feeding of stem borers and resulted in lower infection by *F. verticillioides* and *F. proliferatum* and subsequently reduced FUM contamination.[122] FUM detoxification has also been achieved by genetic modification of maize with a degradative enzyme originating from *Exophiala spinifera* and *Rhinocladiella atrovirens*.[123]

Post-harvest control

FUM and DON levels in grain do not increase significantly when grain is harvested at <14% moisture and when optimal moisture and temperature conditions and control of insect pests are maintained during storage.[124-126] The removal of mouldy, broken and underdeveloped kernels can also significantly lower mycotoxin levels in cereal grains. FUM levels of maize were reduced between 26.2% and 69.4% by sieving (<3 mm), and by 71% by separating mouldy from healthy kernels of maize produced by subsistence farmers in the former Transkei.[127,128] An 86% reduction of FUM was also achieved by the removal of *F. verticillioides*-contaminated maize kernels by flotation in water and sodium chloride, as these were less dense than sound kernels.[129] The separation of smaller, underdeveloped and shrivelled wheat kernels by means of the Carter dockage tester resulted in a 6–19% reduction of DON.[130]

Mycotoxins are mostly heat stable; however, the preparation of South African traditional maize porridge through normal household cooking can reduce FUM by 23%.[131] The washing of barley with distilled water has reduced DON levels by 69% and ZEA levels by 2%. In maize, DON levels were reduced by 65% and ZEA levels by 61%. A further reduction in DON and ZEA was achieved by using 1 M sodium carbonate solution for the first wash.[132] The conversion of mycotoxins into non-toxic products can also be achieved through physical or chemical processes. Chemical degradation of DON has been achieved by ammonia, calcium hydroxide, chlorine, hydrochloric acid, ozone, sodium bisulfite, and sodium hydroxide.[133-136] However, the large-scale application of these methods are hampered by costs, safety concerns and the negative impact on grain quality.[137] Biological detoxification, defined as the enzymatic degradation of mycotoxins or modification of their structure that leads to less toxic products, offers an alternative method to reduce the mycotoxin content in food and feed products.[138]

Discussion

Mycotoxigenic *Fusarium* species negatively affect the most important staple food crops grown in South Africa by reducing their yield and quality, and by contaminating the grain with harmful mycotoxins. These effects pose a serious threat to food safety and security for a rapidly expanding population. Efforts to manage harmful *Fusarium* species and their associated mycotoxins, both in commercial and subsistence farming systems, should therefore be made to sustain food production, to reduce health risks to humans and other animals, and to safeguard competitive international trade. A first step in achieving this aim could be the introduction of maximum levels for *Fusarium* mycotoxins in South African food and feed – a directive which has been conspicuously overlooked by the Departments of Health and Agriculture in the country.

A policy brief was compiled in 2009 to[139]:

> *assist national stakeholders in government and industry, as well as commercial and emerging farmers, in understanding and implementing a united monitoring programme for the prevention and control of mycotoxins in foods in South Africa.*

This brief recommended that DON and FUM be added to existing South African regulations in order to align with the guidelines adopted by most other mycotoxin-regulating countries.[94,139] Recently, South Africa has amended regulations regarding the tolerances for fungus-produced toxins in foodstuffs by limiting DON in grains to 2000 and 1000 μg/kg before and after processing, respectively. Maize grain, intended for further processing, is limited to 4000 μg/kg FUM while processed products, ready for human consumption, may not contain more than 2000 μg/kg of FUM.[186] Maximum levels for South Africa should be established by determining the general toxicity, haematotoxicity and immunotoxicity of the different mycotoxins as well as considering consumption levels of grain in the country. Incidences of mycotoxicoses, such as the outbreaks of DON-associated acute gastrointestinal illness in humans in China in 1984/1985 and in India in 1987[73], should also be taken into consideration. The biggest limiting factors in this undertaking would be the costs involved in an extensive regulation programme of foodstuffs, such as the laboratory analyses and the monitoring of revised mycotoxin legislation by health inspectors.

Health workers should be trained to identify symptoms exhibited by humans and animals in cases of mycotoxicoses. A serious call should be made on government to support mycotoxin research and to implement legislation on the levels of the different toxins present in foodstuff. The high intake of grains, in terms of both portion size and frequency, as staple foods by the majority of South Africans should be considered when determining allowable levels of contamination. Coordinated efforts should furthermore be made to launch public awareness campaigns through the distribution of educational information, in a responsible manner, without evoking public fear. These efforts should be particularly focused in subsistence farming communities, in which mycotoxicoses pose a genuine public health threat, as a high incidence of oesophageal cancer in the Transkei region of South Africa has been directly linked to high FUM contamination.[82]

Managing the incidence and severity of mycotoxin contamination in grains, to reduce human and animal health risks and to safeguard competitive international trade, requires continuous efforts to understand and subsequently control the *Fusarium* species responsible for the production of these mycotoxins. South Africa, with its internationally recognised track record in mycotoxin research, possesses the skills, expertise and motivation to continue to work towards food safety and security for all people.

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Authors' contributions

I.B. was responsible for the design and content of the work; for the collection, analysis and interpretation of the data; and for drafting the manuscript. A.V. was responsible for the conception and design of the work. L.J.R., G.S.S., B.C.F. and A.V. critically revised the manuscript. All authors approved the final version.

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