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The impact of environmental factors on the infection of cereals with *Fusarium* species and mycotoxin production – a review

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ABSTRACT

Several phytopathogenic *Fusarium* species occurring worldwide on cereals as causal agents of 'head blight' (scab) of small grain cereals and 'ear rot' of maize, are capable of accumulating, in infected kernels, several mycotoxins some of which of notable impact to human and animal health. *Fusarium graminearum, F. culmorum*, *F. poae*, *F. avenaceum* and *Microdochium nivale* predominantly cause *Fusarium* diseases of small-grain cereals. Maize is predominantly attacked by *F. graminearum*, *F. moniliforme*, *F. proliferatum* and *F. subglutinans*. The review is focused on the influence of climatic variables, particularly temperature, humidity and rainfall on growth, reproduction, survival, competitive ability, mycotoxicity and pathogenicity of *Fusarium* fungi commonly isolated from wheat, barley and maize.

Key words: *Fusarium* spp., mycotoxins, smal grain cereals, maize, climatic factors

IZVLEČEK

VPLIV OKOLJSKIH DEJAVNIKOV NA OKUŽBO ŽIT Z GLIVAMI *FUSARIUM* SPP. IN TVORBO MIKOTOKSINOV – PREGLEDNI ČLANEK

Številne fitopatogene glive rodu *Fusarium*, ki povzročajo plesnivost klasov žit in koruznih storžev, je sposobnih v okuženih zrnih akumulirati številne mikotoksine, med katerimi so nekateri škodljivi za zdravje ljudi in živali. Žita prvenstveno okužujejo vrste *Fusarium graminearum, F. culmorum*, *F. poae*, *F. avenaceum* in *Microdochium nivale,* medtem ko koruzo *F. graminearum*, *F. moniliforme*, *F. proliferatum* in *F. subglutinans*. V pregledu je poudarek na vplivu vremenskih dejavnikov (temperatura, vlaga in padavine) na rast, razmnoževanje, preživetje, tekmovalno sposobnost, mikotoksičnost in patogenost *Fusarium* vrst, običajno izoliranih iz pšenice, ječmena in koruze.

Ključne besede: *Fusarium* spp., mikotoksini, strna žita, koruza, klimatski dejavniki

1 INTRODUCTION

Fusarium is a common mould in cereal fields. The infestation (superficial contamination) and infection of *Fusarium* in cereals are of great concern worldwide – as plant pathogens and producers of mycotoxins.

The genus *Fusarium* comprises a diverse array of fungi, members of which are phytopathogenic to a wide range of plants under diverse environmental conditions. Phytopathogenic *Fusarium* fungi cause several diseases of small-grain cereals, including seedling blight and foot rot, fusarium head blight (FHB) (also known as 'scab' or ear blight) and ear rot of maize (Parry et al., 1995). The *Fusarium* species *Fusarium graminearum* (teleomorph *Gibberella zeae*), *F. culmorum, F. poae*, *F. avenaceum* (teleomorph *G. avenacea*) and *Microdochium nivale* (formerly known as *Fusarium nivale*, teleomorph *Monographella nivalis*) are common pathogens of wheat and

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barley (Sutton, 1982; Parry et al., 1995; Miedaner, 1997; Tekauz et al., 2000; Brennan et al., 2003).
Three *Fusarium* species are frequently isolated from infected maize: *F. graminearum, F. moniliforme* (syn. *F. verticillioides*, teleomorph *G. fujikuroi* mating population A) and *F. subglutinans* (teleomorph *G. fujikuroi* mating population E). Other species responsible for ear rot of maize include *F. culmorum*, *F. proliferatum* (teleomorph *G. fujikuroi* mating population D) and *F. equiseti* (Sutton, 1982; Leslie et al., 1986; Pomeranz et al., 1990; Odiemah and Manninger, 1994; Vigier et al., 1997; Velluti et al., 2000; Torres et al., 2001).

Fusarium diseases of wheat, barley and maize cause significant yield losses world-wide and are therefore of great economic importance (Sutton, 1982; Parry et al., 1995; Miedaner, 1997; Mesterhazy et al., 1999). In addition, many of these *Fusarium* species have the potential to produce a range of toxic secondary metabolites known as mycotoxins that cause a potential health risk when contaminated grain is consumed in human and animal food products (D'Mello and Macdonald, 1997; D'Mello et al., 1999; Placinta et al., 1999).

