European Journal of Plant Pathology **109:** 755–768, 2003.
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Influence of climatic factors on *Fusarium* species pathogenic to cereals

F.M. Doohan, J. Brennan and B.M. Cooke
Department of Environmental Resource Management, Faculty of Agriculture, University College Dublin, Belfield, Dublin 4, Ireland (Phone: +353 1 7167743; E-mail: Fiona.doohan@ucd.ie)

Key words: water availability, wheat, barley, conidia, ascospores, germination

Abstract

Fusarium head blight of small-grain cereals, ear rot of maize, seedling blight and foot rot of cereals are important diseases throughout the world. *Fusarium graminearum, F. culmorum*, *F. poae*, *F. avenaceum* and *Microdochium nivale* (formerly known as *F. nivale*) predominantly cause *Fusarium* diseases of small-grain cereals. Maize is predominantly attacked by *F. graminearum*, *F. moniliforme*, *F. proliferatum* and *F. subglutinans*. These species differ in their climatic distribution and in the optimum climatic conditions required for their persistence. This review deals with the influence of climate on the production and dispersal of inocula, growth, competition, mycotoxin production and pathogenicity. Most species produce inocula, grow best, and are most pathogenic to cereal heads at warm temperatures and under humid conditions. However, the optimal conditions for *F. moniliforme* and *F. proliferatum* maize ear rot tend to be hot and dry and *M. nivale* head blight, seedling blight and foot rot of small-grain cereals tend to occur under cooler conditions. Seedling blight and foot rot caused by other species are favoured by warm dry weather. Between them, these fungi produce four important classes of mycotoxins: trichothecenes, zearalenone, fumonisins and moniliformin. Conditions favourable for *in vitro* growth are also generally the most favourable for mycotoxin production on cereal grains. These fungi rarely exist in isolation, but occur as a complex with each other and with other *Fusaria* and other fungal genera. Climatic conditions will influence competition between, and the predominance of, different fungi within this complex.

Introduction

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 (Sutton, 1982; 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 barley (Sutton, 1982; Parry et al., 1995; Miedaner, 1997; Tekauz et al., 2000; Brennan et al., 2003). Three species of *Fusarium* 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. equisti* (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 (Conrath et al., 2002).

This review focuses on the influence of climatic variables, particularly temperature, humidity and rainfall, on the *in vitro* and *in vivo* growth, reproduction, survival, competitive ability, mycotoxicity and pathogenicity of *Fusarium* fungi commonly isolated from wheat, barley and maize.

Climatic distribution of *Fusaria*

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 maritime regions of the world such as the UK, while *F. graminearum* tends to be the predominant *Fusarium* species pathogenic to these cereals in hotter regions of the world such as the USA (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. equisti* (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.

Production and dispersal of *Fusaria* inocula

Temperature, humidity, light intensity and wind are the critical climatic factors affecting the production and dispersal of asexual conidia and sexual ascospores of *Fusarium*. Hence these factors critically influence the propagation and survival of *Fusarium* fungi. The optimal environmental conditions for the production and dispersal of inoculum vary depending on whether the fungus reproduces sexually and/or asexually. Of the common causal agents of FHB and ear rot, *F. graminearum, F. avenaceum, M. nivale, F. moniliforme, F. proliferatum* and *F. subglutinans* reproduce both sexually and asexually, while only asexual conidial reproduction has been observed for *F. culmorum* and *F. poae* (Parry et al., 1995; Leslie, 1996).

Production of inoculum

Temperature, water availability (a_w), aeration and light are key climatic factors influencing the production of *Fusarium inoculum*. Sutton (1982) showed that *F. graminearum* inoculum is generally formed under warm rather than cool conditions. In the case of sexual reproduction, the optimal temperatures for *F. graminearum* perithecial and ascospore production were 29 and 25–28 °C, respectively. The discharge of inoculum is triggered by a drop in air temperature accompanied by a rise in relative humidity (Paulitz and Seaman, 1994; Paulitz, 1996). Ascospore release occurs over a range of temperatures (10–30 °C) and this explains why the optimal temperature observed for ascospore dispersal was 16 °C (Sutton, 1982). However, ascospore release is inhibited by rain or continuously high relative humidity (>80%) and Gilbert and Tekauz (2000) postulated that there is a threshold humidity beyond which release slows or stops.

