Symposium contribution / Contribution à un symposium

Epidemiology and biological control of *Gibberella zeae* / *Fusarium graminearum*

J. Gilbert and W.G.D. Fernando

Abstract: A decade of losses and damage due to fusarium head blight in cereals in North America and other parts of the world has resulted in great efforts to understand the factors that cause and intensify the disease. This review considers our current understanding of the importance of the contribution of cultural practices to the increase or decrease of inoculum levels, spore dispersal, and biological control of spore production and fusarium head blight. Perithecia of *Gibberella zeae* develop on aboveground residues, and on maize and wheat kernels rather than maize stems and wheat spikes, at temperatures of 15 and 25 °C, but not below 15 °C or above 30 °C. Ascospores are released during the evening, in response to rising relative humidity, and there is evidence for both local and long-distance dispersal. The effect of rotation and tillage system on the development of inoculum and FHB requires further research, but several studies indicate that weather may be the principal factor in development of the disease. Several fungal and bacterial species have been reported to inhibit hyphal and perithecial formation of *G. zeae*. These are discussed with an appraisal of the conditions and requirements to produce an effective biological control of *G. zeae*.

Key words: Gibberella zeae, *Fusarium graminearum*, epidemiology, biological control, cultural practices, rotation, tillage.

Résumé : Une décennie de pertes et de dommages dus à la fusariose des panicules dans les céréales en Amérique du Nord et dans d'autres régions du monde a suscité des efforts importants afin de comprendre les facteurs qui causent et stimulent la maladie. La présente synthèse examine les connaissances actuelles sur l'importance de la contribution des pratiques culturales à l'augmentation ou à la diminution des niveaux d'inoculum, à la dispersion des spores et à la lutte biologique contre la production de spores et la fusariose des panicules. Les périthèces du *Gibberella zeae* se développent sur les débris végétaux en surface du sol, et sur les grains de maïs et de blé plutôt que sur les tiges de maïs et les épis de blé, à des températures de 15 et 25 °C, mais pas en dessous de 15 °C ou au-dessus de 30 °C. Les ascospores sont libérées le soir, en réaction à l'augmentation de l'humidité relative, et des données indiquent que la dissémination peut se faire localement et sur de longues distances. De plus amples recherches sont nécessaires au sujet de l'effet du système de rotation et de travail du sol sur le développement de l'inoculum et de la fusariose des panicules, mais plusieurs études indiquent que la température pourrait être le principal facteur dans le développement de la maladie. Selon ce qui a été rapporté, plusieurs espèces de champignons et de bactéries seraient capables d'inhiber la formation des hyphes et des périthèces du *G. zeae*. Une discussion de ces cas est présentée ainsi qu'une évaluation des conditions et des exigences pour arriver à une lutte biologique efficace contre le *G. zeae*.

Mots clés : Gibberella zeae, *Fusarium graminearum*, épidémiologie, lutte biologique, pratiques culturales, rotation, travail du sol.

Introduction

Fusarium head blight (FHB) is one of the most serious diseases affecting cereals in North America. The principal pathogen is *Gibberella zeae* (Schwein.) Petch (anamorph *Fusarium graminearum* Schwabe), although other species, such as *Fusarium avenaceum* (Fr.) Sacc., are more important in regions such as the western Canadian prairies. The past decade will be noted as a period in which FHB became more prevalent globally, resulting in intense research activity to find strategies to control and manage the disease while breeders attempted to transfer adequate levels of resistance into adapted wheat backgrounds (Gilbert and Tekauz 2000). The epidemiology of FHB has also been

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J. Gilbert.[1] Cereal Research Centre, Agriculture and Agri-Food Canada, 195 Dafoe Road, Winnipeg, MB R3T 2M9, Canada.
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W.G.D. Fernando. Department of Plant Science, University of Manitoba, Winnipeg, MB R3T 2N2, Canada.

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[1]Corresponding author (e-mail: jgilbert@agr.gc.ca).

reexamined. Environmental conditions have been favourable to the disease for several consecutive years, permitting a local buildup of inoculum and the development of FHB to epidemic levels (Clear and Patrick 2000; Gilbert et al. 1999). This review covers the last 5 years and provides an update of our understanding of factors that influence the sources, dispersal, and control of inoculum and may contribute to changes in FHB levels in space and time.

