

Daily and seasonal dynamics of airborne spores of *Fusarium graminearum* and other *Fusarium* species sampled over wheat plots

W.G.D. Fernando, J.D. Miller, W.L. Seaman, K. Seifert, and T.C. Paulitz

Abstract: Spores were sampled during 2 years over wheat plots at Ottawa, Ontario. Plots were treated with corn colonized with *Gibberella zeae* (Schwein.) Petch (anamorph *Fusarium graminearum* Schwabe). In 1994, viable spores were sampled with four Burkard high-throughput jet samplers. *Gibberella zeae* ascospores were recovered mostly at night and showed four main release events during the 20-day sampling period, 1–3 days after rain events. Highest density of *G. zeae* spores (1500 spores/m³) were sampled 1.5 m away from the inoculum source, with fewer spores 5 m away. Recovery of other *Fusarium* species was sporadic. For all species, there were no statistical differences among the daily sampling times, although for most species, morning counts were the lowest. Other *Fusarium* species detected, in decreasing order of spore density, were *F. crookwellense*, *F. sporotrichioides*, *F. moniliforme*, *F. equiseti*, *F. subglutinans*, and *F. culmorum*. Most spore release events did not correlate with rainfall events. In 1995, a Burkard continuous 7-day spore sampler was used to investigate the release of ascospores and macroconidia of *G. zeae*. Ascospores, but not macroconidia, showed a daily periodicity. Daily average densities of macroconidia were an order of magnitude less than ascospores. Ascospore release was correlated with rainfall events and the time of day.

Key words: spore sampling, *Gibberella zeae*, *Fusarium graminearum*, *Fusarium* sp. ascospores, macroconidia.

Résumé : Les auteurs ont recueilli des échantillons de spores au dessus de champs de blé, au cours de deux années, à Ottawa, en Ontario. Les parcelles ont reçu du maïs colonisé avec le *Gibberella zeae* (Schwein.) Petch (l'anamorphe du *Fusarium gramineorum* Schwabe). En 1994, ils ont capté les spores viables avec quatre échantillonneurs 'Burkard high-throughput' à jet. Les ascospores du *G. zeae* ont été captées surtout la nuit et montrent 4 évènements principaux d'émission au cours de la période de 20 jours d'échantillonnage, 1–3 jours après une pluie. Les plus fortes densités de spores du *G. zeae* (1500 spores/m³) ont été obtenues à une distance de 1,5 m de la source d'inoculum, les spores étant moins nombreuses à 5 m. On retrouve sporadiquement d'autres espèces de *Fusarium*. Chez toutes ces espèces, il n'y a pas de différences statistiques entre les moments d'échantillonnage quotidien, bien que chez la plupart des espèces les mesures du matin soient les plus faibles. Les autres espèces de *Fusarium* récoltées, en ordre décroissant d'abondance, sont: *F. crookwellense*, *F. sporotrichioides*, *F. moniliforme*, *F. equisetii*, *F. subglutinans*, et *F. culmorum*. La plupart des émissions de spores ne sont pas corrélées avec l'avènement de précipitations. En 1995, les auteurs ont utilisé un échantillonneur Burkard en continue, pendant 7 jours, afin d'examiner l'émission des ascospores et des macroconidies du *G. zeae*. Les ascospores, mais non les macroconidies, montrent une périodicité quotidienne. Les densités quotidiennes moyennes sont d'un ordre de grandeur plus bas que celles des ascospore. L'émission des ascospore est corrélée avec l'avènement de précipitations et le moment du jour.

Mots clés : échantillonnage de spores, *Gibberella zeae*, *Fusarium gramineorum*, *Fusarium* sp., ascospores, macroconidies.

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Introduction

Fusarium head blight of wheat and gibberella ear rot of corn are important diseases in eastern Canada. The causal agent *Gibberella zeae* (Schwein.) Petch (anamorph *Fusar-*

ium graminearum Schwabe, group 2) produces mycotoxins in the grain, particularly deoxynivalenol (DON), and in corn, zearalenone (Miller 1994). Although epidemics are sporadic (Sutton 1982), economic loss can be significant. Mycotoxins are of concern to grain growers, livestock producers, and ce-

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real processors (Trenholm et al. 1983).

Gibberella zeae forms perithecia and sporodochia on host tissue and debris. The perithecia forcibly discharge ascospores, and the sporodochia give rise to macroconidia. The pathogen is known to overwinter in crop debris in the field and to produce perithecia and sporodochia the following growing season (Reis 1990; Fernandez and Fernandes 1990). Under favorable weather conditions, the spores infect the heads and other parts of the wheat plant, and the fungus produces pinkish mycelia and orange-colored sporodochia on the surface of host tissues. Although much of the life cycle is known (Parry et al. 1995), knowledge of the microclimate factors influencing spore release and dispersal is limited. However, more associations have been made with macroclimatic factors. In Canada, Sutton (1982) reported that epidemics of wheat scab were associated with years of high rainfall. In Manitoba, abnormally high rainfall during the wheat growing seasons of 1984 and 1985 resulted in a high incidence of *Fusarium*-infected wheat (Abramson et al. 1987). During 1993 and 1994, years with higher than normal summer rainfall, an extensive epidemic occurred on wheat in the upper midwest of the U.S. and the Red River Valley (McMullen et al. 1997). In 1996, an epidemic on soft white winter wheat in southern Ontario resulted in losses of over 80% (Schaafsma et al. 1998). Rainfall was frequent during anthesis of this crop.