Host and climatic factors influence the growth, survival, dissemination and hence the incidence of *Fusarium* fungi and the disease severity. The influence of host cultivars on the pathogenicity and toxicity of *Fusarium* fungi has been extensively reviewed (Miedaner, 1997; Miedaner et al., 2001; Mesterhazy et al., 1999; Magg et al., 2002).

The influence of climatic factors on *Fusarium* diseases is complicated by the fact that *Fusarium* fungi can cause disease individually or in complex infections (Doohan et al., 1998), and there are numerous reports on how species differentially respond to different environmental variations, particularly temperature and humidity.

Also, host susceptibility to fungal disease is directly influenced by temperature and osmotic stress. This review is focused on the influence of climatic variables, particularly temperature, humidity and rainfall, on grain infection, growth, reproduction, survival, competitive ability, mycotoxicity and pathogenicity of *Fusarium* fungi commonly isolated from wheat, barley and maize.

2 CLIMATIC DISTRIBUTION OF *FUSARIUM* SPP.

Several factors influence the occurrence of *Fusarium* in the soil and the infestation and infection it generates in cereal plants. Geographical factors including climate are of superior importance for the occurrence of *Fusarium* and for the pattern of infestation by various *Fusarium* species.

The incidence of the causal organisms of FHB of wheat, barley and ear rot of maize is often correlated to different climatic conditions (temperature and rainfall) in different geographic locations. *F. culmorum*, *F. poae, F. avenaceum* and *M. nivale* are common pathogens of wheat and barley in the cooler temperate regions of the world, while *F. graminearum* tends to be the predominant *Fusarium* species pathogenic to these cereals in hotter regions of the world (Parry et al., 1995; Brennan et al., 2003).

F. graminearum, *F. moniliforme* and *F. subglutinans* are the *Fusarium* species most frequently isolated from infected maize, but depending on geographical location, other causal species of ear rot include *F. culmorum*, *F. proliferatum* and *F. equiseti* (Leslie et al., 1986; Vigier et al., 1997; Pomeranz et al., 1990; Odiemah and Manninger., 1994; Velluti et al., 2000; Torres et al., 2001).

Varying the temperature in a simple model ecosystem produces changes in the community structure of *Fusarium* species that mimic those found along climatic temperature and rainfall gradients (Saremi et al., 1999). The influence of climatic conditions on the incidence of *Fusarium* species is probably both direct (e.g. an effect on mode of reproduction) and indirect (e.g. an effect of soil and vegetation type).

More research is required to determine the indirect effect of climate on the incidence of *Fusarium* fungi and how this affects species-specific factors.

3 GERMINATION, GROWTH AND COMPETITION BETWEEN *Fusarium* spp.

Germination, growth and competition between *Fusarium* spp. are dependent upon the availability of nutrients and environmental factors such as temperature, pH, humidity, aeration and light. The influence of nutritional availability is outside the scope of this review. It is generally not a limiting factor during infection and colonisation of host tissue, but may be limiting or growth-inhibiting during saprophytic survival (e.g. humic acids in soil) (Moliszewska and Pisarek, 1996).

3.1 Germination

Germination is influenced by water availability (*a*w) and temperature: warm humid conditions favour this developmental stage. Marín et al. (1996) found that the *a*w minima for the microconidial germination of Spanish isolates of *F. moniliforme* and *F. proliferatum* were 0.88 on maize meal extract medium.

Microconidia of *F. moniliforme* germinated optimally at 25–37 °C and 0.96–0.98 *a*w, but at 30 °C when the *a*w was 0.90–0.94, with intraisolate variation. The germination of microconidia of *F. proliferatum* was optimal at 30 °C, regardless of *a*w, and with significant intra-isolate variation. However, Etcheverry et al. (2002) found that Argentinean isolates of *F. moniliforme* and *F. proliferatum* grew very slowly, if at all, at *a*w 0.93 and 25 °C. At marginal temperatures and *a*w levels, the germination lag time increases (Marín et al., 1996; Etcheverry et al., 2002). Earlier, Francis and Burgess (1977) found that the percentage germination of conidia, ascospores and chlamydospores of *F. graminearum* Group II isolates was reduced as water potential was lowered from −1 to −20 bars.

