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REVIEW PAPER

The aerobiology of *Fusarium graminearum*

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Abstract Current knowledge of the aerobiology of *Fusarium graminearum* sensu lato is based on decades of published research documenting the processes of spore discharge, atmospheric transport, and deposition in this important pathogen of cereal crops worldwide. Spores from both local and more distant sources have been shown to cause infection in susceptible cereal crops when environmental conditions are favorable. Susceptible crops may be exposed throughout a growing season to airborne spores deposited in rain events and in night-time hours through gravitational settling. Given that spores deposited on cereal florets originate from distant as well as local sources, disease risk forecasts, based currently on weather favoring local spore production during the days before peak infection (i.e., initiation of crop flowering), might be improved by placing greater emphasis on local weather directly favoring infection at and following the time of flowering. Also, considering the genetic diversity of fungal spores introduced to local agricultural fields following atmospheric transport, crop breeders should select resistant varieties based on screening against a set of fungal isolates that represent the range of virulence observed in fungal populations across a broader geographic region. An increased understanding of the aerobiology of *F. graminearum* contributes to the overall knowledge of plant pathogen transport in the atmosphere.

Keywords Spore transport · Fusarium head blight · *Gibberella zeae* · Disease forecasting

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1 Introduction

Researchers have long debated the contribution of local and atmospheric inocula to local epidemics of *Fusarium graminearum* sensu lato [teleomorph: *Gibberella zeae* (Schwein.) Petch] in cereal crops and more recently to the influence of atmospheric inoculum on the accuracy of risk assessment models. Atanasoff (1920) attributed *G. saubinetti* (a synonym of *F. graminearum*) infection of a rye field to the movement of spores in air currents influenced by local topographical features. In a US Department of Agriculture Farmer's Bulletin, Johnson and Dickson (1921) described how *F. graminearum* ascospores are easily blown by wind and air currents. They suggested if environmental conditions were favorable, *F. graminearum* infection might spread rapidly over an entire region causing immense loss (Johnson and

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Dickson 1921). It is evident from these statements that the long-distance movement of *F. graminearum* was accepted as early as the 1920s.

Several plant pathogens are known to be transported long distances, and their aerobiological mechanisms have been well documented. For example, *Venturia inaequalis* (ascospore average size = 6 × 13 μm), the causal agent of apple scab (Aylor 1998), *Puccinia graminis* subsp. *graminis* Pers. (urediniospore average size = 32 × 19 μm), the causal agent of wheat stem rust (Roelfs 1985; Stakman and Harrar 1957) and *Peronospora hyoscyami* de Bary (sporangiospore average size = 20 μm), the causal agent of tobacco blue mold (Aylor and Taylor 1983) are among the fungal pathogens with well-documented aerial transport capabilities. Ragweed pollen (20 μm) is reported to move great distances within plant canopies during the day before impacting on plant surfaces or settling by gravity (Aylor 1975). Ragweed pollen has a similar size to many fungal spores (Gregory 1973) including *F. graminearum* which has an average ascospore size of 21 μm × 3.5 μm (Trail et al. 2005). Booth (1971) described ascospores as 19–24 × 3–4 μm and macroconidia as 25–50 × 3–4 μm.

Aerobiology is the study of factors and processes that influence the movement of biota in the atmosphere and involves biota liberation from inoculum sources, horizontal transport, deposition, and the ecological and environmental factors that contribute to each (Isard and Gage 2001). Many plant pathogens such as *F. graminearum* have adapted to move long distances in the atmosphere by taking advantage of aerial transport. The ability of a plant pathogen such as *F. graminearum* to move long distances is essential to its evolutionary survival. Atmospheric movement may result in invasion of new sites, utilization of new resources, and gene transfer among populations (Rabb 1985). It can also result in the introduction of a disease to a region or continent or the frequent re-introduction of a pathogen to a region (Aylor 1986). Recent aerial sampling in the middle-to-upper troposphere indicates microbial communities to exist, including fungi that are available for long-range transcontinental transport (DeLeon-Rodriguez et al. 2013).

Fusarium graminearum is the most common causal agent of Fusarium head blight (FHB) in North America and many other parts of the world (Sutton 1982; Weise 1987). In addition to FHB, *F. graminearum* can also cause Gibberella ear and stalk rot of corn. FHB is internationally recognized as one of the most destructive diseases of wheat, barley, and other small grains due to decreased market value based on low test weights and mycotoxin accumulation. This disease can devastate potentially high-yielding small grains within weeks of harvest (McMullen et al. 1997) and has caused the loss of billions of dollars in Asia, Europe, South America, and North America (Goswami and Kistler 2004; McMullen et al. 2012).

In addition to the direct impact on yield, some strains of *F. graminearum* produce a mycotoxin known as deoxynivalenol (DON) in infected grain. DON is an important inhibitor of protein synthesis and may cause adverse health effects in humans (Pestka 2010; Pestka and Smolinski 2005) and domestic animals (Pestka 2007) if contaminated grain is consumed. The United States Food and Drug Administration's recommended tolerance level for DON is 1 ppm in finished food products for human consumption. DON tolerances are set at different levels depending on the grain usage and the sensitivity of the animal consuming the grain or grain by-products (US Food and Drug Administration 2010). As a result, research on *F. graminearum* has been rigorous and comprehensive.

Though specific aspects of *F. graminearum* aerobiology have been thoroughly investigated, aerial transport mechanisms of *F. graminearum* have been largely ignored (Bai and Shaner 1994, 2004; Gilbert and Tekauz 2000; Goswami and Kistler 2004; McMullen et al. 1997; Snijders 1990; Stack 1999; Tekauz et al. 2000). Apart from one brief review concerning the aerobiology of this organism (Schmale and Bergstrom 2007), other reviews have only briefly addressed long-distance transport of *F. graminearum* without using the term aerobiology (Atanasoff 1920; Gilbert and Fernando 2004; Johnson and Dickson 1921; McMullen et al. 2012; Munkvold 2003; Osborne and Stein 2007; Parry et al. 1995; Shaner 2003; Sutton 1982). A review of decades of literature reveals considerable accumulated knowledge of the aerial transport of *F. graminearum*.

2 Inoculum sources of *F. graminearum*

Since the early 1900s, overwintered crop residue has been recognized as the primary inoculum source of *F. graminearum* (Atanasoff 1920; McMullen et al. 1997;

Sutton 1982) during crop rotations involving susceptible crops. Corn and wheat grown in rotation can provide an abundant source of inoculum for subsequent infection. Hoffer et al. (1918) reported incidence of FHB increased when wheat was grown immediately after corn. More recent research shows similar trends in continuous wheat rotations (Snyder and Nash 1968) as well as corn-wheat rotations (Dill-Macky and Jones 2000; Schaafsma et al. 2005; Teich and Hamilton 1985; Teich and Nelson 1984). Alternative hosts such as gramineous weeds, fescue, and sunflower residue have been reported to support *F. graminearum* establishment, although perithecia production has not been seen on sunflower (Pereyra and Dill-Macky 2008). Soybean has also been reported as a possible host (Martinelli et al. 2001) especially when soybean residue is present in a no-tillage system (Baird et al. 1997).

Fusarium graminearum-infested wheat and corn residue contain haploid mycelia that will grow through the vascular system and pith and radially colonize the stem tissue (Guenther and Trail 2005). Sexual spore-containing structures called perithecia emerge from nodes and internodes and are associated with stomatal openings and silica cells of the colonized residue (Guenther and Trail 2005). Tschanz et al. (1976) reported light was required for perithecia maturation which may explain the association between perithecia and light-transmitting silica cells. *F. graminearum* has been reported to survive at least 1–2 years (Khonga and Sutton 1988) and for more than 2 years (Pereyra et al. 2004) in residue on or above the soil surface, indicating that this residue can be a long-term source of inoculum. Khonga and Sutton (1988) also reported limited *F. graminearum* survival on buried residue which Pereyra et al. (2004) confirmed and that survival within residues was found beyond *F. graminearum*'s ability to sporulate (Khonga and Sutton 1988). The survival of *F. graminearum* in soil has been documented (McMullen and Stack 1983), but is thought to be of little importance compared with crop residue located on the soil surface (Shaner 2003).

