European Journal of Plant Pathology **109:** 683–689, 2003.

Effects of environmental conditions on the development of *Fusarium* ear blight

Xiangming Xu
Horticulture Research International, East Malling, West Malling, Kent, ME19 6BJ, UK
(Fax: +44173284906; E-mail: xiangming.xu@hri.ac.uk)

Key words: Fusarium, inoculum, infection, forecasting

Abstract

Recent research on the epidemiology of *Fusarium* ear (or head) blight (FEB or FHB) of small-grain cereals is reviewed, focusing on inoculum, infection and disease forecasting. Both conidia and ascospores have been shown to be important for causing FEB. For *Fusarium graminearum*, propagules from crop debris are the main source of initial inoculum. Inoculum production is critically dependent on rainfall although the precise relationship is not clear. Recent work on understanding the effects of climatic variables on FEB development has been based on field observations. These field-based studies confirmed that warm and moist conditions during anthesis are the key factors for FEB development. Several empirical models were derived from the field data and proposed for use in disease forecasting. However, these models may not be applicable to a broader range of areas because of the limited nature of the field data. Several areas are proposed for future research, focusing on the development of more generally applicable forecasting models and on understanding the relationships between disease severity, fungal biomass and the production of associated mycotoxins.

Introduction

Fusarium ear (or head) blight (FEB or FHB) of small grains has recently become an important issue for two reasons. First, the incidence and severity of FEB has increased worldwide and these have resulted in significant yield losses. The International Maize and Wheat Improvement Centre (CIMMYT) has identified FHB as a major factor limiting wheat production in many parts of the world. In addition to causing yield losses, FEB is of greater significance under certain circumstances because of mycotoxin accumulation which can occur in *Fusarium*-infected grain. Grain contaminated with *Fusarium* mycotoxins is unsuitable for both human and animal consumption because of adverse health effects of such toxins.

The main causal agents of FEB are *Fusarium culmorum*, *F. graminearum*, *Microdochium nivale* var *nivale* and var *majus* (formerly *F. nivale*), *F. avenaceum* and *F. poae*. The distribution and predominance of these pathogens is, to a large extent, determined by climatic parameters, particularly temperature and moisture. Hence, in hotter regions, *F. graminearum* predominates, whereas in cooler maritime areas *M. nivale* is favoured. In addition to small-grain crops, *Fusarium* has a wide host range among other grass hosts. Combinations of these pathogens can often occur on wheat ears. The impact of the environment on such disease complexes is poorly understood. The sporadic nature of FEB is largely attributed to the observation that wheat plants are most susceptible to the disease during anthesis, which is a relatively short phase of the growth. For successful infection during anthesis, inoculum must be available and optimum weather conditions must prevail. There is a general consensus, which has been arrived at largely through anecdotal evidence, that FEB is most severe in cereals where warm and wet conditions occur. However, there are still insufficient quantitative data on the impact of environmental parameters on FEB development caused by individual species, and combinations of species, to draw any firm conclusions.

Because of its economic importance, there is an immense literature on FEB worldwide. Central to the understanding of FEB development is the nature of the initial inoculum of *Fusarium* from the soil, which survives either as saprophytic mycelium or as thick-walled resting chlamydospores, depending on the species. This initial inoculum may result in the infection of seedlings, resulting in the development of seedling blight and foot rot. Later, during anthesis and the early seed development period, airborne conidia or ascospores may infect the ears of cereal plants and consequently this results in development of FEB. Research on FEB has been reviewed by Parry et al. (1995) and Dubin et al. (1997). The FEB situation in North America has also been reviewed (Bai and Shaner, 1994; McMullen et al., 1997). Consequently, this paper concentrates on reviewing research on FHB conducted over the last 7–8 years, focusing on three aspects of the epidemiology of the disease: inoculum, infection and forecasting.

Inoculum

Most species of *Fusarium* are spread by the dispersal of conidia that are blown or splashed to new infection courts. Among the species causing FEB, *F. graminearum* has an additional epidemiological advantage because it regularly forms abundant perithecia (*Gibberella zeae*), resulting in production of ascospores. Ascospores are forcibly discharged into the air, which greatly increases the dispersal distance from the colonised residue where perithecia form. Ascospores and conidia cause significant infections (Fernado et al., 1997; Scholz and Steffenson, 2001). A genetically modified strain of *G. zeae* was obtained by deleting the entire mating type locus (MAT) that controls sexual reproduction from a wild type (Brown et al., 2001). This MAT-deleted strain appears similar to the wild type in morphology and in its ability to produce macroconidia. Field inoculations showed that the MAT-deleted strain resulted in less disease and less trichothecenes than the wild strain, indicating that ascospores play an important role in the development of FEB epidemics and the production of FEB associated mycotoxins.