3.2 Growth

Temperature and *a*w differentially affect the growth of *Fusarium* species (Table 1, Figure 1). *Fusarium* species differed in their temperature requirements for optimal growth on potato dextrose agar (Cook and Christen, 1976; Pettitt et al., 1996; Brennan et al., 2003). Irrespective of the European origin of isolates, *in vitro* culture experiments showed that optimal growth occurred at 25 °C for *F. graminearum*, at 20–25 °C for *F. culmorum and F. poae* and at 20 °C for *F. avenaceum* and *M. nivale*.

In general, *F. culmorum* had the fastest growth rate of all five species over the range 10–30 °C. Species accounted for 51–63% and country of origin accounted for 23–52% of growth rate variation. At the low temperature of 5 °C, Pettitt et al. (1996) found that of *F. culmorum*, *F. avenaceum* and *M. nivale*, the latter species was significantly the fastest growing. At the higher temperature of 35 °C, Cook and Christen (1976) found that *F. graminearum* did not grow, even after 30 days. Marín et al. (1998a) found that the maize pathogens *F. moniliforme* and *F. proliferatum* had a faster growth rate than *Eurotium* and *Penicillium* species and on sterile layers of maize grew best at 30 °C (Table 1).

The temperature optima for growth of *Fusarium* spp. appears to be dependent on *a*w. Cook and Christen (1976) found that the optimal growth temperature for European isolates of *F. graminearum* (24–28 °C) increased slightly when lower water potentials prevailed. *Fusarium graminearum* grew optimally at −10 to −20 bars and *F. culmorum* at −8 to −14 bars. Increasing *a*w (>0.925) favoured growth of *F. moniliforme* and *F. proliferatum* on sterile layers of maize at 30 °C (Marín et al., 1995). More research is required to better understand the influence of *a*w on the growth of *F. culmorum*, *F. poae* and *M. nivale.* It must be noted that drawing comparisons between growth rate studies is difficult, as the rates are very dependent on the growth substrates used. For example, on maize culture media *F. subglutinans* grew optimally at 20–25 °C, but faster on rice culture media at 15 °C (Castellá et al., 1999).

Table 1: Optimum temperature and water potential/availability for the *in vitro* growth of *Fusarium* species.
Preglednica 1: Optimalne temperature in vodni potencial/dostopnost za *in vitro* rast *Fusarium* vrst.

Species	Substrate[a]	Optimum growth conditions		References
		Temperature (°C)	Water potential/availability[b]	
F. graminearum	BM, PDA	24–28	−10 to −20 bars	Cook and Christen (1976), Brennan et al. (2003)
F. culmorum	BM, CMA, PDA	20–25	−8 to −14 bars	Cook and Christen (1976), Parry et al. (1994), Brennan et al. (2003)
F. avenaceum	PDA	20–25	ND	Parry et al. (1994), Brennan et al. (2003)
F. poae	PDA	20–25	ND	Brennan et al. (2003)
M. nivale	PDA	15–20	ND	Parry et al. (1994), Brennan et al. (2003)
F. moniliforme	Sterile maize layers	30	a_w > 0.925	Marín et al. (1995)
F. proliferatum	Sterile maize layers	30	a_w > 0.925	Marín et al. (1995)
F. subglutinans	MCM, RCM	15–25	ND	Castellá et al. (1999)

[a] BM = basal medium, PDA = potato dextrose agar, CMA = corn meal agar, MCM = maize culture media, RCM = rice culture media.
[b] ND = no data.