One reason for the limited information on this disease could be its sporadic nature, making it difficult to study under natural conditions. Over half of reported observations about environmental effects were from experiments in controlled conditions, such as those of Tschanz et al. (1975). Fauzi and Paulitz (1994) developed a reproducible method of establishing head blight from ascospores in field plots by using corn kernels colonized with *G. zeae*. Mature perithecia were produced on the corn kernels, and ascospores were released over a 3-week period. Paulitz (1996) used a Burkard 7-day continuous spore trap to determine the daily and seasonal release of ascospores of *G. zeae* in inoculated field plots in Quebec. He determined that ascospores were released in the evening, beginning around 1700–1800 h, before leaf wetness was detected, with most of the release occurring before midnight. Rainfall was not required but rather inhibited ascospore release. The time of ascospore release was correlated with the time when relative humidity (RH) increased in the early evening, in association with a decrease in temperature. The sampler used by Paulitz (1996), however, did not permit the identification and characterization of other species of *Fusarium* that occurred over a wheat field. Volumetric spore samplers, such as the Burkard 7-day continuous spore sampler, use an adhesive-coated surface, and the trapped spores do not remain viable. Martin (1988) used a high-throughput jet sampler, which overcame some of these limitations, by allowing species identification, and providing cultures that could be used for further study through molecular work. The jet sampler collects spores by impaction onto selective media, and resultant colonies can be transferred to other culture media for identification. This could help to determine the relative frequency of the species present over a wheat field and also enable the identification to the strain or isolate level through the use of DNA fingerprinting techniques (Ouellet and Seifert 1993). A

known strain could be released and collected by samplers to study survival and distribution of a fungus over a given time period and its pathogenicity and virulence.

Another unknown factor in the epidemiology of this disease in Eastern Canada is the role of macroconidia, which are produced in sporodochia on crop debris. Macroconidia could play a role in infection, but spores would have to be splashed a distance of 70–90 cm to be deposited on the heads. This would only occur with very intense rainfall and large raindrops with the kinetic energy to propel the spores that distance (Madden 1992). The closed crop canopy at the time of anthesis would also intercept the drops, reducing their dispersal even further. However, macroconidia are also produced on blighted heads later in the season, and these could be wind dispersed and serve as a source of inoculum for heads of secondary tillers, provided the heads were still susceptible. Paulitz (1996) counted only ascospores, but the same spore sampler that collects spores on a sticky tape could be used to quantify macroconidia over the season. However, this trap would not sample splash-dispersed spores.

The objectives of our work were to (i) determine the daily and seasonal patterns of airborne spores of *Fusarium* spp. over wheat plots during head and seed formation by use of high throughput traps, (ii) determine the daily and seasonal patterns of airborne spores of *Fusarium graminearum* in inoculated field plots, and (iii) determine the relative frequency, daily, and seasonal patterns of ascospores versus macroconidia of *G. zeae*. Preliminary results were reported previously (Fernando et al. 1996).

Materials and methods

Inoculum preparation

Gibberella zeae strain DAOM 178148, obtained from the Canadian Collection of Fungal Cultures, is pathogenic to wheat (Miller et al. 1985) and has a characteristic yellow colony in culture that differentiates it from the more common carmine-coloured wild type. In independent field experiments on the Central Experimental Farm, Agriculture and Agri-Food Canada, Ottawa, Ont., the yellow cultural phenotype was recovered only from plots inoculated with this strain. The fungus was grown on synthetic nutrient agar (SNA) for 10 days, and plugs (0.5 cm diam.) were placed in a fresh tomato medium (Fernando et al. 1997). The medium was prepared by soaking 100 g of fresh ripe tomatoes, cut into 2-cm pieces, in 1 L distilled water for 2 h, and then filtering out the tomatoes with cheesecloth. NaCl (16 g/L) was added, and the solution was autoclaved in 2-L flasks. A 1-cm piece of *G. zeae* from a PDA culture was added to the autoclaved medium. Flasks were aerated by bubbling with filtered air and incubated under near-UV light for 7 days (until macroconidia were present). Twenty-millilitre aliquots (50 000 spores/mL) were added into 1-L jars containing 500 g of previously autoclaved corn kernels. The jars were sealed with a canning lid with two holes (6 mm diam). A 70-mm diameter filter disk was placed on the inside of the lid to prevent contamination while allowing air to exchange. Jars were incubated at 20°C under 16 h/day fluorescent lighting for 6 weeks and were gently shaken every day to break up clumps of kernels.

Field plots

In 1994, the experiments were carried out at the Central Experimental Farm (CEF) in Ottawa in plots of spring wheat (*Triticum aestivum* L. cv. Roblin), a susceptible cultivar. Locations A (Base-

line site) and B (Morningside site) each had a 50 × 50 m plot area. In 1995, the experiment was done in a 10 × 10 m plot area at one location. Rows were 18 cm apart, with a planting density of approximately 450 plants/m². Two litres of the infested corn inoculum was scattered on the soil of the central 1 × 1 m area of each plot on 15 June 1994 and 15 June 1995 (day 166).