Dill-Macky and Jones (2000) found lower FHB incidence and severity in wheat plots where residue was minimized using a moldboard plow when compared with no-till or when using a chisel plow. In addition, wheat planted after corn resulted in the highest FHB infection when compared with wheat planted after soybean (Dill-Macky and Jones 2000). Nita et al. (2006) found higher amounts of *F. graminearum* inoculum to elevate disease levels when environmental conditions were moderately favorable for disease. However, amount of inoculum was not correlated with disease incidence when conditions were highly favorable or unfavorable for FHB (Nita et al. 2006). In a similar study, Stein et al. (2009) reported FHB incidence, FHB severity, and DON levels to increase with an increasing number of *F. graminearum* spores applied.

3 Spore discharge

Spore dissemination is a critical step for fungi to colonize new substrates and habitats. To escape thin laminar layers of air surrounding plant parts (i.e., crop residue and small grain spikes) into the atmospheric turbulent layers, spores must be dislodged by the wind and rain or use ejection mechanisms (Aylor 1990; Isard and Gage 2001). Once spores have escaped into the turbulent layers of the atmosphere, spores can move throughout the canopy or escape into the lower atmosphere to transport long distances.

Some ascospores (sexual spores) are known to be released independently of wind speed by active mechanisms of the perithecia (Aylor 1990). In contrast, macroconidia (asexual spores) are dependent upon wind speed for liberation (Aylor 1990). Both ascospores and macroconidia of *F. graminearum* have been shown to cause disease epidemics (Stack 1989). Macroconidia have been produced under moist conditions between 16 and 36 °C with an optimal temperature of 32 °C from a single isolate of *F. graminearum* (Andersen 1948). Macroconidia are typically reported to be splash-dispersed short distances within the canopy (Parry et al. 1995; Sutton 1982) and thus thought only to be a local (within-field) source of inoculum. Ascospores are typically reported to be the primary source of airborne inoculum (Andersen 1948; Fernando et al. 1997), but airborne macroconidia have also been captured and could contribute to airborne inoculum (Fernando et al. 2000; Maldonado-Ramirez 2001; Markell and Francl 2003).

Although twice as many ascospores were observed as macroconidia in aerial samples and on infected plant tissue, Markell and Francl (2003) found macroconidia to be present on days with high inoculum amounts. Maldonado-Ramirez (2001) was able to collect both macroconidia and ascospores 60 m above

ground level on an adhesive-coated surface mounted on unmanned aircraft systems (UAS) sampling the lower atmosphere. Paul et al. (2004) placed rain splash collectors at 0, 30, and 100 cm above the soil surface, and both macroconidia and ascospores were recorded. Macroconidia were collected at all three heights for all rain events, but it is noted the spores collected at 100 cm may have splashed from both the upper leaves and from the ground. Rain shields were placed over each collector to minimize incident raindrops. A greater number of spores was captured at 0 and 30 cm, although, only 30 % less at 100 cm (Paul et al. 2004).

The forcible discharge of *F. graminearum* ascospores from perithecia (Trail and Common 2000) is associated with environmental conditions specific to release. The production of *F. graminearum* perithecia occurs between 16 and 31 °C (Tschanz et al. 1976), and ascospores are produced within perithecia between 13 and 33 °C with optimal temperatures between 25 and 28 °C (Ye 1980). *Fusarium graminearum* ascospores have been reported to launch 4.6 mm from perithecia at speeds of 34.5 m s^{-1} under controlled conditions (Trail et al. 2005). If there are 8 ascospores and their epiplasm within each ascus, a pressure of 1.54 MPa and an acceleration of 8.5 × 10^6 m s^{-2} or 870,000*g* would be required for *F. graminearum* ascospore discharge. This is one of the highest accelerations reported by a biological system (Trail et al. 2005). The asci inside perithecia act as a spore cannon with a relatively long range. Ascospores of *Podospora fimicola* have been documented to discharge distances up to 50 cm, but most species have ranges from 0.5 to 2.0 cm (Ingold 1967). Trail et al. (2005) reported *F. graminearum* ascospores to have a horizontal discharge distance ranging from 2.8 to 8.5 mm with the majority of ascospores discharging at distances between 4.5 and 6.5 mm. Other research in controlled conditions has reported *F. graminearum* ascospores to discharge at distances between <1 and 10 mm with an average distance of 4 mm (Schmale et al. 2005a). Once discharged, *F. graminearum* ascospores take less than 3 s to settle to a surface (Schmale et al. 2005a). Aylor et al. (1993) calculated relatively quiescent periods of air movement that lasted less than 1 s and occurred less than 8 % of the total time examined within grass canopies. Infrequent and short-term quiescent periods close to the ground within the canopy may prevent ascospores from settling out of the air, causing them to become airborne instead.

Under controlled conditions, Tschanz et al. (1975) reported peak capture of *F. graminearum* ascospores after an atmospheric moisture saturation deficit following a period of four or more hours of light. Tschanz et al. (1976) determined maximum discharge to be at 16.6 °C and to cease at 26 °C. Trail et al. (2002) found 8 to 30 % higher *F. graminearum* ascospore discharge at 20 °C under light and at relative humidity greater than 92 %. The trigger for *F. graminearum* ascospore discharge was reported to be turgor pressure generated by potassium ion flux (Trail et al. 2002). Although light may be linked to perithecial formation (Tschanz et al. 1976), light was not reported to be a requirement for *F. graminearum* ascospore discharge. However, an increase in ascospore discharge was reported under lighted conditions when compared with complete darkness (Trail et al. 2002).

Rainfall may affect the water potential of *F. graminearum*-infested crop residues and encourage germination. *F. graminearum* spore concentrations are reported to increase within the 4 days after rain events (Fernando et al. 2000; Inch et al. 2005; Paulitz 1996). Sung and Cook (1981) reported *F. graminearum* to germinate best at −1.4 bars (−0.14 MPa), the highest water potential tested, and showed less germination as the water potential decreased. Macroconidia germinated between −25 (−2.5 MPa) and −65 bars (−6.5 MPa). Perithecial production was maximum at −15 bars (−1.5 MPa), but discontinued below −50 bars (−5.0 MPa) (Sung and Cook 1981). Their conclusions state that *F. graminearum* macroconidia production lowered and perithecia production increased as water potential was lowered. Based on this conclusion, Sung and Cook (1981) suggested *F. graminearum* produces macroconidia in wet conditions and perithecia in dry conditions. Similar observations were made by Paulitz (1996) and Trail et al. (2002). *F. graminearum* ascospores were reported to lose the ability to germinate with exposure to low (<50 %) relative humidity suggesting limited infectivity after long-distance dispersal in these environmental conditions (Beyer and Verreet 2005). However, Beyer et al. (2005) found ascospores to require ≥53 % relative humidity while macroconidia required ≥80 % relative humidity for germination, an advantage of airborne ascospores over macroconidia in colonizing susceptible hosts.

Under natural conditions, Ayers et al. (1975) reported the maximum *F. graminearum* ascospore

collection from corn and wheat residue at temperatures of 13–22 °C and at 95–100 % relative humidity. Maldonado-Ramirez (2001) placed artificially inoculated corn stalk pieces directly in front of a Burkard sampler inlet on a rooftop to minimize impact from other inoculum sources. *F. graminearum* ascospores were reported to discharge from the corn stalk pieces predominantly during daylight hours when atmospheric turbulence is high, providing opportunity for spores to escape into the atmosphere (Maldonado-Ramirez 2001).

Reports by Maldonado-Ramirez (2001) of daylight release of ascospores contradict two previous reports of predominant ascospore release at night (Fernando et al. 2000; Paulitz 1996). Fernando et al. (2000) and Paulitz (1996) quantified aerial concentrations of ascospores, not necessarily discharged spores, using Burkard samplers placed within 1 and 1.5 m, respectively, from an artificially inoculated source. A Burkard can sample approximately 10 L min^{-1} of air. However, the results were unable to distinguish between newly discharged ascospores and those from atmospheric settling and washout by rainfall. Gravitational settling occurs after the termination of vertical atmospheric mixing, typically around sundown (Isard and Gage 2001; Levizzani et al. 1998). The results from Fernando et al. (2000) and Paulitz (1996) are reported to be relevant to ascospore release, but we suggest they more appropriately represent ascospore concentration measurements as they will be referred to here. Fernando et al. (2000) reported the highest concentration of *F. graminearum* ascospores (1,500 spores/m^3) occurred 1–3 days after rainfall and between 2000 and 0800 hours. Ascospore concentration was reported to increase between 1700 and 1800 hours with a peak at 1800 to 1900 hours (Fernando et al. 2000). Paulitz (1996) reported ascospore concentration to increase with a rise in relative humidity between 1600 and 1800 hours, peak before midnight, and to decline between 0600 and 0800 hours. The lowest concentrations were found between 0800 and 1600 hours. Higher ascospore concentrations were reported to occur 2–4 days after rainfall and with relative humidity <80 % (Paulitz 1996). Other research confirms higher ascospore concentrations following periods of rainfall (Rossi et al. 2002). While a portion of the ascospore concentrations reported may have originated from the artificially inoculated field plots, it is also likely the captured spores included those from background sources (i.e., atmospheric settling and washout originating from distant sources) as supported by recent data (Bergstrom and Waxman 2008; Keller et al. 2010; Keller et al. 2011). The topic of night-time ascospore collection will be further explored in Sect. 5.