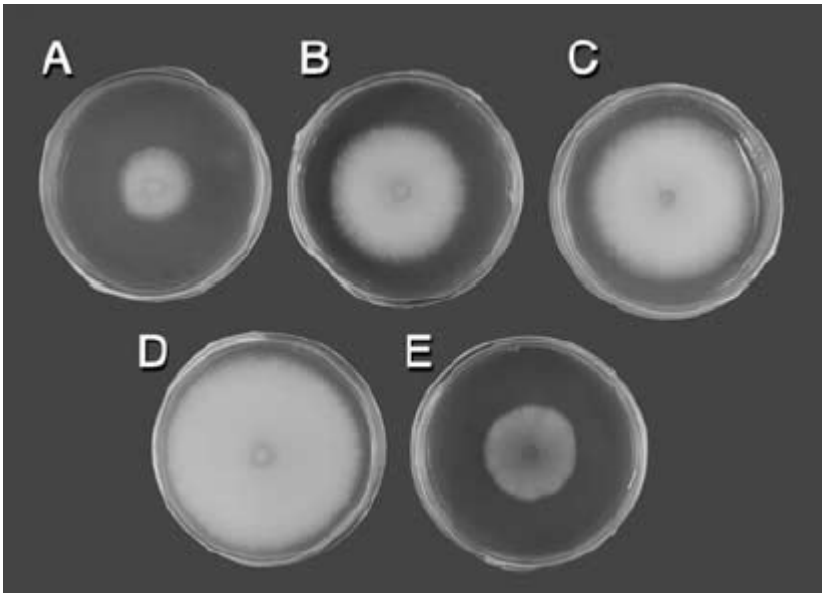

Figure 1: *In vitro* growth rate of *F. poae* (strain CC359B) at 10 (A), 15 (B), 20 (C), 25 (D) and 30 °C (E) (Brennan et al., 2003).
Slika 1: *In vitro* priraščanje glive *F. poae* (izolat CC359) pri 10 (A), 15 (B), 20 (C), 25 (D) in 30 °C (E) (Brennan et al., 2003).

3.3 Competition: Temperature and water availability (*a*w)

Fusarium fungi do not exist in isolation, either in the soil, on debris, or on the host, but are continually competing with other organisms, particularly microorganisms. Microbial interactions and the balance between microbial communities are influenced by the prevailing environmental conditions. It has previously been shown that temperature and *a*w significantly influence the growth and interaction between *F. moniliforme* and *F. proliferatum*, and between *F. graminearum*, *F. subglutinans*, *F. proliferatum, Aspergillus, Penicillium*, *Eurotium* and *Trichoderma* species (Marín et al., 1998a,b).

In a study of the competing abilities of *Fusarium*, *Aspergillus*, *Penicillium*, *Eurotium* and *Trichoderma* species, Marín et al.(1998a) found that *Fusarium* species were only dominant at high *a*w (0.995). Magan and Lacey (1984) found that of a range of field fungi, *F. culmorum* was the only one able to compete with and dominate other fungi, particularly at *a*w > 0.95. Within the *Fusarium* genus, *F. graminearum* appears to have a competitive advantage over other species under cooler conditions (Marín et al., 1998b; Velluti et al., 2000). Marín et al. (1998b) suggested that *F. graminearum* has a competitive advantage over *F. moniliforme* and *F. proliferatum* at 15 ^{o}C, while at 25–30 ^{o}C, these species coexisted in the same niche. Similar results were found by Velluti et al. (2000), regardless of *a*w (0.93, 0.95 and 0.98). Later in this seminar, the occurrence of *Fusarium* complexes and their impact on mycotoxin production will be discussed.

4 *FUSARIUM* SPECIES INVOLVED AND MYCOTOXIN PRODUCED

4.1 *Fusarium* species involved

The species of *Fusarium* (teleomorph *Gibberella*) causing fusariosis of cereals are worldwide in distribution and can cause several diseases generally recognized, according to the host, as *Gibberella* seedling blight, foot rot, and head blight (scab) of small grain cereals (wheat, oats, barley, rye, triticale); and *Gibberella* stalk and ear rot, and seedling blight of maize. From the mycotoxicological point of view, the phases of disease of greatest concern are certainly scab of small cereals and ear rot of maize, for the potential accumulation of mycotoxins in grains. The etiological characteristic of both these phases, is the co-occurrence or the quick succession of several species of *Fusarium* usually referred to as a ‘complex’. In fact, it is quite common to isolate up to nine different *Fusarium* species, from a single fragment of infected tissues or up to seventeen different species from freshly harvested wheat samples collected in a limited area. However only a restricted number of species have been regarded as pathogenic and generally only very few of them predominate in a particular host-agroclimatic system (Burgess et al., 1997).

But, like the strains of the pathogenic and predominant *Fusarium* species, also several strains of the other less pathogenic or opportunistic *Fusarium* species are capable of producing considerable amounts of toxins. Therefore, the toxigenic profile of a contaminated crop is determined not only by the predominant pathogenic species, but also by the opportunistic species included in the “complex” (Burgess et al., 1997).