Macroconidia of *F. graminearum* are produced at an optimal temperature of 28–32 °C and their production is severely inhibited below 16 and above 36 °C (Tschanz et al., 1976). On wheat spikelets, Andersen (1948) showed that millions of conidia of *F. graminearum* were produced on moist wheat heads at 20–30 °C on, and lesser numbers at 15 °C. Macroconidia appeared within 5 days at 20 °C and within 3 days at 25–30 °C. Exposure of spikelets to moisture reduced conidial formation time to 1–2 days, with conidial numbers increasing with increasing humidity. Using osmotically adjusted agar plates, maximal ascospore and/or conidial production for *F. culmorum*, *F. graminearum*

Group I and *F. avenaceum* occurred at approximately −10 to −20 bars (Cook and Christen, 1976; Sung and Cook 1981). However, Sung and Cook (1981) found that for *F. graminearum* Group II, conidial production was maximal at −1.4 to 3.0 bars. Although macroconidia are more readily formed in older *in vitro* cultures (Winder, 1999), which have decreased water potential, such cultures may also be depleted in nutrients and perhaps contain increased levels of toxic metabolites.

Chlamydospores are produced by some species of *Fusarium* fungi in response to adverse conditions (Griffiths, 1974). High temperatures and anaerobic conditions favoured the conversion of macroconidia of *F. sulphureum* to chlamydospores (Barran et al., 1977). The switch between the production of ascospores, macroconidia, mesoconidia, microconidia and chlamydospore formation may well be related to both nutritional and environmental factors, such as temperature and water potential. Higher daytime temperatures (30 vs. 20 °C) caused a greater proportion of macroconidia to form, and lowered the abundance of mesoconidia in *in vitro* cultures of *F. avenaceum* (Winder, 1999).

Light levels influence the production of inoculum by *Fusarium* fungi. Low intensity ultraviolet light (<390 nm) is required for perithecial initiation: the most effective wavelength range being 300–320 nm (Tschanz et al., 1976). Continuous darkness, continuous illumination, or a transition from light to darkness failed to induce conidiation in cultures of *F. solani* (Das and Busse, 1990). Conidia were only produced from hyphae that grew in darkness for less than 20 h and were subsequently illuminated.

Dispersal of inoculum

Parry et al. (1995) have extensively reviewed the role of wind and rain-splash in the dispersal of Fusaria inocula. Splash dispersal of *Fusarium* conidia has previously been demonstrated (Jenkinson and Parry, 1994; Hörberg, 2002; Rossi et al., 2002) and Parry et al. (1995) suggested that macroconidia are more suited for splash rather than wind dispersal. Rossi et al. (2002) studied the dynamics of airborne Fusarium macroconidia in wheat fields naturally infected by head blight. They detected no or very few conidia before rainfall, but their numbers progressively increasing during rainfall. With subsequent humid conditions, conidia continued to be produced for some hours after rainfall and usually reached their peak under these conditions. Fernando et al. (1997) showed that *F. graminearum* inoculum (macroconidia and ascospores) was usually displaced downwind from inoculated wheat heads and that the incidence of disease was higher and more diffuse in irrigated as opposed to non-irrigated plots. High humidity is required for the initial release of ascospores, although dry periods may be required for their forceful discharge into the air from perithecia (Parry et al., 1995). Also, the *F. graminearum* disease development gradients in wheat plots were more diffuse from ascospores (from infected maize grain) than from macroconidia (inoculated wheat heads) applied at anthesis (Fernando et al. 1997). Presumably air-borne dispersal of facilitates more widespread displacement of ascospores than does splash/rain dispersal of conidia.