When a large source of inoculum (225-m^2 inoculated area) was used, ascospore concentrations measured with rotorod-type samplers were reported to decrease by 50 % within 20–50 m from the source and 90 % within 60–70 m (de Luna et al. 2002). de Luna et al. (2002) explained spore gradients to reach an asymptote at longer distances and the remaining 10 % of spores may be in concentrations high enough to cause infection. This observation was in reference to the FHB risk to surrounding fields which has been confirmed by Francl et al. (1999). Francl et al. (1999) reported spore concentrations of *F. graminearum* on plants exposed in infested fields and at remote sites distances from any known sources of inoculum. Within infested fields, they collected 20 colony-forming units (CFU)/spike/day in infested fields and 4 CFU/spike/day at remote sites, strongly suggesting ascospore movement over mesoscale distances (Francl et al. 1999). A wide-scale NY survey of FHB spatial patterns in wheat fields identified the patterns to be random and concluded the majority of *F. graminearum* inoculum to be from atmospheric sources (Del Ponte et al. 2003).

Previous research has attempted to measure spore dispersal from an inoculum source by observing *F. graminearum* infection. Stack (1997) observed a 50 % decrease in incidence of FHB within 2–3 m of a 1-m^2 *F. graminearum*-infested source area and a 50 % decrease within 20–50 m of a 30-m^2 source area. Fernando et al. (1997) modeled the dispersal of inoculum by measuring disease gradients in two dimensions from 1-m^2 inoculum sources in the center of susceptible wheat cultivar plots. They found FHB infection to decrease by 50 % between 1 and 10 m and 90 % between 10 and 25 m from the center of the inoculum source. Disease gradients were also reported to be steeper on the upwind side of the center of the inoculated source than that of the downwind side (Fernando et al. 1997). The assumption made by Stack (1997) and Fernando et al. (1997) is that ascospores causing FHB infection originated from the established inoculum source and not from atmospheric settling or washout of spores originating distances from the

infection site. Reporting conclusions about spore dispersal from an inoculum source by measuring disease patterns may discount (1) the importance of airborne spores of long-distance origin, and (2) escape of spores from the canopy into the lower atmosphere for long-range movement.

Using a molecular fingerprinting technique, Miller et al. (1998) reported conventional tillage reduced kernel infection from their introduced *F. graminearum* strains. In the no-till plots, the introduced strains represented 79 % of all strains present in kernels harvested in the first season following introduction, 55 % in the second, and 46 % in the third. However, in the tilled plots, 20, 40, and 13 % of the introduced strains were present, respectively (Miller et al. 1998). It was proposed that the second year increase in the introduced inoculum in the tilled plots was the result of inoculum re-introduction from neighboring no-till plots where 55–79 % of inoculum was attributed to introduced strains, supporting the concept of aerial transport of ascospores.

Other research has been conducted using a PCR-based genotyping technique called amplified fragment length polymorphism (AFLP) to distinguish the contribution of artificially introduced inoculum from the background (naturally occurring) inoculum. Incidence of spike infection attributable to introduced *F. graminearum* strains averaged 15, 2, 1, and <1 % at 0, 3, 6, and ≥24 m from approximately 1-m^2 inoculum source areas (Keller et al. 2010). Infection decreased an average of 90 % between 3 and 6 m suggesting a steeper gradient than presented by Fernando et al. (1997) and Stack (1997). Infection gradients from small-area sources have been shown to be steeper than gradients from large-area sources (Gregory 1968). The low incidence of spike infection from the released *F. graminearum* isolates strongly suggests that contribution from background inoculum was greater than 80 %, and most likely from aerial sources. The reduction in introduced *F. graminearum* strains within a few meters from approximately 1-m^2 sources was confirmed using both large and small amounts of *F. graminearum*-infested residue and both susceptible and moderately resistant cultivars (Keller et al. 2011). These results suggest ascospores from the released isolates within the sources are vertically escaping the canopy and moving to distant locations rather than remaining in the local field and causing disease.

4 Atmospheric transport

Atmospheric turbulence affects the ascent of spores before they become airborne (Pedgley 1985). The planetary boundary layer (PBL) extends from the earth's surface to an altitude of a few hundred meters at night and 1–3 km during the day (Isard and Gage 2001). The surface boundary layer (SBL) is the lower 10–20 % of the PBL and contains large and variable vertical gradients of wind speed, temperature, and humidity (Isard and Gage 2001). Vertical mixing occurs in the PBL when the sun heats the surface of the earth, warming the air in contact with the surface. Warm air then rises carrying biota from near the surface aloft. Cooler air replaces the rising warm air to be subsequently warmed with contact to the earth's surface. Solar radiation and moderate wind speeds increase daytime convection while nocturnal cooling of surface air inhibits convection in the atmosphere (Sparks et al. 1985). Thermal convection promotes the mixing of surface air and spores with the air aloft (Sparks et al. 1985). Spores may be carried aloft to heights of several km through a succession of updrafts. These updrafts create a mixing layer which can be greater in the afternoon and warmer months and can be the shallowest on calm nights (Pedgley 1985). Organisms may successfully escape from the turbulent PBL where higher wind speeds and air flow disperse the biota long distances (Cox 1987). It is important to remember *F. graminearum* has been documented to discharge ascospores approximately 4–5 mm from perithecia (Schmale et al. 2005a; Trail et al. 2005) which may easily propel spores beyond the laminar layer surrounding crop residues or plant substrates and into the turbulent SBL (Isard and Gage 2001).

In 1921, slides were exposed from airplane windows and mechanical spore traps were attached to full-scale aircraft. During one of these sampling flights, a *Fusarium* spore was captured at an altitude of 3,200 m (Stakman et al. 1923) confirming the possibility that the forces of turbulence and convection are capable of transporting *F. graminearum* to great altitudes allowing long-distance transport. More recently, approximately 13,000 *F. graminearum* CFU were collected 60 m above the ground in collectors mounted on UAS during 158 flights in central NY (Maldonado-Ramirez et al. 2005). No significant difference was found between average day- and night-time collections. Flights with the greatest number of *F. graminearum*

CFU occurred between 0700 and 1000, at 1300 hours, and 2000 hours (Maldonado-Ramirez et al. 2005). The aerial density of *F. graminearum* has been reported to be 0–1,000 ascospores per 1,000 m^3 (<0.001–1.0 m^3) of air sampled with 30 ascospores per 100 m^3 (0.3 per m^3) typical (Maldonado-Ramirez 2001; Shields and Testa 1999). Less *F. graminearum* CFU were collected in the PBL during clear and rainy conditions than in cloudy conditions (Maldonado-Ramirez et al. 2005). Recent UAS flights have occurred to capture *Fusarium* spores for the purpose of improving UAS sampling efficiency (Keller and Shields 2013) and for determining the role large-scale atmospheric changes have on the long-distance transport of populations of *Fusarium* (Tallapragada et al. 2011).

Collection of greater numbers of viable *F. graminearum* spores in cloudy conditions may be due to spore exposure to UV radiation on clear days (Aylor 1986). The amount of UV resulting in 100 % *F. graminearum* ascospore mortality has been reported to be $\geq$19.8 MJ m^{-2} (Nita et al. 2007), but there is a lack of comprehensive information on *F. graminearum* UV sensitivity. Research on UV radiation effects on *V. inaequalis* and *Sclerotinia sclerotiorum* ascospores has been published. *V. inaequalis* ascospores typically release in cloudy conditions when low levels of UVB radiation are present; therefore, the mortality rate has been reported to be negligible (Aylor 1998). Caesar and Pearson (1983) observed 99 % mortality of *S. sclerotiorum* within 32 h when exposed to between 250 and 279 nm which is equivalent to $\sim$19.2 J m^{-2}; these are much lower UV levels than what *F. graminearum* has been shown to withstand.