Production of conidia is critically influenced by temperature as well as moisture. Rossi et al. (pers. comm.) studied the effect of constant temperature regimes on sporulation of *F. avenaceum*, *F. culmorum*, *F. graminearium* and *M. nivale* on potato dextrose agar media. Different isolates within each species showed similar relationships of sporulation with temperature. *F. avenaceum* produced the greatest amount of spores, followed by *M. nivale* and then by *F. graminearium* and *F. culmorum*. The optimum temperature for production of macroconidia was 32 °C for *F. culmorum* and *F. graminearium*, 28 °C for *F. avenaceum* and 26 °C for *M. nivale*. Mathematical models were developed to describe these relationships for each species and validated against data obtained on artificially inoculated wheat stems.

Conidia are generally splash dispersed and thus the dispersal distance is generally limited. Laboratory research showed that the maximum dispersal height and distance of *F. culmorum* and *F. poae* are 60 cm and 70 cm, respectively (Horberg, 2002). Furthermore, the splash dispersal patterns are indistinguishable for the two species. Thus only a very small proportion of conidia on the crop debris at soil level can reach the ears by rain splash. It has been speculated that symptomless infections on green leaves, such as the flag leaf, may provide an important bridge between conidia on crop debris and ears. Isolation of apparently healthy and diseased leaves (with necrotic leaf spots) indicated that *Fusarium* species associated with FEB survive parasitically and saprophytically on leaves throughout the season (Ali and Francl, 2001).

One of the main sources of inoculum is colonised crop debris. This provides a site for abundant sporulation during the next growing season. The mixture of maize, wheat and barley production, especially when combined with widespread use of reduced tillage, has increased residue retention and set the stage for major epidemics of FHB to occur in small-grain cereals whenever weather is favourable for disease during flowering and heading. Andries et al. (2000) found that in Michigan the peak of perithecial production occurred just prior to flowering and that most (83%) of these perithecia were on maize debris. The proportion of mature perithecia was highly correlated with temperature during the 14 days prior to sampling, but not with relative humidity (RH). Temperatures below 3 °C appeared to inhibit perithecium formation. These findings closely parallel the 2-week cycle of development and maturation of perithecia demonstrated in the laboratory (Trail and Common, 2000). In China, where rice is rotated with wheat, the incidence of rice debris bearing ascospores could be as high as 80% (Lu et al., 2001). Ascospore production appears to be critically dependent on soil moisture. When the soil moisture content is below 30%, ascospore production is not possible. When it is greater than 80%, ascospore production is at its maximum. Minimum and optimum temperatures for ascospore production are about 7–10 and 15–20 °C, respectively. Burning crop residues reduces the inoculum potential of *F. graminearium* present in residues and hence the potential inoculum for FEB (Dill-Macky and Salas, 2001). However, there are many other hosts, such as grasses and some broad-leaved weeds, which may provide an important alternative inoculum source.

Several researchers have observed a clear diurnal pattern of ascospore discharge (Paulitz, 1996; Fernado et al., 2000; Francl et al., 2000), beginning from 1600–1800 h, which peaked around midnight and then gradually declined. Peak ascospore release occurred 2–4 days after rainfall (>5 mm). Similarly, in China, ascospore release only occurred at near-saturation humidity (Lu et al., 2001). Paradoxically, Maldonado-Ramirez and Bergstrom (2000) found that most ascospores were discharged during daylight hours when atmospheric turbulence was highest. This pattern may provide the maximum opportunities for ascospores to be moved into the planetary layer, where vertical mixing occurs up to cloud level and the potential for long distance dispersal is greatest.

In general, ascospore dispersal is associated with rainfall events, although Thomas et al. (1999) and Francl et al. (1999) did not find any consistent relationships between the numbers of ascospores caught in trapping experiments and the actual amount of rainfall. The numbers of spores caught during anthesis were generally low but increased substantially thereafter (Thomas et al., 1999). Spores were not detected or only occurred sporadically during dry periods (Francl et al., 1999). Inoculum increased during rainy periods but the timing of this increase was variable. These results suggest that, whilst rainfall may be needed for perithecial and ascospore formation and maturation, it may not actually trigger the release of ascospores.