While large differences in spore morphology (e.g. ascospore vs. macroconidum) influence inoculum dispersal, it appears that smaller inter-species differences in macroconidial shape do not. Hörberg (2002) compared the splash dispersal of *F. culmorum* and *F. poae* macroconidia and found essentially identical patterns, although *F. culmorum* produced fewer colonies than *F. poae*. However, it would be interesting to investigate whether there are differences in the splash dispersal patterns of macro and microconidia of *F. poae*.

Germination, growth and competition between *Fusaria*

Germination, growth and competition between *Fusaria* 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).

Germination

Germination is influenced by 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 intra-isolate 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.

Growth

Temperature and a_w differentially affect the growth of *Fusarium* species (Table 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*. *M. nivale* and *F. culmorum* were the fastest growing of all five species over the range 20–30 °C. Figure 1 depicts the typical growth of *F. graminearum*, *F. poae* and *M. nivale* and *F. poae* following 5 days incubation at 10 and 30 °C on potato dextrose agar. The fastest growing species at 10 °C was *M. nivale*, while at 30 °C they were *F. graminearum* and *F. culmorum* (Figure 1) (Brennan et al., submitted for publication). 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 *Fusaria* 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

Table 1. Optimum temperature and water potential/availability for the *in vitro* growth of *Fusarium* species

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	$a_w > 0.925$	Marin et al. (1995)
F. proliferatum	Sterile maize layers	30	$a_w > 0.925$	Marin 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.