In addition to mortality from UV, desiccation in a dry atmosphere may also be detrimental to ascospores moving long distances. Beyer and Verreet (2005) reported germination of *F. graminearum* ascospores to be hindered by low relative humidity within only a few minutes and viability to be hindered up to 21 days after discharge. They concluded long-distance ascospore dispersal will not be effective at relative humidities <50 % due to their inability to germinate (Beyer and Verreet 2005). Gilbert et al. (2008) reported at 15, 20, and 30 °C after 48 h, germination rate ranged from 74 to 85%, 52 to 72 %, and 13 to 47 %, respectively. Germination rate was highest at 90 % relative humidity (except at 30 °C) and lowest at 60 % relative humidity (Gilbert et al. 2008).

5 Deposition

There are two types of spore deposition. Dry deposition involves the use of air currents and gravitational settling, and wet deposition occurs when spores are carried by rain droplets to receptor crops (Aylor 1986). Washout of airborne spores may occur due to rain (Aylor 1998; Oke 1987). The contributions of wet and dry deposition are suggested to be more equal in number even though there are more dry hours than wet hours within an average season (Aylor 1986). It is possible wet deposition may provide a better environment for infection than dry deposition. Reis (1990) observed removal of spores from the air after four consecutive rainy days. Paulitz (1996) observed spores to be removed from the air during sequential rain events, and complete washout of spores during heavy rain events.

The settling of spores from the atmosphere may explain the higher percentages of deposition observed in the evenings by previous research. At night, an inversion layer coupled with little to no wind, can allow spores to settle (Oke 1987). Using Petri plates of selective media attached to a platform, *F. graminearum* CFU were collected mostly at night (82–94 %) during 8 h of night-time exposure. Most (87 %) *F. graminearum* CFU were deposited between 1200 and 0600 hours, with the majority between 0400 and 0600 hours (Schmale et al. 2006b). In 2003, 91 % of CFU deposited on media plates exposed from sunset to sunrise or from sunrise to sunset inside corn canopies were collected at night at average temperatures of 21 °C and total rainfall of 10.65 mm from July to September (Schmale and Bergstrom 2004). They found an average of 74 colonies deposited per plate at night compared with only 12 colonies during daytime deposition. Deposition was observed for 45 days and nights and night-time spore deposition was reported to be more prevalent than day-time deposition (Del Ponte et al. 2005). In research using a similar platform sampler, 76 % of the 1,031 *F. graminearum* CFU were collected at night, and with Petri plates mounted on a wind-driven sampler, 56 % of the 512 CFU were collected at night. Rain events and relative humidity over 90 % coincided with the greatest number of *F. graminearum* CFU collected (Del Ponte et al. 2005). These results confirm previous observations of night-time settling from 1999 to 2001

with averages of 0 to 70 colonies per plate (Maldonado-Ramirez 2001).

When vertical mixing stops, gravitational settling of the spores can begin. With a settling velocity between 1 and 2 mm s^{-1} in still air, discharged *F. graminearum* spores will settle to a surface between 3.1 and 3.6 s from perithecia on crop residue (Schmale et al. 2005a). Similarly, ascospores of *V. inaequalis* have been reported to settle approximately 2 mm s^{-1} in still air (Aylor 1998). Based on a settling velocity of 1 and 2 mm s^{-1}, *F. graminearum* spores will only have time (8.5 h.) to settle from the lower 30 to 60 m of the PBL. This leaves spores mixed in the atmosphere from 60 to 1,000 m above ground level to be re-mixed in the atmosphere at sunrise and transported horizontally for another 16 h before the next settling period at sundown the following day. If winds aloft are 20–30 km h^{-1}, spores will be moved between 170 and 255 km before the next gravitational settling period the following evening. Depending upon the resistance of *F. graminearum* ascospores to UV and desiccation, viable spores can be transported many hundreds of km in a few days and settle from the lower atmosphere in new geographical locations each evening.

An increase in ascospore concentration in and above crop canopies has been reported during night-time hours. In field experiments, Ayers et al. (1975) reported the maximum ascospore collection between 2100 and 0600 hours. Spore collection from Kramer-Collins samplers ranged from 106 to 2,825 ascospores/m^3/h in a corn plot and from 106 to 1,413 ascospores/m^3/h in a wheat plot (Ayers et al. 1975). Zinkernagel et al. (1997) reported ascospores mostly at night between 2300 and 0400 hours using a Burkard sampler in winter wheat plots. Average values of 5.1 to 13.1 CFUs were reported on spore trap media plates in naturally infected wheat fields during anthesis from 1700 to 0900 hours (Schaafsma et al. 2005). Rotorod spore samplers used by Inch et al. (2005) collected spores from artificially inoculated plots between 1800 and 0200 coinciding with lowest daily relative humidities. When using a Burkard sampler, an increase in spore concentration occurred between 1500 and 1700 hours with the highest ascospore concentration (15,233 m^{-3}) at 2100 hours and continuing until 0400 hours (Inch et al. 2005). Daily ascospore concentrations ranged from 0 to 214 m^{-3} and macroconidia concentrations ranged from 0 to 42 m^{-3}. This confirms previous reports of high night-time aerial concentrations of *F. graminearum* (Fernando et al. 2000; Paulitz 1996). Fernando et al. (2000) reported the highest concentration of *F. graminearum* spores (1,500 spores/m^3) occurred between 2000 and 0800 hours. Ascospore concentration was reported to increase between 1700 and 1800 hours with a peak at 1800–1900 hours (Fernando et al. 2000). Paulitz (1996) reported ascospore concentration to increase with a rise in relative humidity between 1600 and 1800 hours, peak before midnight, and to decline between 0600 and 0800 hours. The lowest concentrations were found between 0800 and 1600 hours.

Spatial patterns in wheat fields of viable spore deposition were reported to be random in the majority (93 %) of day and night-time periods (Schmale et al. 2005b). Turbulence in the SBL during day-time hours (Isard and Gage 2001; Levizzani et al. 1998; Sparks et al. 1985) most likely influences random deposition pattern. Aggregated patterns at night were reported (Schmale et al. 2005b) and are most likely due to more stable night-time settling spore events (Aylor 1986; Isard and Gage 2001). Other research has reported random spatial patterns of FHB incidence in rotational wheat fields; however, aggregated patterns were reported when large amounts of naturally overwintered corn residue were present (Del Ponte et al. 2003). This suggests a greater contribution of local inoculum to epidemics when large amounts of crop residue are present. These patterns assume spores are airborne as solitary entities; however, spore clustering has been shown to occur in urediniospores in approximately half of the total number of dispersal units (Ferrandino and Aylor 1987). It was estimated that the number of dispersed spores counted would have been 20–30 % greater if all spores had been dispersed and deposited individually.

Transport of *F. graminearum* in the atmosphere is responsible for initiating disease many km from inoculum sources. Wheat and barley are most susceptible from flowering through soft dough stages (Andersen 1948; Schroeder and Christensen 1963; Sutton 1982) and possibly into later stages of kernel development (Cowger et al. 2009; Del Ponte et al. 2007). Yoshida et al. (2007) reported mycotoxin accumulation even without the presence of visible FHB symptoms confirming previous research by Walker et al. (2001). Airborne and rain-splashed spores are deposited on susceptible hosts where they germinate and initiate infection. Detailed explanations of the infection process have been published (Bushnell et al. 2003; Sutton 1982).

Research was performed in New York and Virginia to determine the contribution of released isolates of *F. graminearum* from that of background isolates. Using AFLP, released isolates could be identified in heterogeneous populations of *F. graminearum* and tracked distances from source plots. Background inoculum accounted for more than 80 % of spike infection directly above and distances from source areas (Keller et al. 2010). This contribution may change from year-to-year based on local environmental conditions and amounts of local (within-field) inoculum present. In 21 winter wheat environments over two years, the addition of corn residue to microplots in rotated wheat fields in corn-production regions resulted in very little increase in FHB and DON above background levels in those fields suggesting that atmospheric spores were predominant (Bergstrom et al. 2010).