The species predominantly found associated with head blight of wheat and other small cereals are *F. graminearum* Schwabe and its widespread teleomorph *G. zeae* (Schw.) Petch, *F. culmorum* (Wm.G. Sm.) Sacc. and *F. avenaceum* (Fr.) Sacc. (*G. avenacea* R.J. Cooke). Among the other less frequently isolated species there are *F. poae* (Peck) Wollenw., *F. crookwellense* L.W. Burgess, P.E. Nelson & T.A. Toussoun (syn. *F. cerealis* Cooke), *F. equiseti* (Corda) Sacc. (syn. *F. scirpi*) (*G. intricans* Wollenw.), *F. sporotrichioides* Sherb., and *F. tricinctum* (Corda) Sacc. Several other species may be sporadically encountered, including *F. acuminatum* Ellis & Everh. (*G. acuminata* Wollenw.), *F. subglutinans* (Wollenw. & Reink.) P.E. Nelson, T.A. Toussoun & Marasas (syn. *F. sacchari*), *F. solani* (Mart.) Sacc. (*Nectria haematococca* Berk. & Broome), *F. oxysporum* Schlecht., and *F. semitectum* Berk. & Rav. (syn. *F. pallidoroseum*, *F. incarnatum*) (Burgess et al., 1997).

Fusarium species may be responsible for at least two kinds of maize ear rot, commonly called as 'red ear rot' mainly caused by species of the *Discolor* section, and 'pink ear rot', mainly caused by representatives of the *Liseola* section. The predominant species causing maize 'red ear rot' are *F. graminearum*, *F. culmorum* and *F. crookwellense*. Among the other less frequently isolated species there are *F. subglutinans*, *F. avenaceum*, *F. moniliforme* J. Sheld. [syn. *F. verticillioides* (Sacc.) Nirenberg]. The species more frequently isolated from maize 'pink ear rot' and related 'random kernel rot', are essentially the widespread anamorphs of the rather rare *G. fujikuroi* (Sawada) Ito in Ito & K. Kimura, namely, *F. moniliforme*, *F. proliferatum* (T. Matsushima) Nirenberg and *F. subglutinans* (Wollenw. & Reinking) P.E. Nelson. Among the other toxigenic *Fusarium* species less frequently isolated from molded maizeears, there are: *F. equiseti*, *F. poae*, *F. sporotrichioides*, *F. acuminatum*, *F. semitectum*, *F. solani* and *F. oxysporum* (Burgess et al., 1997).

Finally, there are many other species only sporadically isolated from cereals, but in some occasion reported as emerging problem, such as *F. anthophilum* (A. Braun) Wollenw., *F. chlamydosporum* Wollenw. & Reink. (syn. *F. fusarioides*), *F. compactum* (Wollenw.) Gordon, *F. flocciferum* Corda, *F. heterosporum* Nees (syn. *F. reticulatum*, *F. graminum*), *F. lateritium* Nees, *F. sambucinum* Fuckel, *F. torulosum* (Berk. & Curt.) Nirenberg, and *F. venenatum* Nirenberg (Burgess et al., 1997).

Within *F. graminearum* (*G. zeae*) were characterized two populations designated as Group 1 and Group 2, with almost the same toxigenic potentiality. The Group 1 very rarely forms perithecia in nature and mainly causes crown rot of cereals and grasses; Group 2 readily forms abundant perithecia in nature and mainly causes head blight of grain cereals and stalk and ear rot of maize. Studies on genetic diversity indicated that *F. graminearum* Group 2 have greater affinity to *F. culmorum* and *F. crookwellense* than to *F. graminearum* Group 1 (Burgess et al., 1997).

In addition, the toxigenic strains of *F. graminearum* were classified in two chemotypes: DON and NIV producers, according to the main type B trichothecenes synthesized. Furthermore, DON-chemotype strains of *F. graminearum* were subclassified into two types: 3-AcDON and 15-AcDON producers (Miller *et al*., 1991; Logrieco et al., 1992; Szécsi and Bartok, 1995; Yoshizawa, 1997).

Ecological differences in chemotype distribution may contribute to characterizing a regional grain contamination. Toxigenic strains of *F. culmorum* can be divided into two types: DON and NIV chemotypes, according to the main type B trichothecenes produced. DON-type strains produced also AcDON (3-AcDON) (Gang et al., 1998; D'Mello et al., 1997).