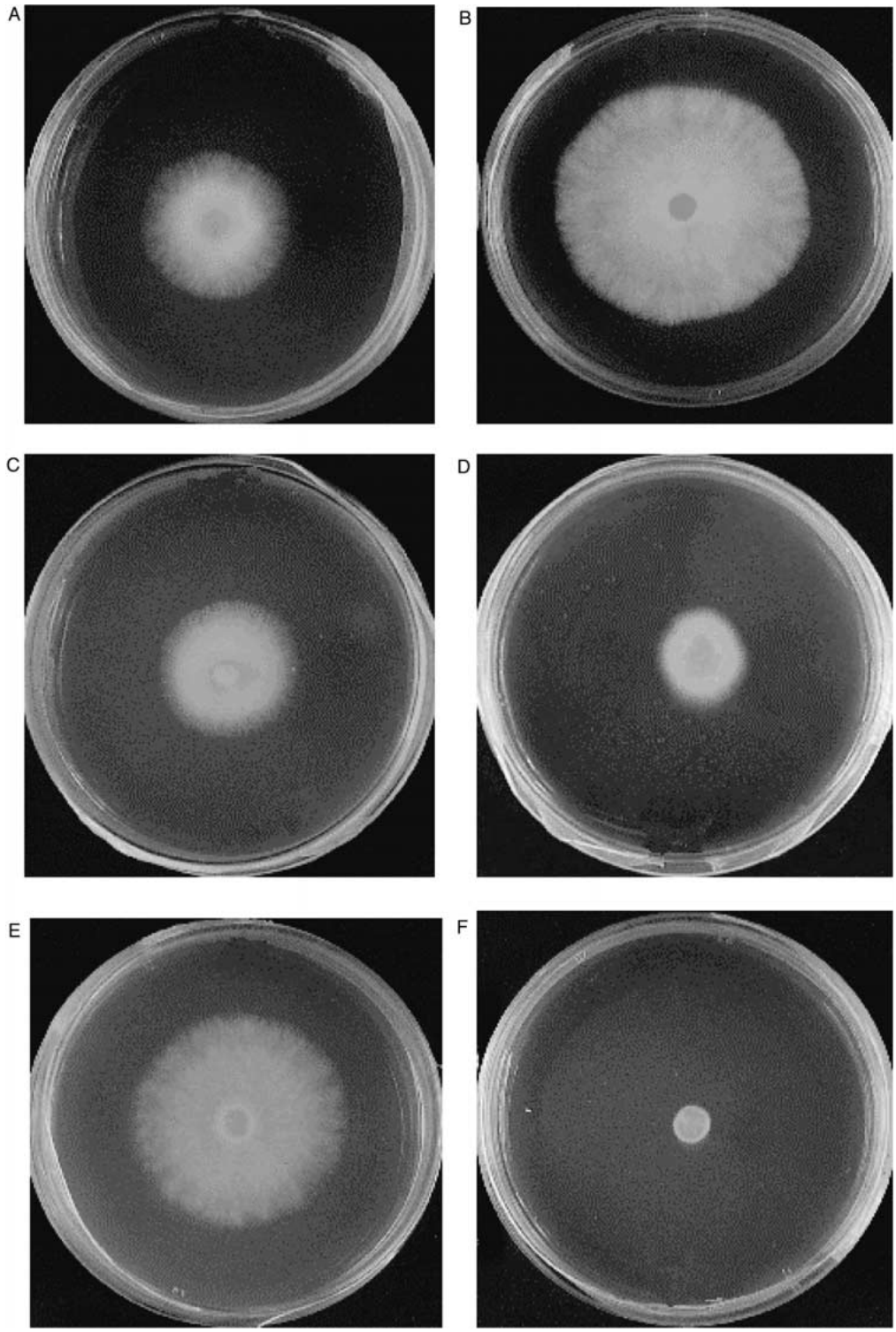

Figure 1. Growth of *F. graminearum* (strain HugR8) (A and B), *F. poae* (strain I105) (C and D) and *M. nivale* (strain 12/1/N) (E and F) on potato dextrose agar, following 5 days incubation at 10 and 30 °C, respectively (Brennan et al., 2003).

at 20–25 °C, but faster on rice culture media at 15 °C (Castellá et al., 1999).

Competition: Temperature and 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 °C, while at 25–30 °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 review, the occurrence of *Fusarium* complexes and their impact on mycotoxin production will be discussed.

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 B_1 (FB_1) and B_2 (FB_2) 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 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 °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

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

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), Marin 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.

stored at 25 °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; Martin and Martins, 2002) (Table 2). Martins and Martins (2002) found that on *F. graminearum*-infected cracked corn ($a_w = 0.97$), 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 $a_w \sim 0.98$ and fumonisin production generally decreases with temperature and higher a_w (Cahagnier et al., 1995; Marin 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 FB_1 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).

Microbial interactions and mycotoxin production

Fusaria and other microorganisms often occur as a complex on cereal crops, but limited information is available regarding the effects of fungal interactions on mycotoxin production by *Fusarium* complexes under different environmental conditions. The two fumonisin-producing species *F. moniliforme* and *F. proliferatum* are dominant over other fungal genera that contaminate maize over a wide range of temperature and a_w conditions, but little is known about the effect of such interactions on mycotoxin production. Orsi et al. (2000) found that in a mixed mycoflora-infected maize, FB_2 correlated positively with maize grain moisture content; significant negative correlations existed between relative FB_1 and FB_2 contents of maize and relative humidity, and between FB_2 and mean temperature. In terms of inter-species interactions, it is known that growth and FB_1 production by these pathogens on irradiated maize grain was significantly reduced at 15 °C in the presence of *F. graminearum* (Marín et al., 1998b; Velluti et al., 2000). More interestingly, at 25 °C, growth was not significantly affected, but there was an increase in FB_1 production by *F. moniliforme* in the presence of *F. graminearum*, regardless of a_w (0.92–0.98) (Velluti et al., 2000). ZEA production by *F. graminearum* was not significantly higher in the presence of *F. moniliforme* or *F. proliferatum*, regardless of temperature or a_w.