Fusarium graminearum spores were deposited on Petri plates of selective media placed in corn and wheat fields from 2002 to 2004. The high genetic diversity found in the *F. graminearum* populations from the plates (Schmale et al. 2006a) is consistent with reports of high genotypic diversity in populations collected from infected fields (Dusabenyagasani et al. 1999; Schilling et al. 1997; Walker et. al. 2001; Zeller et al. 2003). Zeller et al. (2004) surveyed the genetic structure of 523 *F. graminearum* isolates from 8 different populations from infected small grains across the USA. The results indicated the populations were genetically diverse and that extensive inter-population genetic exchange had occurred over geographic distances. They state that if pathogenicity and aggressiveness genes are just as diversely distributed within *F. graminearum* populations, then cultivars must be exposed to a representative *F. graminearum* population (Zeller et al. 2004).

6 Implications for management

An accurate evaluation of atmospheric inoculum sources is critical to successful integrated management strategies (Aylor 1999) and researchers have long debated the importance of local and atmospheric inoculum to epidemics from *F. graminearum* infection. During the infection window for the current season crop, both local and more distant sources have been shown to cause infection in susceptible crops when environmental conditions are favorable. In agricultural scale wheat plots following corn harvest, with and without plowing of corn residues, in 14 US environments from Nebraska to Vermont, Bergstrom et al. (2012) observed that plowing resulted in only small reductions in mycotoxin levels and suggested that DON accumulation was influenced more by infections from spores in the regional atmospheric population than from spores originating from within-field residue. Susceptible crops may be exposed to viable spores deposited from atmospheric sources during every rain event (wet deposition) and during every evening (gravitational settling, dry deposition). When a susceptible crop is present and environmental conditions are favorable, FHB may result from as little as one viable *F. graminearum* spore. Post-season establishment of the next year's local inoculum source is created from a combination of local and airborne spores settling from both wet and dry deposition on crop residue remaining in the field. The intensity of the disease depends on the amount of inoculum and/or the length of environmentally favorable conditions for spore germination and host penetration.

The current risk assessment model (De Wolf et al. 2003) is based on pre-flowering environmental conditions and prediction accuracy has been reported to be 80 %. Increasing the model's accuracy for post-flowering infection and DON production would allow additional assessments based on post-flowering environmental conditions. Local environmental conditions are appropriate for predicting incidence of disease whether it originated from local or distant inoculum sources.

Billions of dollars has been lost to epidemics of FHB caused predominantly by *F. graminearum* populations (Cowger and Sutton 2005; McMullen et al. 2012; McMullen et al. 1997; Windels 2000). Integrated management strategies have been suggested to minimize FHB epidemics by *F. graminearum*. Studies performed in North Dakota found using a combination of cultivar resistance, fungicides, and crop rotation, rather than a single strategy, reduced disease and mycotoxin levels while increasing yield and kernel test weight (McMullen et al. 2008). The purpose for conservation tillage (no-till or reduced tillage) is to prevent soil erosion by leaving crop residue on the soil surface after harvest. The increasing adoption of conservation tillage practices (Dill-Macky 2008; McMullen et al. 1997) creates an increase in the amount of crop residue available for *F. graminearum* infection.

Without the reduction in crop residue, populations of *F. graminearum* may proliferate and continue to provide both within-field and atmospheric sources for infection.

Utilizing moderately resistant cultivars and appropriately timed fungicides are still the most effective strategies against both within-field and atmospheric sources of inoculum. Research has shown large genotypic diversity among isolates of *F. graminearum* (Dusabenyagasani et al. 1999; Schilling et al. 1997; Schmale et al. 2006a; Walker et al. 2001; Zeller et al. 2003). Research in North Carolina found *F. graminearum* populations to be highly pathogenic and to produce high levels of DON indicating future threat of infection (Walker et al. 2001). Ward et al. (2008) reported the recent spread of isolates with the 3-acetyldeoxynivalenol chemotype of *F. graminearum* from eastern into western provinces of Canada suggesting long-distance dispersal by some means. A recent expansion of isolates of *F. graminearum* with the 15-acetyldeoxynivalenol chemotype into western Canada has also been reported (Mishra et al. 2009).

The aggressiveness and specific virulence of *F. graminearum* isolates from regional inoculum sources must be considered when developing wheat cultivars resistant to infection. It has been recommended that a variety of local isolates are needed to appropriately screen for *F. graminearum* resistance (Bai and Shaner 1996) and this is especially relevant if there is a known isolate(s) with increased infectivity and/or mycotoxin production capabilities. For example, resistance of wheat in Arkansas and Louisiana to both DON and nivalenol (NIV) chemotypes is now necessary after the discovery of the NIV chemotype of *F. graminearum* within the region (Horevaj et al. 2011). Cuomo et al. (2007) described sequence information relevant for future molecular research on the interaction of *F. graminearum* with plant hosts. Collaboration between the Broad Fungal Genome Initiative and the International *G. zeae* Genomics Consortium has resulted in a comparative genomics database of *Fusarium* spp. including the sequenced genome of *F. graminearum* PH-1 (NRRL 31084) (http://www.broadinstitute.org/annotation/genome/fusarium_group/MultiHome.html).

7 Concluding remarks

A review of the literature has revealed a broad understanding of the aerobiological mechanisms of *F. graminearum*. Research shows *F. graminearum* discharges spores during daylight time periods when the spores can be easily transported aloft with turbulence caused by vertical mixing or wind. Viable spores have been collected aloft regardless of the time of day/night or the time of year. Deposition of aerial spores occurs because of rain and gravitational settling in the night-time hours. We have identified two areas where research would contribute significantly to our broader understanding of these mechanisms. The first area would include the environmental conditions influencing the release of ascospores. Much of the current literature cited as having ascospore release information is actually more suited to citation of ascospore deposition. The second area would be an extensive study regarding the survivability of ascospores and the UV intensity encountered during aerial transport.

The quantitative contribution of long-distance sources versus local sources of *F. graminearum* to regional epidemics is less understood. An improved knowledge of inoculum magnitude and timing of arrival will facilitate an understanding of how quickly and by what atmospheric pathways new genetic variants of the pathogen with changed mycotoxin profiles, virulence patterns, or with resistance to fungicides could be disseminated within and between regions. Genetic evaluation of fungal isolates causing local disease epidemics indicates a very diverse genetic background and strongly supports the concept of consistent mixing from geographically diverse sources. Crop breeders should select resistant cultivars based on screening against a set of fungal isolates that represent the range of virulence observed in fungal populations across a broader geographic region. Crops are constantly exposed to both local and aerial sources of inoculum, so the focus of FHB risk prediction on local environmental conditions that directly favor infection is appropriate.

The last few decades of *F. graminearum* research have validated the conclusions of Johnson and Dickson (1921) when they warned producers of regional epidemics caused by the movement of airborne *F. graminearum* spores in the 1920s. An increased understanding of the aerobiology of *F. graminearum* contributes to the overall knowledge of plant pathogen transport in the atmosphere. Aerobiology continues to play a role in modeling efforts and biosecurity protocols for the protection of agricultural crops.

References

Andersen, A. L. (1948). The development of *Gibberella zeae* head blight of wheat. *Phytopathology, 38*, 599–611.

Atanasoff, D. (1920). Fusarium blight (scab) of wheat and other cereals. *Journal of Agricultural Research, 20*, 1–41.

Ayers, J. E., Pennypacker, S. P., Nelson, P. E., Pennypacker, B. W. (1975). Environmental factors associated with airborne ascospores of *Gibberella zeae* in corn and wheat fields. *Phytopathology*, *65*, 835 (Abstr.).

Aylor, D. E. (1975). Deposition of particles in a plant canopy. *Journal of Applied Meteorology, 14*, 52–57.

Aylor, D. E. (1986). A framework for examining inter-regional aerial transport of fungal spores. *Agricultural and Forest Meteorology, 38*, 263–288.

Aylor, D. E. (1990). The role of intermittent wind in the dispersal of fungal pathogens. *Annual review of Phytopathology, 28*, 73–92.

Aylor, D. E. (1998). The aerobiology of apple scab. *Plant Disease, 82*, 838–849.

Aylor, D. (1999). Biophysical scaling and the passive dispersal of fungus spores: relationship to integrated pest management strategies. *Agricultural and Forest Meteorology, 97*, 275–292.

Aylor, D. E., & Taylor, G. S. (1983). Escape of *Peronospora tabacina* spores from a field of diseased tobacco plants. *Phytopathology, 73*, 525–529.

Aylor, D. E., Wang, Y., & Miller, D. R. (1993). Intermittent wind close to the ground within a grass canopy. *Boundary-Layer Meteorology, 66*, 427–448.