The species G. *fujikuroi* has been subdivided into seven distinct mating populations (biological species), indicated as A to G, and covering several *Fusarium* anamorphs (Leslie, 1995). From these, the most frequently found on maize were *F. moniliforme* (A), *F. proliferatum* (D), and *F. subglutinans* (E), which were also differentiated by their toxigenic capability (Moretti et al., 1997). *F. nivale* Ces. ex Berl. & Voglino is a well known pathogen of cereals, very frequently found among the major fungi included in the species complex causing 'foot rot' and 'head blight (scab)' of small cereals. *F. nivale* is no longer considered a *Fusarium*, first it was placed in the genus *Gerlachia* [*G. nivalis* (Ces. ex Berl. & Voglino) W. Gams & E. Müller], and then transferred to *Microdochium* as *M. nivalis* (Fr.) Samuels & I.C. Hallett [teleomorph *Monographella nivalis* (Schaff.) E. Müller]. Therefore *M. nivalis* is not included in this paper dedicated to cereal fusarioses, also because it has a very low toxicity, and proved to be incapable of producing the typical *Fusarium* mycotoxins (Logrieco *et al*., 1991).

4.2 Mycotoxin production

One of the most serious consequences of FHB and ear rot of cereals is the contamination of grain with mycotoxins (D'Mello and Macdonald, 1997; D'Mello et al., 1999; Placinta et al., 1999). The most important classes of *Fusarium* mycotoxins, based on their harmful effects on human and animal health, are the trichothecenes, fumonisins, moniliformin and zearalenone (ZEA) (D'Mello et al., 1999).

Trichothecene mycotoxins are tricyclic sesquiterpenes and two classes; types A and B, are commonly found in cereals along with the oestrogenic mycotoxin ZEA (D'Mello and MacDonald, 1997; D'Mello et al., 1999). The fumonisin class of mycotoxins comprises a group of structurally related metabolites of which fumonisin B1 (FB1*)* and B2 (FB2*)* are commonly found in maize grain with moniliformin (D'Mello and Macdonald, 1997; D'Mello et al., 1999). Mycotoxin production in grain can begin in the field and continue throughout storage. Mycotoxin production is dependent mainly on both well-defined ranges of temperature and *a*w. But in turn, the optimum climatic conditions for mycotoxin production in infected grains depends on the substrate, *Fusarium* species and isolate. The influence of temperature and *a*w on mycotoxin production by *Fusarium* fungi is probably not entirely direct but rather a function of the influence of these parameters on fungal growth.

- Trichothecenes and zearalenone (ZEA)

Many *Fusarium* species, including *F. graminearum*, *F. culmorum*, *F. poae*, *F. oxysporum* and *F. sporotrichioides* are producers of trichothecenes and ZEA (D'Mello and Macdonald, 1997; D'Mello et al., 1999) (Table 2). *F. sporotrichioides* and perhaps *F. poae* predominately produce type A trichothecenes, which includes T-2 toxin, HT-2 toxin, neosolaniol and diacetooxyscirpenol (DAS). *F. culmorum* and *F. graminearum* predominately produce type B trichothecenes, including deoxynivalenol (DON, also known as vomitoxin), its 3-acetyl and 15-acetyl derivatives (3-ACDON and 15-ACDON, respectively) and nivalenol (NIV). Most studies indicate that high moisture favours the production of both classes of mycotoxins, but the optimum temperatures for trichothecene and ZEA production in *Fusarium*-infected grain appears to be specific to the substrate, species and individual metabolites (Table 2). Moderate rather than warm temperatures favour the production of type A trichothecenes by *F. sporotrichioides* (Miller, 1994; Mateo et al., 2002) (Table 2). While the optimum production conditions varied depending on the substrate and toxic metabolite, in general *F. sporotrichioides*-infected maize, wheat and rice grains contained more type A trichothecenes when moistened with 35% water (*a*w = 0.990) and incubated at 20 ^{o}C for 3 weeks than when incubated at higher temperatures or *a*w. However, Rabie et al. (1986) detected relatively large amounts of T-2 toxin in *F. acuminatum*-infected oats stored at 25 ^{o}C, although a comparison was not drawn between different incubation conditions. In the case of type B trichothecenes, warm humid conditions favour their production during storage of *F. culmorum* and *F. graminearum*-infected grain (Greenhlagh et al., 1983; Lori et al., 1990; Beattie et al., 1998; Homdork et al., 2000; Martins and Martins, 2002) (Table 2).