Pathogenicity of *Fusaria*

Ultimately, all of the above factors, i.e. production and dispersal of inoculum, germination, growth, competition and mycotoxin production might facilitate the pathogenesis of plants by *Fusarium* fungi. Hence, even prior to infection of the host, climate influences *Fusarium* potential for disease incidence and severity. Once *Fusarium* inoculum has been dispersed to the host, temperature and humidity play a significant role in the infection and colonisation of cereals by *Fusarium* fungi. The optimum conditions for disease development vary depending on the species, inoculum type and virulence and the affected tissue, i.e. seed, stem-base or head (Sutton, 1982; Miller, 1994; Parry et al., 1994; 1995; Miller et al., 1995; Tekauz et al., 2000; Vigier et al., 1997; Velluti et al., 2000; Bateman and Murray, 2001). Osmotic or temperature stress may indirectly affect disease development by inducing or 'priming' the host antifungal defence mechanisms prior to pathogen attack (Conrath et al., 2002). While *in vitro* growth tests suggested that temperature ecotypes existed amongst *Fusarium* on the basis of both species and country of origin, *in vitro* pathogenicity tests indicated that species is a much more important factor than climatic origin in determining the pathogenicity of *Fusarium*, irrespective of temperature (Brennan et al., 2003).

As discussed earlier, climate can influence the quantity and type of inoculum produced, but the production conditions may also influence the subsequent pathogenicity of inoculum. Winder (1999) showed that incubation temperature affected the pathogenicity of *F. avenaceum* inoculum (as did substrate type). Inoculum produced at 20 °C caused significantly more leaf damage on marsh reed grass plants that did that produced at 30 °C. More research is required to determine the effect of climatic conditions on the pathogenicity of FHB and maize ear rot inoculum.

FHB and ear rot

The climatic conditions optimal for the development of maize ear rot differ from those for small-grain cereals. This is more a function of the causal species rather than the host (Parry et al., 1995; Vigier et al., 1997) (Table 3). Precipitation plays a key role in the development of epidemics of FHB of small-grain cereals, which are usually associated with warm wet weather at the time of anthesis (Parry et al., 1995; Tekauz et al., 2000). Risk assessment and disease forecasting models for FHB are usually based on climatic conditions around the flowering to the early milky-ripe stage. For wheat, wetness periods of at least 24 h and temperatures above 15 °C are required for significant infection of heads by *F. graminearum*, *F. culmorum*, *F. poae*, *F. avenaceum* and *M. nivale*. The temperature optima for infection were 25, 25, 25, 25 and 15 °C, respectively (Parry et al., 1994; 1995).

In the first half of the twentieth century, it was recognised that temperature and humidity influence the severity of FHB (Atanasoff, 1920; Dickson et al., 1921; Pugh et al., 1933; Andersen, 1948). Under damp

Table 3. Optimal climatic conditions for the development of *Fusarium* cereal diseases

Species	Optimal conditions for disease development		References
	FHB and ear rot	Seedling blight and foot rot	
F. graminearum, *F. culmorum*, *F. poae*, *F. avenaceum*	Warm wet weather at anthesis (25 °C and >20 h rainfall)	Warm dry weather (>16 °C)	Atansoff (1920), Dickson et al. (1921), Pugh et al. (1933), Andersen (1948), Sutton (1982), Parry et al. (1994; 1995) Reid et al. (1995), McMullen et al. (1997), Hall and Sutton (1998), Tekauz et al. (2000), Brennan et al. (2003)
M. nivale	Moderately warm wet weather at anthesis (20 °C and >20 h rainfall)	Cool dry weather (10–15 °C)	Parry et al. (1994; 1995), Brennan et al. (2003)
F. moniliforme, *F. proliferatum*	Hot and dry conditions, especially at maize silking	—	Miller et al. (1995), Vigier et al. (1997), Reid et al. (2002)
F. subglutinans	Moderately warm humid climates	—	Vigier et al. (1997), Reid et al. (2002)

conditions, FHB symptoms on wheat developed 6 days post-*F. graminearum* inoculation, while under dry conditions symptoms were not observed until the onset of rain or heavy dew (Atansoff, 1920). Pugh et al. (1933) and Andersen (1948) found that the period of continuous wetness required for the development of moderate *F. graminearum* FHB disease scores was dependent on temperature (20–48 h at 25 °C and 60–72 h at 20 °C), with negligible symptoms developing at 15 °C. However, severe FHB infections can occur below 20 °C if precipitation is abundant (McMullen et al., 1997; Hall and Sutton, 1998). Tekauz et al. (2000) postulated that the increase in the incidence of *F. graminearum* in barley and wheat grown in the cooler and moist Black Soil Zone of the Canadian prairies supports the view that moisture is the overriding determinant of FHB severity.