Bai, G., & Shaner, G. (1994). Scab of wheat: Prospects for control. *Plant Disease, 78*, 760–766.

Bai, G.-H., & Shaner, G. (1996). Variation in *Fusarium graminearum* and cultivar resistance to wheat scab. *Plant Disease, 80*, 975–979.

Bai, G., & Shaner, G. (2004). Management and resistance in wheat and barley to Fusarium head blight. *Annual review of Phytopathology, 42*, 135–161.

Baird, R. E., Mullinix, B. G., Peery, A. B., & Lang, M. L. (1997). Diversity and longevity of the soybean residue mycobiota in a no-tillage system. *Plant Disease, 81*, 530–534.

Bergstrom, G.C., Cummings, J.A., Waxman, K.D., Bradley, C.A., Hazelrigg, A.L., Hershman, D.E., Nagelkirk, M., Sweets, L.E., Wegulo, S.N. (2012). Effects of local corn debris management on FHB and DON levels in fourteen U.S. wheat environments in 2011 and 2012. In *Proceedings of the 2012 National Fusarium Head Blight Forum* (pp. 5–6). Orlando, FL.

Bergstrom, G. C., Waxman, K. D. (2008). Microplots in commercial wheat fields for quantifying the local contribution of *Gibberella zeae* from natural corn debris to Fusarium head blight and deoxynivalenol accumulation. In *Proceedings of the 2008 National Fusarium Head Blight Forum* (pp. 6–8). Indianapolis, IN.

Bergstrom, G. C., Waxman, K. D., Schmale, D. G., III, Bradley, C. A., Sweets, L. E., Wegulo, S. N., Keller, M. D. (2010). Effects of within-field corn debris in microplots on FHB and DON in eleven U.S. wheat environments in 2010. In *Proceedings of the 2010 National Fusarium Head Blight Forum* (pp. 69–70). Milwaukee, WI.

Beyer, M., & Verreet, J. A. (2005). Germination of *Gibberella zeae* ascospores as affected by age of spores after discharge and environmental factors. *European Journal of Plant Pathology, 111*, 381–389.

Beyer, M., Verreet, J. A., & Ragab, W. S. M. (2005). Effect of relative humidity on germination of ascospores and macroconidia of *Gibberella zeae* and deoxynivalenol production. *International Journal of Food Microbiology, 98*, 233–240.

Booth, C. (1971). *The genus Fusarium*. Farnham Royal: Commonwealth Agricultural Bureaux for the Commonwealth Mycological Institute.

Bushnell, W. R., Hazen, B. E., & Pritsch, C. (2003). Histology and physiology of Fusarium head blight. In K. J. Leonard & W. R. Bushnell (Eds.), *Fusarium head blight of wheat and barley* (pp. 44–83). St. Paul, MN: APS Press.

Caesar, A. J., & Pearson, R. C. (1983). Environmental factors affecting survival of ascospores of *Sclerotinia sclerotiorum*. *Phytopathology, 73*, 1024–1030.

Cowger, C., Patton-Özkurt, J., Brown-Guedira, G., & Perugini, L. (2009). Post-anthesis moisture increased Fusarium head blight and deoxynivalenol levels in North Carolina winter wheat. *Phytopathology, 99*, 320–327.

Cowger, C., Sutton, A. L. (2005). The Southeastern U.S. Fusarium head blight epidemic of 2003. *Plant Health Progress*. doi:10.1094/PHP-2005-1026-01-RS.

Cox, C. S. (1987). *The aerobiological pathway of microorganisms*. Chichester: John Wiley & Sons.

Cuomo, C. A., Güldener, U., Xu, J., Trail, F., Turgeon, B. G., Di Pietro, A., et al. (2007). The *Fusarium graminearum* genome reveals a link between localized polymorphism and pathogen specialization. *Science, 317*, 1400–1402.

de Luna, L., Bujold, I., Carisse, O., & Paulitz, T. C. (2002). Ascospore gradients of *Gibberella zeae* from overwintered inoculum in wheat fields. *Canadian Journal of Plant Pathology, 24*, 457–464.

De Wolf, E. D., Madden, L. V., & Lipps, P. E. (2003). Risk assessment models for wheat Fusarium head blight epidemics based on within-season weather data. *Phytopathology, 93*, 428–435.

Del Ponte, E. M., Fernandes, J. M. C., & Bergstrom, G. C. (2007). Influence of growth stage on Fusarium head blight and deoxynivalenol production in wheat. *Journal of Phytopathology, 155*, 577–581.

Del Ponte, E. M., Fernandes, J. M. C., & Pierobom, C. R. (2005). Factors affecting density of airborne *Gibberella zeae* inoculum. *Fitopatologia Brasileira, 30*, 55–60.

Del Ponte, E. M., Shah, D. A., & Bergstrom, G. C. (2003). Spatial patterns of Fusarium head blight in New York wheat fields suggest role of airborne inoculum. *Plant Health Progress,*. doi:10.1094/PHP-2003-0418-01-RS.

DeLeon-Rodriguez, N., Lathem, T. L., Rodriguez-R, L. M., Barazesh, J. M., Anderson, B. E., Beyersdorf, A. J., et al. (2013). Microbiome of the upper troposphere: species composition and prevalence, effects of tropical storms, and atmospheric implications. *Proceedings of the National Academy of Sciences, USA, 110*, 2575–2580.

Dill-Macky, R. (2008). Cultural control practices for Fusarium head blight: problems and solutions. In *Cereal research communications 3rd international FHB symposium*. Szeged, Hungary.

Dill-Macky, R., & Jones, R. K. (2000). The effect of previous crop residue and tillage on Fusarium head blight of wheat. *Plant Disease, 84*, 71–76.

Dusabenyagasani, M., Dostaler, D., & Hamelin, R. C. (1999). Genetic diversity among *Fusarium graminearum* strains from Ontario and Quebec. *Canadian Journal of Plant Pathology, 21*, 308–314.

Fernando, W. G. D., Miller, J. D., Seaman, W. L., Seifert, K., & Paulitz, T. C. (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, W. G. D., Paulitz, T. C., Seaman, W. L., Dutilleul, P., & Miller, J. D. (1997). Head blight gradients caused by *Gibberella zeae* from area sources of inoculum in wheat field plots. *Phytopathology, 87*, 414–421.

Ferrandino, F. J., & Aylor, D. E. (1987). Relative abundance and deposition gradients of clusters of urediniospores of *Uromyces phaseoli*. *Phytopathology, 77*, 107–111.

Francl, L., Shaner, G., Bergstrom, G., Gilbert, J., Pederson, W., Dill-Macky, R., et al. (1999). Daily inoculum levels of *Gibberella zeae* on wheat spikes. *Plant Disease, 83*, 662–666.

Gilbert, J., & Fernando, W. G. D. (2004). Epidemiology and biological control of *Gibberella zeae/Fusarium graminearum*. *Canadian Journal of Plant Pathology, 26*, 464–472.

Gilbert, J., & Tekauz, A. (2000). Review: recent developments in research on Fusarium head blight of wheat in Canada. *Canadian Journal of Plant Pathology, 22*, 1–8.

Gilbert, J., Woods, S. M., & Kromer, U. (2008). Germination of ascospores of *Gibberella zeae* after exposure to various levels of relative humidity and temperature. *Phytopathology, 98*, 504–508.

Goswami, R. S., & Kistler, H. C. (2004). Heading for disaster: *Fusarium graminearum* on cereal crops. *Molecular Plant Pathology, 5*, 515–525.

Gregory, P. H. (1968). Interpreting plant disease dispersal gradients. *Annual review of Phytopathology, 6*, 189–212.

Gregory, P. H. (1973). *The microbiology of the atmosphere*. New York: John Wiley and Sons.

Guenther, J. C., & Trail, F. (2005). The development and differentiation of *Gibberella zeae* (anamorph: *Fusarium graminearum*) during colonization of wheat. *Mycologia, 97*, 229–237.

Hoffer, G. N., Johnson, A. G., & Atanasoff, D. (1918). Corn-rootrot and wheatscab. *Journal of Agricultural Research, 13*, 611–612.

Horevaj, P., Gale, L. R., & Milus, E. A. (2011). Resistance in winter wheat lines to initial infection and spread within spikes by deoxynivalenol and nivalenol chemotypes of *Fusarium graminearum*. *Plant Disease, 95*, 31–37.