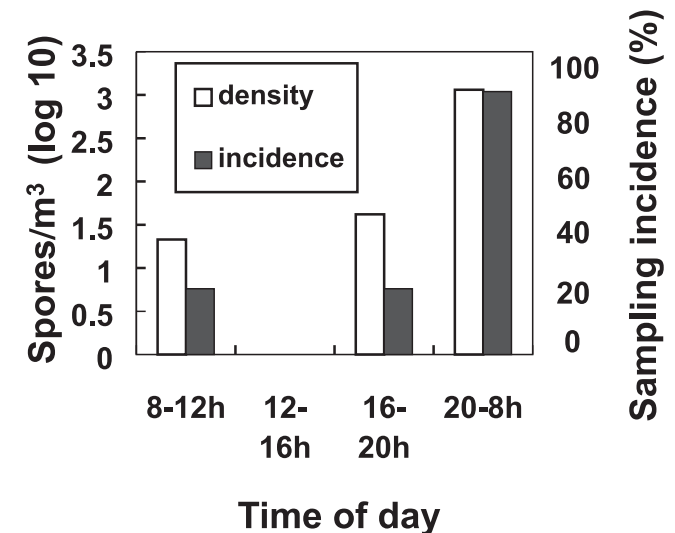
Spore sampling

Four Burkard jet spore samplers (Burkard Manufacturing Co. Ltd., Rickmansworth, England) were used for the experiment in 1994. Spore traps were calibrated with a Reuter centrifugal sampler (RCS) (Biotest Diagnostics, Frankfurt, Germany). The calibration was done on the top of a four-story building on the farm in the early crop season, with the RCS sampler and the jet spore samplers side by side and with a number of trials. Spores trapped included *Cladosporium herbarum*, *Cladosporium cladosporioides*, *Aureobasidium pullulans*, and *Fusarium* spp. The RCS sampler (40 L/min) trapped 15.3 times as many spores as the jet spore samplers. Each jet spore sampler was placed inside a plywood enclosure with a cylindrical intake chimney, which had a flat lid and screening to exclude insects and rain water. The opening of the chimney was 70 cm from the ground. Traps were placed 1.5 and 5.0 m (location A), and 5.0 and 10.0 m (location B), southwest (downwind of the predominant wind direction) of the edge of the infested area. A Petri plate (100 × 15 mm) containing a semi-selective medium for *Fusarium* species (Nash and Snyder 1962) was placed in each sampler. The sampler was operated by a timer that activated the air flow for 2 min at 30-min intervals. Plates were collected from the spore sampler at 0800, 1200, 1600, and 2000 h each day for 21 days beginning 6 July 1994, and were incubated at 26°C under incandescent light for 4–6 days. Colonies of *Fusarium* species were counted and identified. For identification of species, randomly selected colonies were transferred to SNA plates with a piece of no. 1 Whatman filter paper (4.25 cm²) in the center of the plate (Nirenberg 1976). Plates were incubated for another 3–5 days under fluorescent light, and sporulating colonies were identified under the microscope following the concepts of Nelson et al. (1983). Colony counts were converted to cfu/m³ air.

In 1995, a Burkard 7-day wind-oriented spore sampler was used to examine the densities of airborne ascospores and macroconidia over time, in relation to rain events. The spore trap was set up 1 m downwind from the corner of the inoculated area with the sampler orifice (2 × 14 mm) at the level of the wheat heads. The sampler was adjusted to a flow rate of 10 L/min, with a tape speed of 2 mm/h. Spores and other particles entering the sampler impinged on a rotating drum covered with 19-mm-wide Melenex® tape coated with a thin layer of white petroleum jelly (Sutton Industries, Woodbridge, Ont.). The tape was replaced every 7 days. After removal from the drum, the strip of spore-bearing tape (336 mm long) was cut into segments representing 24-h periods and then mounted on glass slides for examination. The spore counts were converted to ascospores or macroconidia/m³ air. In 1995, spore sampling was initiated on 9 June, before heading of the wheat plants. The incidences of infection of *F. graminearum* in seeds from the plot was determined as described in Fernando et al. (1997).

In 1994, weather data were obtained from the CEF meteorological station, approximately 1 km away from both inoculated plot locations. In 1995, temperature, relative humidity, and rainfall data were recorded at the inoculation site, with a Campbell CR 21× micrologger (Campbell Scientific Inc., Logan, Utah). Temperature was monitored using a Fenwal Electronics UUT51J1 thermistor (model HMC35C), relative humidity was measured with a probe (Campbell Scientific Inc.), containing a Vaisala captive relative humidity sensor and a rain gauge that were installed 2 m above the ground on a post. All weather data were recorded every 5 min and saved as 1-h averages. Wind velocity and wind direction data were

obtained from the CEF meteorological station approximately 0.5 km from the plot site.