Fusarium spp. infect maize heads either by growing down the silks, or through wounds created by birds or insects. Optimal conditions for the development of maize ear rot vary from warm to hot dry weather, depending on the causal species (Sutton, 1982; Vigier et al., 1997) (Table 3). *F. graminearum* and *F. subglutinans* tend to be the causal organisms in cooler to moderately warm and humid climates, while *F. moniliforme* and *F. proliferatum* are common causal organisms under hot and dry conditions (Sutton, 1982; Miller et al., 1995; Vigier et al., 1997). A survey of maize in Ontario during 1991–1993 showed that *F. subglutinans* was the predominant species and its incidence was negatively correlated with rainfall. Incidence of *F. graminearum* increased with precipitation and the results were consistent with a previous finding that lower *F. graminearum* infection levels were observed in Canada during dry years (Reid et al., 1995). In a 2-year study (1994–1995), Reid et al. (2002) observed lower disease severity in heads inoculated with *F. moniliforme* than in those inoculated with *F. graminearum* or *F. subglutinans.* This may have been due to the fact that the temperature never exceeded 25 °C or to the fact that the pathogenicity of *F. moniliforme* is considered moderate in comparison to that of *F. graminearum* and *F. subglutinans* (Miller, 1994).

Seedling blight and foot rot

Fusarium seedling blight arises mainly as a result of seed-borne inoculum, although inoculum may be soil-borne. Data on the influence of climatic factors on *Fusarium* seedling blight and foot rot is limited, but it is known that periods of dry weather predispose cereals to seedling blight and foot rot disease, the optimum temperature for the development of both diseases being dependent upon the causal species (Table 3) (Parry et al., 1994; Bateman and Murray, 2001). While cooler temperatures favour *M. nivale* seedling blight (10–15 °C), warmer conditions favour disease development for the other causal species (>16 °C) (Brennan et al., submitted for publication, Parry et al., 1994). Similar results were obtained in *in vitro* seedling blight experiments (Brennan et al., 2003). The effect of temperature (10–30 °C) on coleoptile growth retardation caused by *Fusarium* infection was examined. Greatest retardation was caused by *F. graminearum*, *F. poae* and *F. avenaceum* at 20–25 °C (>83% reduction), and by *F. poae* and *M. nivale* at 10–15 °C (>45.6% reduction). Figure 2 depicts the differences in the *in vitro* pathogenicity of *F.culmorum* and *M. nivale* at 25 °C (Brennan et al., 2003).

Conclusions

Temperature and humidity/wetness are the main climatic factors influencing the development of *Fusarium* 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 *Fusaria.* Knowledge of the influence of climatic conditions on *Fusarium* diseases may prove useful towards developing novel disease control methods. More research is required to understand whether osmotic or temperature stress affect *Fusarium* disease development by inducing or 'priming' the host antifungal defence mechanisms prior to pathogen attack (Conrath et al., 2002). In terms of manipulating environmental conditions to control *Fusarium* diseases, adjustment of soil temperature and moisture through soil solarisation has successfully been applied in