Inch, S., Fernando, D., & Gilbert, J. (2005). Seasonal and daily variation in the airborne concentration of *Gibberella zeae* (Schw.) Petch spores in Manitoba. *Canadian Journal of Plant Pathology, 27*, 357–363.

Ingold, C. T. (1967). Liberation mechanisms of fungi. In *Airborne microbes: Seventeenth symposium of the society for general microbiology held at the Imperial College*. London: Cambridge University Press.

Isard, S. A., & Gage, S. H. (2001). *Flow of life in the atmosphere*. East Lansing: Michigan State University Press.

Johnson, A.G., Dickson, J. G. (1921). Wheat scab and its control. *USDA Farmers Bulletin* (1224).

Keller, M. D., & Shields, E. J. (2013). Aerobiological sampling efficiency of media-containing Petri plates for use in lower atmosphere spore collection. *Aerobiologia,*. doi:10.1007/s10453-013-9306-2.

Keller, M. D., Thomason, W. E., & Schmale, D. G, I. I. I. (2011). The spread of a released clone of *Gibberella zeae* from different amounts of infested corn residue. *Plant Disease, 95*, 1458–1464.

Keller, M. D., Waxman, K. D., Bergstrom, G. C., & Schmale, D. G, I. I. I. (2010). Local distance of wheat spike infection by released clones of *Gibberella zeae* disseminated from infested corn residue. *Plant Disease, 94*, 1151–1155.

Khonga, E. B., & Sutton, J. C. (1988). Inoculum production and survival of *Gibberella zeae* in maize and wheat residue. *Canadian Journal of Plant Pathology, 10*, 232–239.

Levizzani, V., Georgiadis, T., & Isard, S. A. (1998). Meteorological aspects of the aerobiological pathway. In P. Mandrioli, P. Comtois, & V. Levizzani (Eds.), *Methods of aerobiology*. Bologna, Italy: Associazione italiana di aerobiologia.

Maldonado-Ramirez, S. L. (2001). *Aerobiology of the wheat scab fungus, Gibberella zeae: Discharge, atmospheric dispersal, and deposition of ascospores*. Ph.D. dissertation. Ithaca: Cornell University.

Maldonado-Ramirez, S. L., Schmale, D. G, I. I. I., Shields, E. J., & Bergstrom, G. C. (2005). The relative abundance of viable spores of *Gibberella zeae* in the planetary boundary layer suggests the role of long-distance transport in regional epidemics of Fusarium head blight. *Agricultural and Forest Meteorology, 132*, 20–27.

Markell, S. G., & Francl, L. J. (2003). Fusarium head blight inoculum: Species prevalence and *Gibberella zeae* spore type. *Plant Disease, 87*, 814–820.

Martinelli, J., Bocchese, C., Gale, L., Weiping, X., ODonnell, K., Kistler, H. (2001). Soybean is a host for *Fusarium graminearum*. In *Proceedings of the 2001 National Fusarium Head Blight Forum* (p. 136). Erlanger, KY.

McMullen, M., Bergstrom, G., De Wolf, E., Dill-Macky, R., Hershman, R., Shaner, G., et al. (2012). A unified effort to fight an enemy of wheat and barley: Fusarium head blight. *Plant Disease, 96*, 1712–1728.

McMullen, M., Halley, S., Schatz, B., Meyer, S., Jordahl, J., Ransom, J. (2008). Integrated strategies for Fusarium head blight management in the United States. In *Cereal research communications 3rd international FHB symposium*. Szeged, Hungary.

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

McMullen, M. P., & Stack, R. W. (1983). *Fusarium* species associated with grassland soils. *Canadian Journal of Botany, 61*, 2530–2538.

Miller, J. D., Culley, J., Fraser, K., Hubbard, S., Meloche, F., Ouellet, T., et al. (1998). Effect of tillage practice on Fusarium head blight of wheat. *Canadian Journal of Plant Pathology, 20*, 95–103.

Mishra, P. K., Tewari, J. P., Turkington, T. K., & Clear, R. M. (2009). Genetic evidence for a recent geographic expansion of 15-acetyldeoxynivalenol chemotypes of *Fusarium*

graminearum in Canada. *Canadian Journal of Plant Pathology, 31*, 468–474.

Munkvold, G. P. (2003). Epidemiology of *Fusarium* diseases and their mycotoxin in maize ears. *European Journal of Plant Pathology, 109*, 705–713.

Nita, M., De Wolf, E., Isard, S. (2007). Effects of solar radiation on the viability of *Gibberella zeae* ascospores. In *Proceedings of the 2007 National Fusarium Head Blight Forum* (p. 107). Kansas City, MO.

Nita, M., De Wolf, E., Madden, L., Paul, P., Shaner, G., Adhikari, T., Ali, S., Stein, J., Osborne, L. (2006). Effect of corn residue level on disease intensity of Fusarium head blight (FHB) and on deoxynivalenol (DON) concentration: A multi-state field study. *Phytopathology*, *96*, S85. (Abstr.).

Oke, T. R. (1987). *Boundary layer climates* (2nd ed.). Cambridge: Cambridge University Press.

Osborne, L. E., & Stein, J. M. (2007). Epidemiology of *Fusarium* head blight on small-grain cereals. *International Journal of Food Microbiology, 119*, 103–108.

Parry, D. W., Jenkinson, P., & McLeod, L. (1995). *Fusarium* ear blight (scab) in small grain cereals—a review. *Plant Pathology, 44*, 207–238.

Paul, P. A., El-Allaf, S. M., Lipps, P. E., & Madden, L. V. (2004). Rain splash dispersal of *Gibberella zeae* within wheat canopies in Ohio. *Phytopathology, 94*, 1342–1349.

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

Pedgley, D. E. (1985). Concepts in atmospheric science as they relate to the movement of biotic agents. In Mackenzie, Barfield, Kennedy, & Berger (Eds.) *The movement and dispersal of agriculturally important biotic agents* (pp. 175–178). Baton Rouge, Louisiana: Claitors Publishing Division.

Pereyra, S. A., & Dill-Macky, R. (2008). Colonization of the residue of diverse plant species by *Gibberella zeae* and their contribution to Fusarium head blight inoculum. *Plant Disease, 92*, 800–807.

Pereyra, S. A., Dill-Macky, R., & Sims, A. L. (2004). Survival and inoculum production of *Gibberella zeae* in wheat residue. *Plant Disease, 88*, 724–730.

Pestka, J. J. (2007). Deoxynivalenol: Toxicity, mechanisms, and animal health risks. *Animal Feed Science and Technology, 137*, 283–298.

Pestka, J. J. (2010). Deoxynivalenol: Mechanisms of action, human exposure, and toxicological relevance. *Archives of Toxicology, 84*, 663–679.

Pestka, J. J., & Smolinski, A. T. (2005). Deoxynivalenol: Toxicology and potential effects on humans. *Journal of Toxicology & Environmental Health Part B: Critical Reviews, 8*, 39–69.

Rabb, R. L. (1985). Conceptual bases to develop and use information on the movement and dispersal of biotic agents in agriculture. In Mackenzie, Barfield, Kennedy, & Berger (Eds.) *The movement and dispersal of agriculturally important biotic agents* (pp. 5–34). Baton Rouge, LA: Claitors Publishing Division.

Reis, E. M. (1990). Effect of rain and relative humidity on the release of ascospores and on the infection of wheat heads by *Gibberella zeae*. *Fitopatologia Brasileira, 15*, 339–343.

Roelfs, A. P. (1985). Epidemiology in North America. In W. R. Bushnell & A. P. Roelfs (Eds.), *The cereal rusts* (Vol. II, pp. 403–434). London: Academic Press.

Rossi, V., Languasco, E., Pattori, E., & Giosuè, S. (2002). Dynamics of airborne *Fusarium* macroconidia in wheat fields naturally affected by head blight. *Journal of Plant Pathology, 84*, 53–64.

Schaafsma, A. W., Tamburic-Ilinic, L., & Hooker, D. C. (2005). Effect of previous crop, tillage, field size, adjacent crop, and sampling direction on airborne propagules of *Gibberella zeae*/*Fusarium graminearum*, fusarium head blight severity, and deoxynivalenol accumulation in winter wheat. *Canadian Journal of Plant Pathology, 27*, 217–224.

Schilling, A. G., Miedaner, T., & Geiger, H. H. (1997). Molecular variation and genetic structure in field populations of *Fusarium* species causing head blight in wheat. *Cereal Research Communications, 25*, 549–554.