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Data analysis

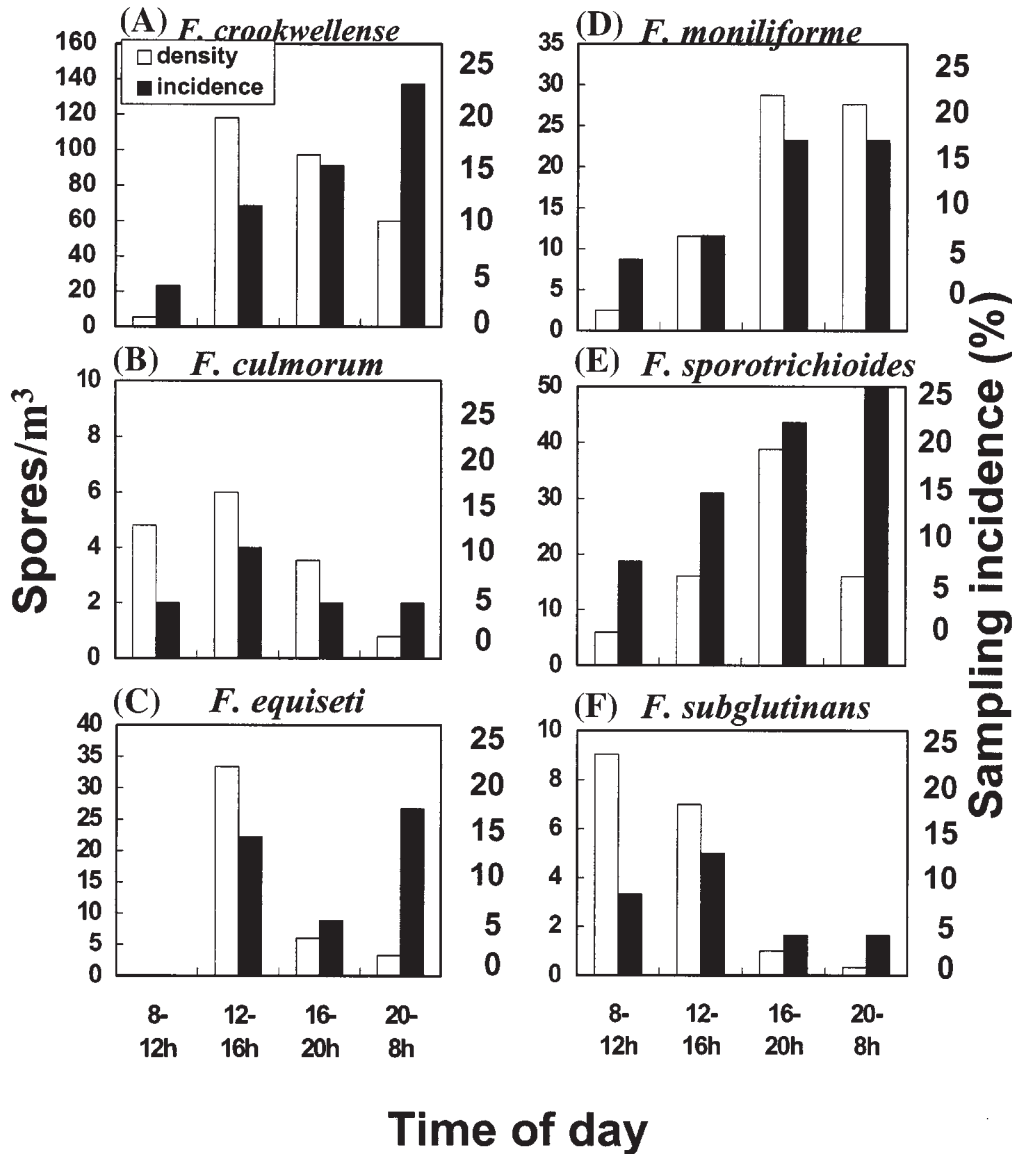
In 1994, because there were no significant differences among spore samplers for all *Fusarium* spp. (except the inoculated *F. graminearum*) in terms of spore densities, the spore numbers for all species except *F. graminearum* were averaged over the four samplers. For daily periodicity data, only days in which the particular species were sampled were included in the spore density and sampling incidence calculations. Sampling incidence at each of four sampling times was calculated as follows. First, all the days in which any spore of that species appeared on any trap at any time during the day were counted. Then, for each trap at each sampling time, the number of times the species was detected was counted and divided by the total number of days that the spores appeared on any trap. For example, if species X appeared on 10 of the 21 total sampling days, and during the 8- to 12-h period, it was found on 2 of the 10 days, the sampling incidence for that trap during that sampling period would be 20%. The sampling incidence from the four traps were averaged and used for the statistical analysis. For *F. graminearum*, only the results from the 1.5-m sampler at site A were used for calculating daily spore sampling patterns. In 1995, daily spore densities of ascospores and macroconidia were sampled. All spore densities were converted into log values for statistical analysis. Homogeneity of variances was determined with the Bartlett's test (Steel and Torrie 1980). If the means were homogeneous, the daily spore sampling data were analyzed with ANOVA tests. The Kruskal-Wallis nonparametric test was used to compare means when the Bartlett's test showed lack of homogeneity of variances (Daniel 1978).

Results

Daily patterns of spore release in 1994

Among *Fusarium* species sampled, *G. zeae* was the only species with marked daily periodicity and statistically significant differences among daily sampling periods (Fig. 1). Most spores were trapped at 2000–800 h (approximately

Fig. 2. Average spore density and sampling incidence of *Fusarium* spp. on days in which spores were sampled, 1994. Data was averaged over two sites (four samplers). (A) *Fusarium crookwellense*. (B) *Fusarium culmorum*. (C) *Fusarium equiseti*. (D) *Fusarium moniliforme*. (E) *Fusarium sporotrichioides*. (F) *Fusarium subglutinans*.



1500 cfu/m³), with 1.5 log fewer spores in the late afternoon (1600–2000 h) and morning (800–1200 h).

Other *Fusarium* species detected, in decreasing order of spore density, were *F. crookwellense*, *F. sporotrichioides*, *F. moniliforme*, *F. equiseti*, *F. subglutinans*, and *F. culmorum* (Figs. 2A–2F). Average spore densities of these species ranged from 1 to 120 cfu/m³. With these *Fusarium* species, spore release was very sporadic, the samples obtained were not consistent, and there was a high degree of variability among sample sites. This resulted in significant heterogeneity of variances. Comparison of means using Kruskal–Wallis tests showed no significant difference in densities of spores among the sampling periods for any of the species, which implied a lack of periodicity in spore release. However, for the four of the six most prevalent species (*F. crookwellense*, *F. equiseti*, *F. moniliforme*, and *F. sporotrichioides*), there was a trend of a lower spore density during the morning hours.