Infection

As outlined above, anthesis appears to be a period of increased susceptibility of ears to *Fusarium* infection. Much research has been directed towards understanding the exact pathways through which *Fusarium* spores infect and colonise ears. To facilitate such research, Bushnell et al. (1999) produced a transformed isolate of *F. graminearum* with a constitutively expressed gene for green fluorescent protein (GFP). Preliminary investigations using this GFP-transformed isolate showed that hyphae within host tissues were subcuticular and intercellular and that hyphae also appeared to grow into and out of leaf stomata. Furthermore, fungal development was limited in paleas, lemmas and coleoptiles. Infection and colonisation pathways on ears are currently being further investigated using this fungal isolate. Pritsch et al. (2000) found that spores germinated and penetrated the glume stomata and spread throughout the wheat head resulting in chlorosis of infected kernels. There were no differences in the infection structures between a resistant and a susceptible cultivar investigated. Under warm, mist-irrigated field conditions, colonies that formed on the abaxial (exterior) surface of the palea (near the kernel) and on the adaxial (interior) surface of the palea and lemma facing the floret mouth served as starting points for floret invasion (Lewandowski and Bushnell, 2001).

Infection of seeds by *F. graminearium* was investigated in plots inoculated with colonised corn debris and irrigated prior to and during anthesis (Argyris et al., 2001). The incidence of infection increased from c. 20% at 10 days after anthesis (DAA) to a maximum level >95%v at 37–40 DAA (harvest was at c. 50 DAA; physiological maturity, i.e. maximum dry seed weight, occurred between 30 and 32 DAA). There was a significant relationship between visual estimates of spikelet infection and seed infection in the four cultivars studied. Germination of seeds from inoculated plots declined progressively from 10 DAA to harvest (50 DAA); there was a significant negative correlation between germination and seed infection.

Knowledge of environmental factors that influence infection and subsequent FEB development is essential for assessing the potential disease risks and for developing efficient disease management strategies. There seems little doubt that the most important environmental factor that limits FEB development is moisture. Given a wet environment for an extended time, even a low initial inoculum level or a sub-optimal temperature does not prevent FEB from developing. Most studies which investigated the relationship between environmental factors and FEB development have been based on intensive field monitoring of inoculum strength, weather variables and disease development.

Development of FEB has been monitored in states of the USA over several years (De Wolf et al., 2000; 2001).

Differences in observed disease incidence between different field sites can be attributed partially to the differences in temperature and moisture. Lower temperatures and lack of surface wetness during anthesis are believed to be limiting factors for the low incidence of FEB. Modelling of these field data showed that environmental conditions prior to flowering were less important than those during anthesis. One of the important variables identified was the duration (hours) of RH >90% and temperature at 15–30 °C. Similar results were also obtained in Argentina indicating the importance of warm and moist conditions for FEB development (Moschini and Fortugno, 1996). Chinese researchers showed that ascospore germination is critically affected by temperature and humidity (Lu et al., 2001). At 25 °C and 100% RH, germination can be as high as 97.5% after 8 h and incidence of infection on stamens was about 58% after 20 h. Below 90% RH, germination was only about 0.4%.

The effects of temperature and humidity on the infection of wheat ears by *F. avenaceum*, *F. graminearum*, *F. culmorum* and *M. nivale* were studied recently using detached spikes in controlled environments (Rossi et al., 2001b). Infection of glumes was determined following incubation in wet conditions (4–72 h) at different temperatures. *F. avenaceum* and *F. graminearum* showed the highest incidence of infection, with optima at 28–29 °C. *M. nivale* and *F. culmorum* had lower incidences of infection, with optimum temperatures of 18 and 26.5 °C, respectively. Overall, the incidence of infection increased with increasing duration of wet periods, with *F. avenaceum* and *F. graminearum* increasing at a much faster rate than the other two species. For example, at the optimum temperature 30 °C, the incidence of infection by *F. avenaceum* increased from 0% after an 8 h wet period to 84% after a 72 h wet period, whereas with *M. nivale* at 15 °C, it increased from 0 to 22% under the same conditions. Empirical regression models were developed to relate the incidence of infection to the length of wet period and temperature and these models were used as a basis for developing forecasting models.