Sources of inoculum

It has been recognized since the early years of the last century that overwintered stubble provides inoculum for FHB (Atanasoff 1920). Both rain splash for macroconidia and wind for ascospores were implicated as the means of spore dispersal. More recent studies have attempted to determine the duration of survival of spore-bearing residues in light of an increased move toward tillage practices that leave crop stubble in the field. Khonga and Sutton (1988) examined survival and sporulation of *G. zeae* on wheat spikes, grain, and stems and maize stems and ears. Tissues were buried, left at soil surface, or suspended from a nylon line 10 cm above the ground. No sporulation occurred on buried tissues. During the first year, macroconidia and perithecia developed on tissues placed on the soil surface or suspended above the ground. During the second year, perithecia, but no macroconidia, formed on maize stems and wheat spikelets and grain left at soil surface or suspended, while during the third year, perithecia formed only on wheat spikelets and grain suspended above the ground. A high density of perithecia developed on maize kernels and wheat grain. Similar results were reported for *Fusarium*-infested wheat kernels in Manitoba (Inch and Gilbert 2003a).

There is no evidence of spore production on *Fusarium*-infested residues that are buried (Khonga and Sutton 1988; Inch and Gilbert 2003a), although these have been shown to have the potential to infect root tissues of both cereal and noncereal crops seeded in close proximity (Chongo et al. 2001).The rate of decomposition of residues is more rapid in the soil than above or on the soil surface (Dill-Macky 1999; Khonga and Sutton 1988; Todd et al. 2001) and, in conjunction with the lack of spore production in the soil, it means that buried residues contribute little to inoculum load. Wet soil conditions do not favour fungal survival (Dickson 1923), which may explain, in part, the lack of observed seedling blight in the cool, moist clay soils of the Red River valley, Manitoba, where FHB epidemics have been severe in the last decade.

A number of probably minor sources of inoculum have been examined in an attempt to discover or explain how the disease develops and spreads. Among these, asymptomatic inflorescences of wild grasses have been found to harbour several *Fusarium* spp., including *F. graminearum* (Inch and Gilbert 2003b). The fungus *F. graminearum* survives on kernels of wheat and corn, producing copious perithecia and ascospores on the soil surface for 2 to 3 years (Inch and Gilbert 2003a; Khonga and Sutton 1988), although sowing *Fusarium*-infested wheat seed does not cause FHB (Gilbert et al. 2003a). The fungus survives parasitically and saprophytically on wheat leaves throughout the growing season (Ali and Francl 2001; Osborne et al. 2002). The most prevalent *Fusarium* spp. observed were *F. graminearum* and *F. sporotrichioides* Sherb. From 4% to 52% of the diseased leaf tissue not surface disinfested was infected with *F. graminearum* (Ali and Francl 2001). Osborne et al. (2002) recovered up to 1500 spores per leaf. While ascospores were usually the most prevalent, in some locations, the leaves supported also large macroconidial concentrations, suggesting that the fungus may grow epiphytically, resulting in higher inoculum levels within the canopy. Soybeans have also been reported as a host for *F. graminearum* (Martinelli et al. 2001), and noncereal residues, including canola and field pea, were found to support high levels of sporulation (Gilbert et al. 2003b). In areas at low risk from *Fusarium* spp., such as in Alberta, efforts have been made to reduce incoming inoculum in the form of infested grain for feed lots. While the fungus does not survive passage through the rumen, wasted feed and spills are cited as potential means of introducing the disease to the province (Calpas 2003; McLaren et al. 2003).