Seasonal patterns of spore release: 1994 trial

Four peaks of airborne ascospores of *G. zeae* were observed during the 19-day sampling period (Fig. 3A): days 188–190, 192–194, 197, and 202. The peaks appeared to be triggered by rain in the previous 1–3 days, except for the last peak (Fig. 3B). The first event could have been triggered by rain on days 183 and 186; the second event by rain on days 189–191, the third event by rain on day 196, and the last event by rain on day 202, the same day.

Among the other *Fusarium* spp. encountered, *F. crookwellense* was detected in only two release events during the early sampling period with peaks at days 188 and 193 (Fig. 4A). *Fusarium sporotrichioides* was detected more frequently, although higher densities were seen during the early sampling period (Fig. 4E). *Fusarium moniliforme* was detected on the greatest number of days relative to the other *Fusarium* spp., with releases throughout the sampling period (Fig. 4D). *Fusarium culmorum* and *F. subglutinans* showed

similar patterns of release over the season, with two peaks, one at the beginning of the sampling period (day 187 or 188 and day 195 or 196) (Figs. 4B and 4F). *Fusarium equiseti* was detected in high densities on day 192 (Fig. 4C).

Daily and seasonal patterns of ascospores and macroconidia of *G. zae* in 1995

Ascospore counts exhibited a daily periodicity with initial spores at 1700–1800 h and a peak at 1800–1900 h (day 187, Fig. 5A). The ascospore densities in the air over infested sites were lower in the 1995 trial, probably due to lack of rain during June (Fig. 6C). Due to the drought, the inoculated areas in the plots were irrigated with 4 mm of water each day from day 180 to day 184 (total of 20 mm) to initiate perithecial formation and maturation in the initial period. This was followed by a peak of ascospore release on day 187 (Fig. 6A). Another peak was detected on day 200, following rain on days 195, 197, 198, and 199. However, smaller releases (<10 spores/m³) were detected during the drought period.

The daily pattern of macroconidia sampling on a typical release day (day 162) is shown in Fig. 5B. Macroconidia were detected in low densities throughout the day, with no apparent periodicity. The density of macroconidia was approximately 1 log unit less than the ascospore density. A release of macroconidia was detected on day 162, following a rain event on day 161 (Fig. 6B). Smaller releases occurred during the drought period, with another peak following the irrigation of the inoculated area.

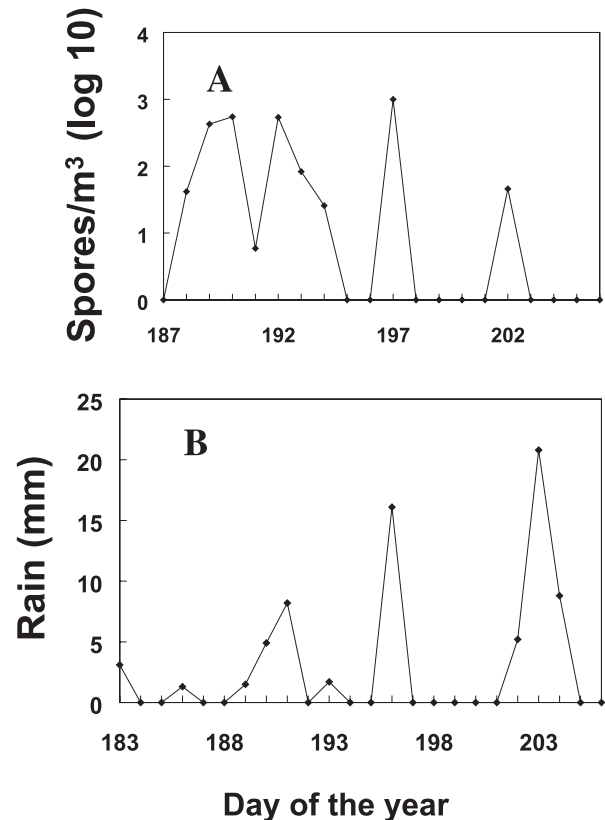
Discussion

Our work has shown the temporal (both seasonal and daily) aspects of spore release by *G. zae* and other *Fusarium* sp. over a wheat field. We have also attempted to separate the release of ascospores from macroconidia by *Fusarium graminearum* (*G. zae*) over wheat fields, and give numbers that appeared on our spore trap over a period of a month. The observed daily density patterns of airborne ascospores of *G. zae* agreed with those found by Paulitz (1996), with a diurnal pattern of spore release beginning during the late afternoon to early evening. Location, year, or size of plot did not affect the diurnal pattern of spore release. Ayers et al. (1975) also noted that the highest numbers of ascospores were trapped during night time (2100–600 h).

Ascospore release of *G. zae* typically followed 1–3 days after rain. In both years, four major release events were detected over a 20- to 30-day period, suggesting that the perithecia on the corn seed may consist of populations at various stages of maturity. In fact, wetting followed by drying may stimulate release (Tschanz et al. 1975). Paulitz (1996) speculated that the increase in RH in the evening following drying during the day could increase the turgor pressure of asci, which contain a vacuole at high osmotic pressure (Ingold 1971).