Schmale, D. G, I. I. I., Arnsten, Q. A., & Bergstrom, G. C. (2005a). The forcible discharge distance of ascospores of *Gibberella zeae*. *Canadian Journal of Plant Pathology, 27*, 376–382.

Schmale, D. G, I. I. I., & Bergstrom, G. C. (2004). Spore deposition of the ear rot pathogen, *Gibberella zeae*, inside corn canopies. *Canadian Journal of Plant Pathology, 26*, 591–595.

Schmale, D. G., III, Bergstrom, G. C. (2007). The aerobiology and population genetic structure of *Gibberella zeae*. *Plant Health Progress*. doi:10.1094/PHP-2007-0726-04-RV.

Schmale, D. G, I. I. I., Leslie, J. F., Zeller, K. A., Saleh, A. A., Shields, E. J., & Bergstrom, G. C. (2006a). Genetic structure of atmospheric populations of *Gibberella zeae*. *Phytopathology, 96*, 1021–1026.

Schmale, D. G, I. I. I., Shah, D. A., & Bergstrom, G. C. (2005b). Spatial patterns of viable spore deposition of *Gibberella zeae* in wheat fields. *Phytopathology, 95*, 472–479.

Schmale, D. G, I. I. I., Shields, E. J., & Bergstrom, G. C. (2006b). Night-time spore deposition of the Fusarium head blight pathogen, *Gibberella zeae*, in rotational wheat fields. *Canadian Journal of Plant Pathology, 28*, 100–108.

Schroeder, H. W., & Christensen, J. J. (1963). Factors affecting resistance of wheat to scab caused by *Gibberella zeae*. *Phytopathology, 53*, 831–838.

Shaner, G. (2003). Epidemiology of Fusarium head blight of small grain cereals in North America. In K. J. Leonard & W. R. Bushnell (Eds.), *Fusarium head blight of wheat and barley* (pp. 84–119). St. Paul, MN: APS Press.

Shields, D. E., & Testa, A. M. (1999). Fall migratory flight initiation of the potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae): Observations in the lower atmosphere using remote piloted vehicles. *Agricultural and Forest Meteorology, 97*, 317–330.

Snijders, C. H. A. (1990). Fusarium head blight and mycotoxin contamination of wheat, a review. *Netherlands Journal of Plant Pathology, 96*, 187–198.

Snyder, W. C., & Nash, S. M. (1968). Relative incidence of *Fusarium* pathogens of cereals in rotation plots at Rothamsted. *Transactions of the British Mycological Society, 51*, 417–425.

Sparks, A. N., Westbrook, J. K., Wolf, W. W., Pair, S. D., Raulston, J. R. (1985). Atmospheric transport of biotic agents on a local scale. In Mackenzie, Barfield, Kennedy,

and Berger (Eds.) *The movement and dispersal of agriculturally important biotic agents* (pp. 203–217). Baton Rouge, LA: Claitors Publishing Division.

Stack, R. (1989). A comparison of the inoculum potential of ascospores and conidia of *Gibberella zeae*. *Canadian Journal of Plant Pathology, 11*, 137–142.

Stack, R. W. (1997). Gradients of Fusarium head blight in wheat along transects away from a concentrated source of *Gibberella zeae* ascospore inoculum. In *Proceedings of the National Fusarium Head Blight Forum*. St. Paul, MN.

Stack, R. W. (1999). Return of an old problem: Fusarium head blight of small grains. *Plant Health Progress,*. doi:10.1094/PHP-2000-0622-01-RV.

Stakman, E. C., & Harrar, J. G. (1957). *Principles of plant pathology*. New York: Ronald Press.

Stakman, E. C., Henry, A. W., Curran, G. C., & Christopher, W. N. (1923). Spores in the upper air. *Journal of Agricultural Research, 24*, 599–606.

Stein, J. M., Osborne, L. E., Bondalapati, K. D., Glover, K. D., & Nelson, C. A. (2009). Fusarium head blight severity and deoxynivalenol concentration in wheat in response to *Gibberella zeae* inoculum concentration. *Phytopathology, 99*, 759–764.

Sung, J.-M., & Cook, R. J. (1981). Effect of water potential on reproduction and spore germination by Fusarium roseum 'Graminearum', 'Culmorum', and 'Avenaceum'. *Phytopathology, 71*, 499–504.

Sutton, J. C. (1982). Epidemiology of wheat head blight and maize ear rot caused by *Fusarium graminearum*. *Canadian Journal of Plant Pathology, 4*, 195–209.

Tallapragada, P., Ross, S. D., & Schmale, D. G, I. I. I. (2011). Lagrangian coherent structures are associated with fluctuations in airborne microbial populations. *Chaos, 21*, 033122.

Teich, A. H., & Hamilton, J. R. (1985). Effect of cultural practices, soil phosphorus, potassium, and pH on the incidence of Fusarium head blight and deoxynivalenol levels in wheat. *Applied and Environmental Microbiology, 49*, 1429–1431.

Teich, A. H., & Nelson, K. (1984). Survey of *Fusarium* head blight and possible effects of cultural practices in wheat fields in Lambton County in 1983. *Canadian Plant Disease Survey, 64*, 11–13.

Tekauz, A., McCallum, B., & Gilbert, J. (2000). Review: Fusarium head blight of barley in western Canada. *Canadian Journal of Plant Pathology, 22*, 9–16.

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

Trail, F., Gaffoor, I., & Vogel, S. (2005). Ejection mechanics and trajectory of the ascospores of *Gibberella zeae* (anamorph *Fusarium graminearum*). *Fungal Genetics and Biology, 42*, 528–533.

Trail, F., Xu, H., Loranger, R., & Gadoury, D. (2002). Physiological and environmental aspects of ascospore discharge in *Gibberella zeae* (anamorph *Fusarium graminearum*). *Mycologia, 94*, 181–189.

Tschanz, A. T., Horst, R. K., & Nelson, P. E. (1975). Ecological aspects of ascospore discharge in *Gibberella zeae*. *Phytopathology, 65*, 597–599.

Tschanz, A. T., Horst, R. K., & Nelson, P. E. (1976). The effect of environment on sexual reproduction of *Gibberella zeae*. *Mycologia, 68*, 327–340.

US Food and Drug Administration guidance for industry and FDA: advisory levels for deoxynivalenol (DON) in finished wheat products for human consumption and grains and grain by-products used for animal feed. (2010). http://www.fda.gov/Food/GuidanceComplianceRegulatoryInformation/GuidanceDocuments/NaturalToxins/ucm120184.htm.

Walker, S. L., Leath, S., Hagler, W. M, Jr, & Murphy, J. P. (2001). Variation among isolates of *Fusarium graminearum* associated with Fusarium head blight in North Carolina. *Plant Disease, 85*, 404–410.

Ward, T. J., Clear, R. M., Rooney, A. P., O'Donnell, K., Gaba, D., Patrick, S., et al. (2008). An adaptive evolutionary shift in Fusarium head blight pathogen populations is driving the rapid spread of more toxigenic *Fusarium graminearum* in North America. *Fungal Genetics and Biology, 45*, 473–484.

Weise, M. V. (1987). Scab (head blight). In *Compendium of wheat diseases* 2nd edn. (pp. 16–18), St. Paul, MN: American Phytopathological Society.

Windels, C. E. (2000). Economic and social impacts of Fusarium head blight: Changing farms and rural communities in the northern Great Plains. *Phytopathology, 90*, 17–21.

Ye, H. Z. (1980). On the biology of the perfect stage of *Fusarium graminearum* Schw. *Acta Phytophylacica Sinica, 7*, 35–42.

Yoshida, M., Kawada, N., & Nakajima, T. (2007). Effect of infection timing on Fusarium head blight and mycotoxin accumulation in open- and closed-flowering barley. *Phytopathology, 97*, 1054–1062.

Zeller, K. A., Bowden, R. L., & Leslie, J. F. (2003). Diversity of epidemic populations of *Gibberella zeae* from small quadrats in Kansas and North Dakota. *Phytopathology, 93*, 874–880.

Zeller, K. A., Bowden, R. L., & Lestlie, J. F. (2004). Population differentiation and recombination in wheat scab populations of *Gibberella zeae* from the United States. *Molecular Ecology, 13*, 563–571.

Zinkernagel, V., Adolf, B., & Haberneyer, J. (1997). The spread of *Fusarium* species from the above ground level to the ears of wheat. *Cereal Research Communications, 25*, 677–679.