Table 2: The major classes of *Fusarium* mycotoxin, their principal producers and optimal production conditions on cereal grains

Preglednica 2: Glavni razredi fuzarijskih mikotoksinov, vrste gliv, ki jih tvorijo in optimalni pogoji za njihovo tvorbo na žitnem zrnju

Toxin	Species	Substrates	Optimum production conditions[a]	References
Type A trichothecenes [T-2 toxin, HT-2 toxin, neosolaniol and diacetoxyscirpenol (DAS)]	*F. sporotrichioides* *F. poae*	Barley, oats, rice, wheat, maize	Moderately warm and humid (20–25 °C, a_w = 0.990)	Mateo et al. (2002), Miller (1994), Rabie et al. (1986)
Type B trichothecenes [deoxynivalenol (DON), 3-acetyl DON, 15-acetyl DON, nivalenol (NIV)]	*F. graminearum* *F.culmorum*	Barley, wheat, rice, maize	Warm and humid (25–28 °C, a_w = 0.97)	Greenhalgh et al. (1983), Lori et al. (1990), Beattie et al. (1998), Homdork et al. (2000)
ZEA	*F. graminearum* *F. culmorum*	Wheat, rice, maize	Warm (17–28 °C), or temperature cycles (e.g. 25–28 °C for 14–15 days; 12–15 °C for 20–28 days) and humid (a_w = 0.97 or 90% RH)	Jiménez et al. (1996), Lori et al. (1990), Ryu and Bullerman (1999), Homdork et al. (2000), Martins and Martins (2002)
Fumonisins	*F. moniliforme* *F. proliferatum* *F. subglutinans*	Maize	Cool to warm conditions and humid (15–30 °C, a_w = 0.98)	Cahagnier et al. (1995), Marín et al. (1999a,b)
Moniliformin	*F. subglutinans* *F. moniliforme* *F. avenaceum*	Wheat, rye, barley, oats, maize	Warm temperatures (25–30 °C)	Kostecki et al. (1999), Schütt (2001)

[a] Optimum temperature and humidity vary depending on substrate, species and isolate; typical conditions are given in parentheses. Time of production varies from 3 to 8 weeks.

Martins and Martins (2002) found that on *F. graminearum*-infected cracked corn (*aw* = 0.97), more of the type B trichothecene DON was produced following incubation at 28 °C for 35 days, rather than at 22 or 28 °C for 15 days followed by 12 °C for 20 days; their results agreed with those of Greenhlagh et al. (1983). Also, maximal DON was produced by *F. graminearum* on infected wheat and polished rice following incubation in the dark at 27 °C, but in hulled rice, DON production was maximised when incubated at 27 °C in the light (Lori et al., 1990).

The effect of initial infection level may outweigh the effect of environmental conditions on mycotoxin contamination of grain, depending on the toxic metabolite in question. Following 7 months storage of barley grain with high initial *Fusarium* infection levels (85%), DON contents did not change significantly, irrespective of conditions (−4, 20 or 24 °C, quiescent or forced aeration), although it was lowest in malt produced from the grain stored at 24 °C (Beattie et al., 1998). Initial infection levels would not normally be so high. In wheat stored for 6–8 weeks under warm humid conditions (25 °C, 90% RH), Homdork et al. (2000) found that, while the DON content significantly increased in grain with a low to moderate (4–15%) initial *F. culmorum* infection level, it did not increase in samples with high (>50%) initial infection levels.

However, the influence of initial infection levels on mycotoxin production may be toxin specific, as

while these conditions were optimal for the production of NIV, unlike DON, it was not present at harvest and levels increased irrespective of initial infection level. As for trichothecenes, the conditions for optimal ZEA production appear to be species, isolate and substrate specific, and may vary from those for DON production. Several studies have found that maximum ZEA was produced in *F. graminearum* and *F. oxysporum*-infected maize at *a*w 0.97 and by cycling the incubation temperatures from 25 to 28 °C for 14–15 days, followed by 12–15 °C for 20–28 days (Jiménez et al., 1996; Ryu and Bullerman, 1999; Martins and Martins, 2002) (Table 2).