Dispersal

Guenther and Trail (2002) reported that perithecia form in wheat through stomates above chlorenchyma of the stem internodes and from epidermal cells of the stem nodes. The light and moisture requirements for *G. zeae* ascospore release have been examined by Trail et al. (2002). Under laboratory conditions, ascospore release was reported to be 8% to 30% greater in light than in complete darkness, and in constant light, discharge reached maximum rates at relative humidities greater than 92%. This is in contrast to data reported by Paulitz (1996) and Inch et al. (2000) who, under natural conditions in Quebec and Manitoba, respectively, found that most ascospores were trapped in the evening, reaching a peak before midnight. Schmale III et al. (2002) also collected more colonies in sampling periods that spanned sunset to sunrise, as opposed to sunrise to sunset. Dufault et al. (2002a, 2002b) identified the conditions under which perithecia develop on corn residues. Under field conditions, an extended period of stalk wetness at temperatures between 15 and 25 °C favoured perithecial development. When temperatures were lower than 15 °C, perithecia stopped developing, but resumed when temperatures rose again (Dufault et al. 2002a). Under controlled conditions, there were no significant differences in rate of perithecial development at 15 or 25 °C, but no perithecia developed at 30 °C (Dufault et al. 2002b).

Ascospores appear to be dispersed relatively short distances when measured by disease levels in wheat plants infected in the neighborhood of the inoculum foci (Fernando et al. 1997). In experiments conducted in Ontario and Quebec, the highest incidence was recorded at 0.5 m from the upwind edge of the inoculum area. There was a 50% decline in spikelet infection within 1.6 to 2.0 m upwind and within 2.7 to 4.9 m downwind from disease foci. Seed infection declined to 10% of the maximum within 5 to 22 m from the focal centre in plots inoculated with corn spawn to promote ascospore infection, and within 5 m in plots inoculated with macroconidia. The suggestion that ascospores might be taken into the planetary boundary layer has re-

cently been given credence by work in New York State. Ascospore occurrence has been recorded at more than 180 m above ground, over lakes and regions remote from farm fields, using remote-controlled model aircrafts and boats fitted with spore traps (Del Ponte et al. 2002). The relative contribution of external and within-field inoculum sources is unknown, but will vary according to region, crops grown, and tillage practices. The experience in New York, in fields where wheat follows corn, for example, indicates a tendency for FHB patterns to be aggregated and for disease incidences to be high. In fields planted to vegetable crops, or where old corn residues (2+ years) were small and scattered, disease incidence was random and low (Del Ponte et al. 2002). A combination of within-field inoculum and inoculum from airborne ascospores may explain the uniform and intense level of infection observed across southern Manitoba wheat fields in the epidemic year of 1993.

Since the work of Fernando et al. (1997) on spore release and dispersal initiated from a point-source inoculum, there have been several studies to understand the epidemiology of spore dispersal in other locations in Canada and the United States, using somewhat different approaches. de Luna et al. (2002) studied *G. zeae* ascospore gradients in a naturally infested field with overwintered residues in Eastern Canada. Ascospore concentrations declined by 50% within 18 m of the point source and by 90% within 60 m. Although this decline was substantial, de Luna et al. (2002) postulated that long-distance transport of spores, beyond the field, could also occur. Paulitz et al. (1999) proposed a generalized two-dimensional Gaussian model to describe disease foci originating from small areas (1–16 m^2) inoculated with corn kernels colonized with *G. zeae* within larger wheat plots (100–2500 m^2). They reported the anisotropic and asymmetric foci arising from ascospores produced in small areas in a field. They claimed wind to be the main factor determining these shapes. Fernando et al. (2000) investigated the abundance of *Fusarium* spp. in a field, using viable spore counts on petri plates containing *Fusarium*-selective medium. Recovery of *Fusarium* spp. other than *F. graminearum* was sporadic. For all *Fusarium* spp. (*F. crookwellense* Burgess et al., *F. moniliforme* Sheldon, *F. sporotrichioides*, *F. culmorum* (W.G. Sm.) Sacc., *F. equiseti* (Corda) Sacc., and *F. subglutinans* (Wollenw. & Reinking) Nelson et al.), there were no statistical differences among the daily sampling times, although for most species, morning counts were the lowest. Also, daily average densities of macroconidia of *F. graminearum* were an order of magnitude lower than ascospores (Fernando et al. 2000). Markell and Francl (2003) reported the presence of several species of *Fusarium* in North Dakota. Most of the species were similar to those reported by Fernando et al. (2000). While *F. graminearum* spores were the most prevalent in the 3-year study in North Dakota, *F. moniliforme* and *Fusarium poae* (Peck) Wollenw. spores were the highest on some days. *Fusarium sporotrichioides* and *F. equiseti* were the other species identified in small numbers. Markell and Francl (2003) artificially inoculated equal amounts of ascospores or conidia on wheat spikes and recovered more colonies from conidia-inoculated spikes. They proposed that conidia play an important role in the primary disease cycle of FHB. In a study using nine locations in Canada and the United States, more colony-forming units were recovered from epidemic as opposed to nonepidemic regions (Francl et al. 1999). Inoculum was either not detected, or occurred sporadically, during dry periods. Francl et al. postulated that FHB epidemics were associated with multiple inoculation episodes and with coincident wet periods. Their study also illustrated corn residue supplying more inoculum than wheat residue to epidemics (Francl et. al. 1999).