Recently, there has been a growing interest in understanding the spatial as well as the temporal dynamics of FEB epidemics. The spatial pattern of disease incidence appeared to be completely random in three out of four sampled fields (Shah et al., 2000; 2001), indicating that the primary inocula for infecting ears were distributed randomly and were thus more likely to be composed of external airborne ascospores. Only in one field was there some degree of clustering of diseased ears within the sampling quadrat. This may indicate that the inoculum was from clustered corn debris in soil. The field with an aggregated pattern had much a higher disease incidence than the other three fields. In another study, infected heads were found to be aggregated, in some cases highly so, within an individual wheat field, with the degree of aggregation increasing over time as disease incidence increased. The proportion of infected seeds varied greatly between seed lots, and this variability in seed infection was significantly greater than would be expected for a binomial (i.e. random) distribution in 72% of data sets (Shah et al., 2002).

Forecasting

A disease forecasting system is generally based on the combined effects of host susceptibility, inoculum strength and meteorological conditions on disease development. For FEB, the most susceptible stage appears to be anthesis, although considerable infection is still possible at the milky stage. Usually, inoculum strength, which is dependent on rainfall, RH, temperature and disease carry-over, etc. is very difficult to estimate. Many forecasting models have been developed for FEB and almost all are empirical regression models derived from long-term field observations. These models describe the overall effects of weather variables on epidemic development such as sporulation, spore dispersal, infection and subsequent disease development. These models may therefore not perform equally well in other regions because of the local nature of the field data. Details of these models are published and the models have been validated, although their usefulness in assisting practical disease management is often not known.

In China, there have been 19 documented forecasting models used in various regions (Lu et al., 2001). Most of these models use rainfall and temperature over various periods of time to estimate FEB risk. Some models also use measures of disease severity in the previous season and current spore catches to predict the disease risk. Similar models have been developed in other countries (Moschini and Fortugno, 1996; Lipps et al., 2001). A prediction model based on a single variable that combines both moisture and temperature correctly identified 83% of epidemic severity classes across several states in the USA (De Wolf et al., 2000; Lipps et al., 2001). In general, these models include the effects of weather variables on two aspects of epidemic development:

1. Spore production. Sufficient rainfall about 8–10 days prior to and during anthesis facilitates production of both ascospores and conidia.
2. Spore dispersal and infection. Sufficient rainfall may be needed to disperse ascospores and/or conidia, followed by prolonged periods of warm humid conditions that are conducive for infection of ears.

The nature of these empirically derived models means that the exact weather variables and their weight in estimating the infection risk differed significantly between each model. This reflects differences in many of the factors in the data sets used to develop the models, such as the frequency/duration of field observations, the cultivars used, fungal pathogen species, inoculum strengths and climates. It remains a challenge for plant pathologists to develop a FEB forecasting model that can be used reliably over a wider range of conditions.

Recently, a system-based model development framework was adopted for developing a risk assessment model for FEB (Ross et al., 2001a). Such system-based models are usually developed by dividing the whole process into several sub-processes such that the individual sub-processes can be predicted accurately from variables that can be easily obtained. Risk indices are then derived by linking individual sub-models sequentially. This model included three sub-processes: sporulation, spore dispersal and infection. The model finally estimates daily infection risks. However, no validation results are yet available.

The future

There are several key areas in the epidemiology of FEB that need to be investigated before an effective management system can be developed for FEB in cereal production.

1. Most current research on the effects of weather conditions on FEB is based on intensive field observations. Such data are very useful for many purposes, but they cannot usually be used to develop a forecasting system applicable to a wide range of conditions. Infection studies need to be conducted in controlled environment conditions on whole plants instead of detached ears or spikelets.
2. The interrelationships between disease incidence/severity, fungal biomass and concentration of the associated mycotoxins need to be understood. Such knowledge should enable disease development to be forecast, and the potential production of mycotoxins to be predicted. Of course, the production of mycotoxins is likely to be influenced by post-infection and post-harvest conditions/events.
3. As FEB is a disease complex in most regions, the consequence of infection by multiple *Fusarium* species on disease development and the production of mycotoxins needs to be understood.
4. A better understanding of the relationship between the actual moisture level on the ear surface and atmospheric moisture, and how this relates to our laboratory measurement of ‘wetness’ is required.
5. There is a need to understand and characterise the spatial heterogeneity and patterns of FEB and their relationships to mycotoxins. Further research is also needed to understand the underlying physical and biological processes that are responsible for the resulting spatial heterogeneity and patterns. Such knowledge will enable an effective sampling scheme for disease assessment and quantification of mycotoxins to be designed.
6. Finally, in addition to the need to develop and validate forecasting models, it is necessary to integrate these models into practical production systems and to demonstrate their usefulness to a wider audience.