However, the optimum temperature for ZEA production may vary with isolate and substrate. Jiménez et al. (1996) found that, while the aforementioned conditions were optimal for ZEA production in maize grain infected by two isolates each of *F. graminearum* and *F. oxysporum*, another *F. graminearum* and two *F. culmorum* isolates produced maximal ZEA after 30 days incubation at room temperature (16–25 °C) rather than at 28 or 37 °C (*a*w = 0.97). In wheat grain with moderate to high levels (4–15%) of *F. culmorum* infection, ZEA production was favoured by warm and humid (25 °C, 90% RH) rather than cool and dry storage conditions.

Most ZEA was produced towards the end of the storage period (6–8 weeks) (Homdork et al., 2000). Lori et al. (1990) reported a lower optimal substrate-dependent temperature for ZEA production by a *F. graminearum* isolate. ZEA production was maximised by incubation of *F. graminearum*-infected wheat and polished rice in the dark at 17 and 21 °C, respectively, while production was maximised in hulled rice incubated at 27 °C in the light (Lori et al., 1990).

- Fumonisins and moniliformin

Fumonisins and moniliformin are commonly produced in maize infected by *F. moniliforme* and *F. proliferatum*, species which tend to grow better at higher temperatures (Keller et al., 1997; Kostechi et al., 1999; Miller, 2001; Marín et al., 1999a,b). Moniliformin has also been detected in cereals infected with *F. avenaceum* and *F. subglutinans* (Kostechi et al., 1999; Torres et al., 2001; Kiecana et al., 2002). While the temperature optima for the production of fumonisins by these pathogens vary, they all prefer *a*w ~ 0.98 and fumonisin production generally decreases with temperature and higher *a*w (Cahagnier et al., 1995; Marín et al., 1999a,b). Marín et al. (1999a,b) found that *a*w had a more significant effect than temperature on total fumonisin production in maize grain and ground maize by *F. moniliforme* and *F. proliferatum*. In general, fumonisin production and fungal biomass decreased with temperature and *a*w and was optimal at 15–30 °C and 0.98 *a*w, depending on the isolate. At marginal temperatures (especially 15 °C), there was an increase in fumonisin production at lower *a*w levels (0.92 and 0.95) when compared to the concentrations produced at higher temperatures and higher *a*w levels. But even at 37 °C, Marín et al. (1999b) found that an isolate of *F. moniliforme* could produce significant amounts of fumonisin.

Ono et al. (1999) attributed the higher fumonisin content of maize in the Northern region of the State of Párana, Brazil compared to the Central-South to higher rainfall in the former during the month preceding harvest (202 and 92.8 mm, respectively). Oxygen limitation retards the growth of *F. moniliforme* and *F. proliferatum* and under such conditions it was found that no FB1 was produced (Keller et al., 1997).

Higher temperatures favour moniliformin production in cereal grains infected by *F. avenaceum* or *F. subglutinans* (Kostecki et al., 1999; Schütt, 2001). Moniliformin production by a *F. subglutinans* isolate from maize was higher at 30 than 20 or 25 °C and on rice rather than on wheat, rye, barley, oat or maize grains (Kostecki et al., 1999). Temperature greatly influenced moniliformin production by *F. avenaceum* on wheat, with more being produced under mediterranean rather than temperate conditions (Schütt, 2001).

5 CONCLUSIONS

Temperature and humidity/wetness are the main climatic factors influencing the development of *Fusarium* fungi causing diseases of cereals, although the influence of these climatic factors is not independent of other environmental and host factors. Many gaps exist in our knowledge of the influence of environmental parameters on *Fusarium* diseases of cereals. A risk assessment model for the forecasting of FHB epidemics in Ireland, based on environmental conditions is currently being developed (van Maanen, Cook and Doohan, unpubl. data). These data will also form part of an EU risk assessment model (EU RAMFIC project QLRT-1999-31517).

Particularly interesting questions for future research are: the influence of humidity on *Fusarium* diseases of small-grain cereals and the influence of environmental parameters on both the mycotoxin profiles (rather than individual metabolites) and biological control of *Fusarium* spp. Knowledge of the influence of climatic conditions on *Fusarium* diseases may prove useful towards developing novel disease control methods.

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