Rainfall probably affects the water potential of the debris in which the perithecia are formed. Laboratory experiments have shown that 94% RH (–9 MPa) is the minimum water potential at which mycelial growth of *G. zae* will occur on corn kernels (T.C. Paulitz, unpublished data). Sung and Cook (1981) showed that perithecial production was greatest

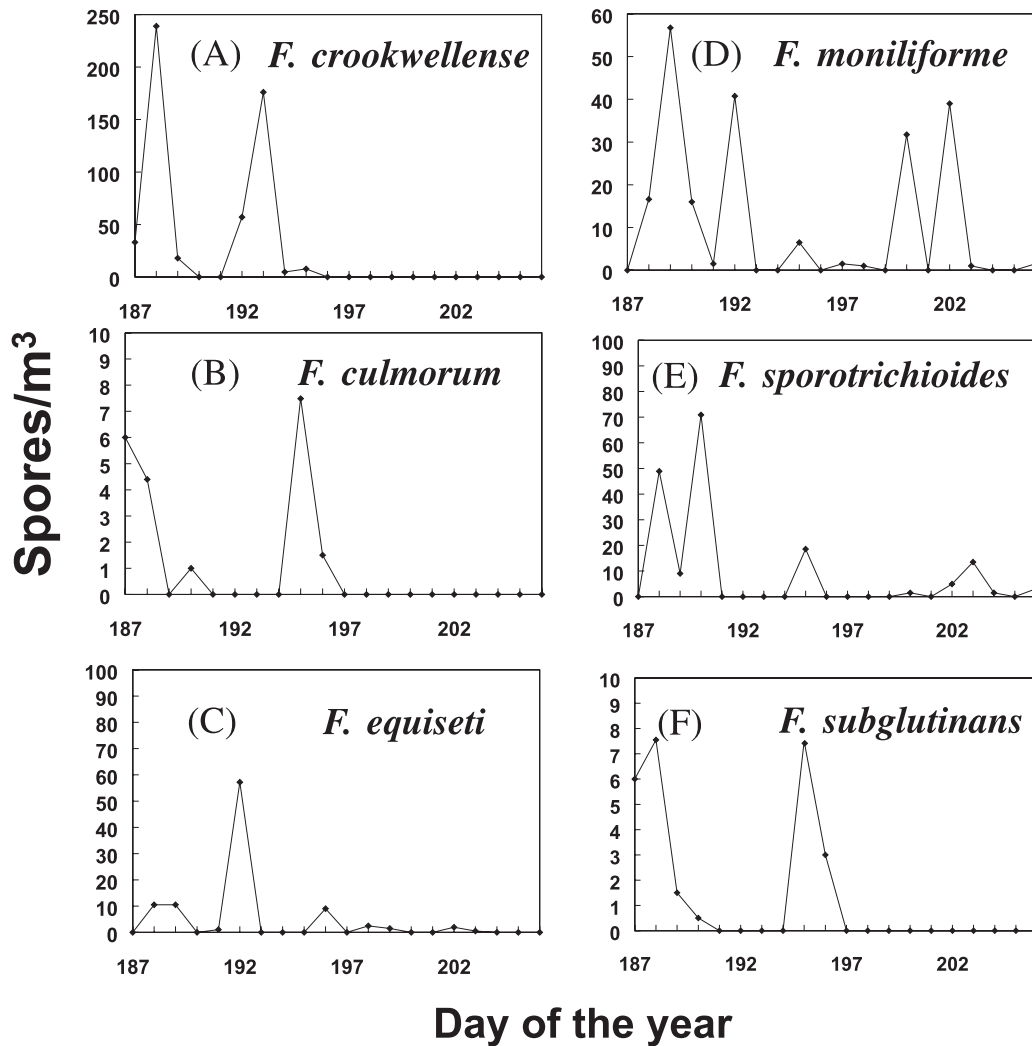
Fig 3. (A) Daily evening spore density of *Gibberella zae* over the sampling period, 1994. The spore sampler was 1.5 m away from the inoculated area, 1994. (B) Daily rainfall during the sampling period, 1994. The y-axis in Fig. 3B starts from day 183 to show the rain events prior to spore capture on day 188. Spore capture was initiated on day 187.



at –1.5 MPa but few were formed below –5.0 MPa. The optimum osmotic potential for growth of mycelium of *G. zae* group 2 on agar medium was around –2 MPa, but some growth was still detected at –12 MPa (Wearing and Burgess 1979). However, colony growth was negligible at –15 MPa. If the water potential in the substrate is not favorable, asci and ascospores may not develop, even though perithecia are already formed, as was seen during the drought of June 1995. The perithecium may be an important survival structure of *G. zae* during dry periods and resume growth after rain occurs. In summary, rainfall is probably important for perithecial formation and ascospore development, but the requirements for ascospore release may be different.

Observations that densities of macroconidia of *F. graminearum* were higher early in the sampling period compared with the period after the inoculum was put out into the field were consistent with the observations that sporodochia and macroconidia formed on the corn kernels after a few days in the field. The macroconidia probably arose from the infested corn kernels placed in the field, since a peak was detected 1 or 2 days after the inoculum was rewetted after a long period of drought. Macroconidia, unlike ascospores, did not show any daily pattern of periodicity. Macroconidia densities were lower than ascospore densities, even though their number in the field should have been artificially elevated from the corn kernel inoculum. This indicates that macroconidia present on

Fig. 4. Daily spore density of *Fusarium* spp. over the sampling period, 1994. Data were averaged over two sites (four samplers). (A) *Fusarium crookwellense*. (B) *Fusarium culmorum*. (C) *Fusarium equiseti*. (D) *Fusarium moniliforme*. (E) *Fusarium sporotrichioides*. (F) *Fusarium subglutinans*.