Currently, HRI-East Malling is co-ordinating an EU-funded project (RAMFIC) that attempts to obtain key knowledge in areas (1)–(3). The overall objective of this project is to obtain a large body of quantitative data on FEB (both visual disease severity and fungal biomass) and the production of associated mycotoxins in controlled environments and to develop quantitative risk assessment models, which will be refined using data collected from a large number of field sites in Europe with contrasting climatic conditions.

Acknowledgements

This research was funded by the European Commission, Quality of Life and Management of Living Resources Programme (QOL), Key Action 5 on Sustainable Agriculture, Contract No. QLK5-CT-2000-01517. I thank Dr Tim Pettitt for critically reviewing the manuscript.

References

Ali S and Francl L (2001) Progression of *Fusarium* species on wheat leaves from seedlings to adult plants in North Dakota. In: Proceedings of 2001 National Fusarium Head Blight Forum (p 99) Erlanger, KY, USA

Andries C, Jarosz A and Trail F (2000) Effects of rainfall and temperature on production of perithecia by *Gibberella zeae* in field debris in Michigan. In: Proceedings of 2000 National Fusarium Head Blight Forum (pp 118–112) Erlanger, KY, USA

Argyris LM, TeKrony DM and VanSanford D (2001) Effect of *Fusarium graminearum* infection during wheat seed development on seed quality. In: Proceedings of 2001 National Fusarium Head Blight Forum (pp 100–104) Erlanger, KY, USA

Bai G and Shaner G (1994) Scab of wheat: prospects for control. Plant Disease 78: 760–766

Brown DW, Desjardins AE, Yun S-H, Plattner R, Lee T, Dyer R and Turgeon BG (2001) Are *Gibberella zeae* sexual spores the critical inoculum leading to FHB epidemics? In: Proceedings of 2001 National Fusarium Head Blight Forum (p 104) Erlanger, KY, USA

Bushnell WR, Skadsen RW, Goff TN and Hohn TM (1999) Use of a GFP strain of *Fusarium graminearum* for histological investigation of infected barley. In: Proceedings of 1999 National Fusarium Head Blight Forum (p 84) Sioux Falls, South Dakota, KY, USA

De Wolf ED, Madden LV and Lipps PE (2000) Prediction of *Fusarium* head blight epidemics. In: Proceedings of 2000 National Fusarium Head Blight Forum (pp 131–135) Erlanger, KY, USA

De Wolf ED, El-Allaf S, Lipps PE, Francl L and Madden LV (2001) Influence of environment on inoculum level and *Fusarium* head blight severity. In: Proceedings of 2001 National Fusarium Head Blight Forum (pp 106–109) Erlanger, KY, USA

Dill-Macky R and Salas B (2001) Effect of burning wheat and barley residues on survival of *Fusarium graminearum* and *Cochliobolus sativus*. In: Proceedings of 2001 National Fusarium Head Blight Forum (p 112) Erlanger, KY, USA

Dubin HJ, Gilchrist L, Reeves J and McNab A (eds) (1997) Fusarium Head Scab: Global Status and Prospects (p 130) CIMMYT, Mexico, DF, Mexico

Fernando WGD, Miller JD, Seaman WL, Seifert K and Paulitz TC (2000) Daily and seasonal dynamics of airborne spores of *Fusarium graminearum* and other *Fusarium* species sampled over wheat plots. Canadian Journal of Botany 78: 497–505

Fernando WGD, Paulitz TC, Seaman WL, Dutilleul P and Miller JD (1997) Head blight gradients caused by *Gibberella zeae* from area sources of inoculum in wheat field plots. Phytopathology 87: 414–421

Francl L, Shaner G, Bergstrom G, Gilbert J, Pedersen W, Dill-Macky R, Sweets L, Corwin B, Jin Y, Gallenberg D and Wiersma J (1999) Daily inoculum levels of *Gibberella zeae* on wheat spikes. Plant Disease 83: 662–666

Francl L, Markell S, Ali S and Friesen T (2000) *Gibberella zeae* Population dynamics: a progress report. In: Proceedings of 2000 National Fusarium Head Blight Forum (pp 144–146) Erlanger, KY, USA.