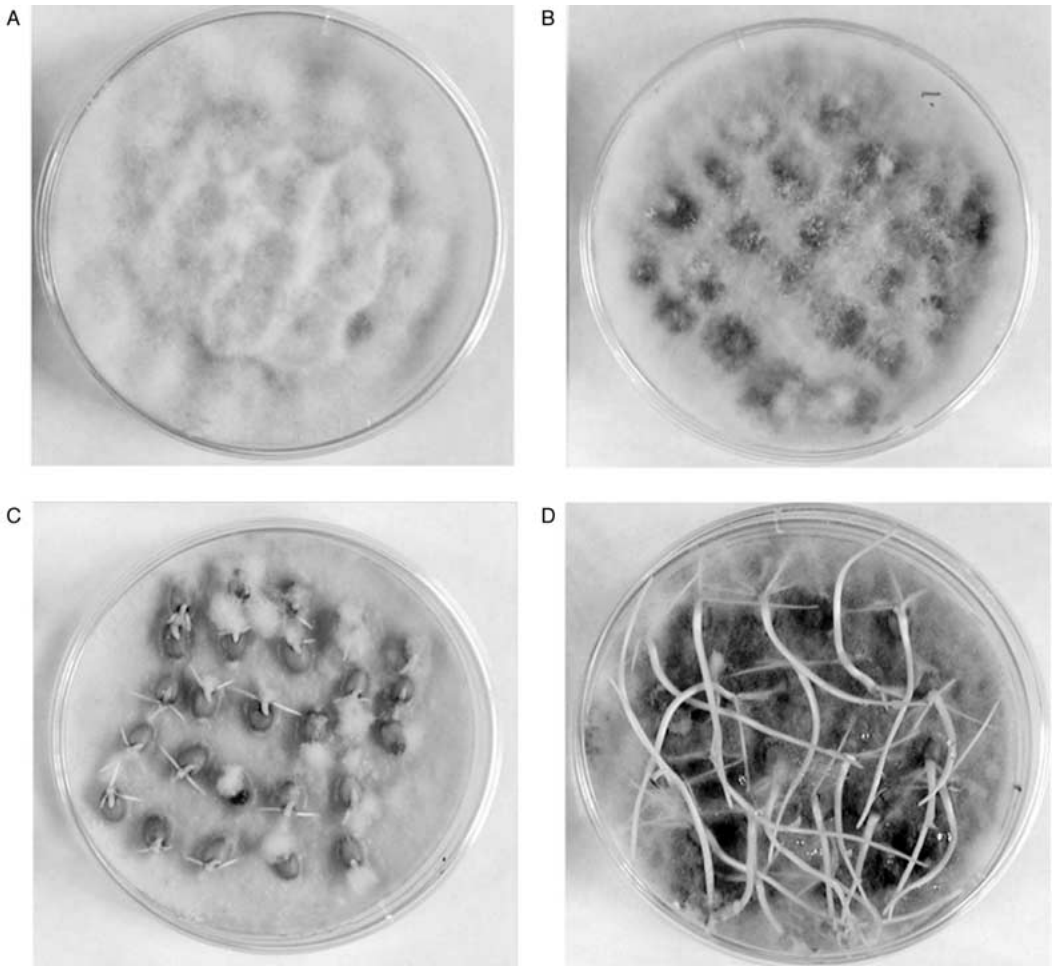

Figure 2. Effect of *F. graminearum* (strain 074) (A and B) and *F. poae* (strain 2742) (C and D) on coleoptile growth rate of wheat seedlings (cv. Falstaff) at 10 and 25 °C, respectively (Brennan et al., 2003).

many countries for the control of soil-borne pathogens (Katan, 1981). Soil solarisation is a method of heating moist soil by covering it with plastic sheets to trap solar radiation. Al-Karraghouli and Al-Kayssi (2001) showed that the efficiency of soil solarisation in killing *F. oxysporum* generally decreased with increasing soil moisture content, as the soil heat capacity increased and maximum soil temperatures decreased with increasing volumetric moisture content. The percentage eradication of the fungus was faster and higher in the soil surface layer (0.05 m) and decreased gradually with depth (as did temperature). While soil solarisation may be effective in eradicating *Fusarium* pathogens of cereals in drier climates, its applicability in maritime climates requires further analyses.

Acknowledgements

The authors thank Damian Egan and Brian Fagan (Department of Environmental Resource Management, University College Dublin) for their technical assistance. Josephine Brennan is funded by the EU 5th Framework Project RAMFIC.

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