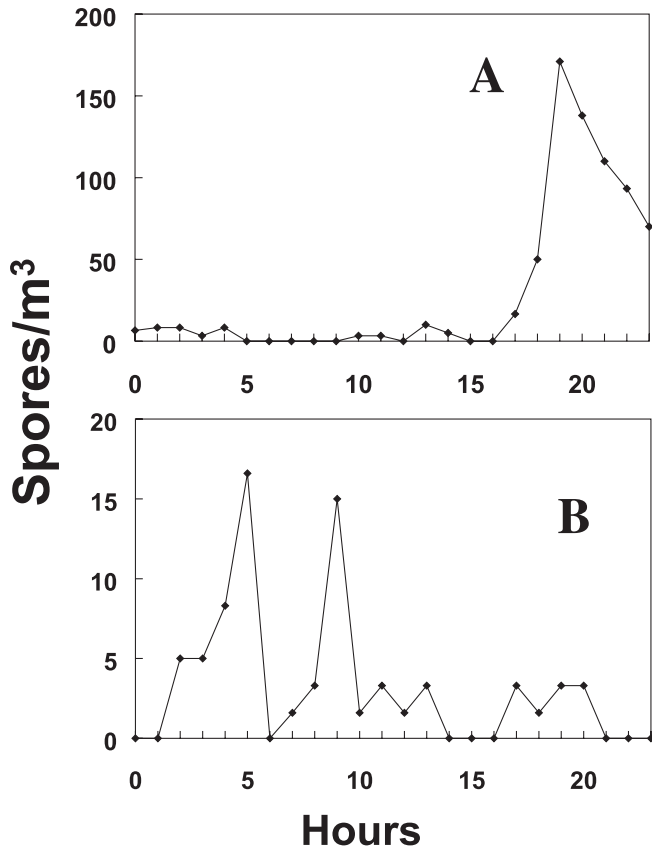


the corn kernels were not liberated into the air in high numbers, and therefore would not serve as a major source of inoculum in fields treated with infested corn kernels. However, we cannot extrapolate these results into naturally infected fields, especially later in the season when macroconidia liberated from sporodochia on the heads may be an important inoculum source for secondary tillers or corn which flowers later. However, Reis (1988) reported that 98% of the spores of *G. zeae* collected through spore trapping were ascospores. This sampling was done on a field of wheat with abundant perithecia, using a suction spore trap with Vaseline-coated microscope slides. In our study, two out of three macroconidial release events followed a rain or irrigation event. In the case of the irrigation event, spore release occurred 7 days later. This long delay was probably due to the drought conditions and the time required to form new sporodochia. Macroconidia probably are mainly splash dispersed (Sutton 1982), and require a heavy rainfall to provide sufficient kinetic energy to propel the spores into the air. However, we cannot preclude the possibility of higher

macroconidia densities in the air, if heads were heavily infected and produced sporodochia later in the season. Due to the drought conditions of 1995, disease incidence in the inoculated plot was low, so sporodochia did not form on the heads.

Other *Fusarium* spp. that were detected included *F. sporotrichioides*, *F. moniliforme*, *F. crookwellense*, *F. culmorum*, *F. equiseti*, and *F. subglutinans*. Martin (1988), using similar spore samplers also found *F. graminearum*, *F. avenaceum*, *F. culmorum*, and *F. poae*. *Fusarium avenaceum*, *F. graminearum*, and *F. sporotrichioides* together made up 93% of the total spores trapped. Duthie et al. (1986) isolated *F. sporotrichioides*, *F. avenaceum*, *F. poae*, and *F. equiseti* from winter wheat seeds in Ontario, and Martin et al. (1991) found a similar range of *Fusarium* spp. on wheat and barley seeds in Atlantic Canada. *Fusarium graminearum* was the most frequently isolated *Fusarium* spp. from Ontario wheat, but *F. sporotrichioides* and *F. poae* were the next most prevalent (Clear and Patrick 1990). Fauzi (1992) found that the four most predominant species on spring wheat in Quebec