Horberg HM (2002) Patterns of splash dispersed conidia of *Fusarium poae* and *Fusarium culmorum*. European Journal of Plant Pathology 108: 73–80

Lewandowski S and Bushnell WR (2001) Development of *Fusarium graminearum* on floret surfaces of field-grown barley. In: Proceedings of 2001 National Fusarium Head Blight Forum (p 128) Erlanger, KY, USA

Lipps PE, Mills D, De Wolf ED and Madden LV (2001) Use of *Fusarium* head scab risk assessment models in Ohio, 2001. In: Proceedings of 2001 National Fusarium Head Blight Forum (p 129) Erlanger, KY, USA

Lu WH, Chen SH and Wang YZ (2001) Research on *Fusarium* Head scab, Science Publisher, Beijing

Maldonado-Ramirez SL and Bergstrom GC (2000) Temporal patterns of ascospore discharge by *Gibberella zeae* from colonized corn stalks under natural conditions. In: Proceedings of 2000 National Fusarium Head Blight Forum (pp 159–162) Erlanger, KY, USA

McMullen MP, Jones R and Gallenberg D (1997) Scab of wheat and barley: a re-emerging disease of devastating impact. Plant Disease 81: 1340–1348

Moschini RC and Fortugno C (1996) Predicting wheat head blight incidence using models based in meteorological factors in Pergamino, Argentina. European Journal of Plant Pathology 102: 211–218

Parry DW, Jenkinson P and McLeod L (1995) Fusarium ear blight (scab) in small grains – a review. Plant Pathology 44: 207–238

Paulitz TC (1996) Diurnal release of ascospores by *Gibberella zeae* in inoculated wheat plots. Plant Disease 80: 674–678

Pritsch C, Muehlbauer GJ, Bushnell WR, Somers DA and Vance CP (2000) Fungal development and induction of defence response genes during early infection of wheat spikes by *Fusarium graminearum*. Molecular Plant–Microbe Interactions 12: 159–169

Rossi V, Giosue S, Pattori E and Languasco L (2001a) Risk of *Fusarium* head blight on wheat: a preliminary model. In: Proceedings of 11th Congress of the Mediterranean Phytopathological Union and the 3rd Congress of the Sociedadae Portuguesa de Fitopatologia, 17–20 September, 2001 (pp 46–48) University of Evora, Portugal

Rossi V, Ravanetti A, Pattori E and Giosue S (2001b) Influence of temperature and humidity on the infection of wheat spikes by some fungi causing *Fusarium* head blight. Journal of Plant Pathology 83: 189–198

Scholz U and Steffenson BJ (2001) Effect of *Gibberella zeae* ascospores and *Fusarium graminearium* on Fusarium head blight severity and deoxynivalenol production in barley. In: Proceedings of 2001 National Fusarium Head Blight Forum (pp 147–150) Erlanger, KY, USA

Shah DA and Bergstrom GC (2001) Spatial patterns of *Fusarium* head blight in New York wheat fields in 2000 and 2001. In: Proceedings of 2001 National Fusarium Head Blight Forum (pp 154–155) Erlanger, KY, USA

Shah DA, Clear RM, Madden LV and Bergstrom GC (2002) Summarising the regional incidence of seed-borne fungi with the β-binomial distribution. Canadian Journal of Plant Pathology 24: 168–175.

Shah DA, Stockwell CA, Kawamoto SO and Bergstrom GC (2000) Spatial patterns of *Fusarium* head blight in New York wheat fields during the epidemic of 2000. In: Proceedings of 2000 National Fusarium Head Blight Forum (pp 174–175) Erlanger, KY, USA

Thomas D, Buechley G and Shaner G (1999) Epidemiology of *Fusarium* head blight of wheat in Indiana. In: Proceedings of 1999 National Fusarium Head Blight Forum, Sioux Falls (pp 100–104) South Dakota, KY, USA

Trail F and Common R (2000) Perithecial development by *Gibberella zeae*: a light microscopy study. Mycologia 92: 130–138