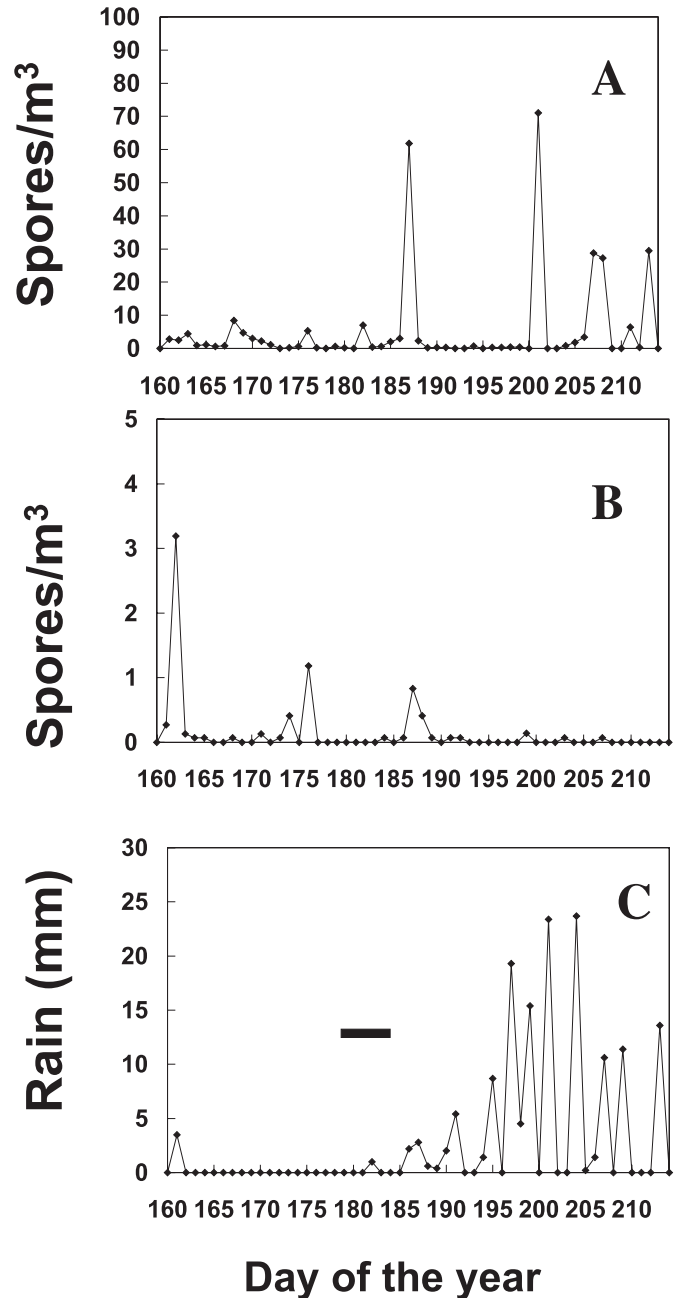
Fig. 5. (A) Hourly density of ascospores of *Gibberella zeae*, day 187, 1995. (B) Hourly density of macroconidia of *Fusarium graminearum*, day 162, 1995. Note: scale on y-axis in Figs. 5A and 5B are different because of the nature of spore numbers represented.



were *F. graminearum*, *F. sporotrichioides*, *F. poae*, and *F. equiseti*.

In contrast to *F. graminearum*, no statistical evidence was found for the daily periodicity of spore dispersal in the other *Fusarium* spp., possibly on account of the high variation and the low spore numbers. Because numbers of spores were lowest in the morning hours for most of the species, this could mean that spores are released after a drying period during the day, or when wind speeds are higher in the afternoon. But much of the literature suggests that macroconidia are dispersed by rain or in splash droplets. Since macroconidia are formed in mucilaginous masses in the sporodochia, rain is needed to liberate them. Jenkinson and Parry (1994) showed that large droplets (4–5 mm) could propel conidia of *F. culmorum* as high as 60 cm vertically, and conidia of *F. avenaceum* as high as 45 cm. We did not observe any close relationship between rainfall events and presence of spores in the air. In most cases, spores were sampled on days with little or no rainfall, the exception being *F. sporotrichioides*, which was sampled on days 191 and 203, two days with rainfall >5 mm. Although these samplers were not designed to directly measure splash-dispersed spores, if spores were liberated into the air by a rain event, they should be sampled in higher numbers. One possibility

Fig. 6. (A) Daily evening ascospore density of *Gibberella zeae* over the sampling period, 1995. (B) Daily macroconidia density of *Fusarium graminearum* over the sampling period, 1995. (C) Daily rainfall during the sampling period, 1995. Bar refers to the period when the plot was irrigated with a total of 20 mm from days 180–184. Note: scale on y-axis in Figs. 6A and 6B are different because of the nature of spore numbers represented.



is that spores liberated and dispersed by rain may deposit on leaves and other surfaces and be blown into the air later.

There were differences among the species in terms of seasonal patterns of sampling. *F. culmorum*, *F. subglutinans*, and *F. crookwellense* were present only in the beginning of the sampling period, while *F. moniliforme* and *F. sporotrichioides* were sampled throughout the sampling period.

Although *F. moniliforme* is not common on wheat, it is common on corn, which was cultivated in adjacent areas of the Central Experimental Farm in Ottawa. This fungus was also the most prevalent, in terms of the number of days in which it was sampled, perhaps a reflection of its tendency to produce abundant chains of dry microconidia. There were also some similarities among the species. *Fusarium culmorum* and *F. subglutinans* showed almost identical patterns of sampling, and all species were sampled on days 188 and 195; the latter was four days after a major rain event. Some of the species may have similar environmental conditions favoring spore release. In the 2 years of our study, the use of viable-spore and nonviable-spore volumetric collectors gave valuable information on spore density, spore release, predominant species of fusaria, and spore type that may be important in the infection of susceptible wheat cultivars. Our data confirm the ability of both types of spore traps to indicate the prevalence trends for *Gibberella* spores. Our results provide estimates of the airborne inoculum load of *Fusarium* spp. Our study shows that certain macroclimatic factors such as rainfall influence spore release, but it does not address the effects of microclimatic factors such as soil moisture, debris moisture, soil surface temperature, wind velocity, and turbulence near or at the soil level or in the crop canopy. These factors require further study to understand the process of spore release and dispersal. An understanding of environmental factors affecting spore formation and release events will be useful in epidemiological modeling and possibly in forecasting epidemics.

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