In a review, McMullen et al. (1997) summed up the FHB situation very well. As for the future outlook on the FHB problem, they mentioned that, while there is still very much to be learned about this disease and its management, the weather will play a significant role. The above studies that reported inocula from *Fusarium* spp., their release, and their dispersal, all showed the role and importance of weather factors. McMullen et al. (1997) also posed the question "where will it strike next?". It did not take too long for a new area to be attacked. In 2003, FHB severely affected the wheat industry in the southeastern States of United States, east of the Mississippi River, such as Kentucky, with yield reductions and deoxynivalenol (DON) content in the grain, (Stewart et al. 2003). Again, weather was a determining factor, with large amounts of rainfall during the flowering period making it conducive for the pathogen to cause infection and subsequently produce DON at high levels in the grain. The problem of DON in grain was further compounded by the fact that it did not fall to lower levels during milling (a concept known as milling loss), because of the presence of plump grain containing DON.

Disease forecasting

Disease forecasts can be used to help producers make decisions about the application of a fungicide or biological control, establish harvest priorities, and pursue markets for grain (De Wolf et al. 2003). Grain buyers can use this information to make preparations for mycotoxin testing, grain cleaning, storage, and processing. Several groups have tested prediction models to manage FHB (De Wolf et al. 2003; Hooker et al. 2002). De Wolf et al. (2003) developed two models based on 50 cases of hourly weather and disease observations from four states in the United States that provide estimates of the probability of occurrence of a scab epidemic greater than 10% severity. These models include a preflowering model that uses weather variables observed prior to flowering to predict disease, and a postflowering model that makes predictions, using weather variables observed both prior to and during the flowering period (De Wolf et al. 2003). Hooker et al. (2002) based their model on empirical relationships between weather variables and concentrations of DON. An early prediction of DON in mature grain was developed using rain and temperature data from 4 to 7 days prior to heading. However, the full predictive model used data from three periods taken from 7 days before heading to 10 days after heading. Hooker et al. (2002) hypothesized that the concentration of DON in mature grain is closely associated with environmental factors influencing both inoculum production and infection in wheat at heading. In Manitoba, the model used for FHB risk forecasting emphasized the importance of high humidity as a key factor in disease development (Kaminski 2003). This system was

based on weather data collected from a network of approximately 50 stations in southern Manitoba. Despite the time and research invested in the development of these models, their use by growers and their accuracy in predicting FHB remains questionable. Additional improvements to, and increased grower awareness of, existing models will help manage FHB and reduce *Fusarium* inoculum.

Control

The most economic and sustainable method of controlling FHB will be through resistant varieties. However, with few registered FHB-resistant varieties, integrated methods of disease management such as chemical applications, cultural practices, and biological control become important to reduce losses. A comprehensive treatment of the effectiveness of chemicals on FHB was recently published (Jones 2000). Here we highlight recent research on cultural practices and biological control.

Cultural practices

Several studies have examined the effect of tillage practice on head blight development. Intuitively, tillage systems that leave the most residues on the soil are expected to produce the greatest amount of inoculum and cause the highest severity of FHB. In light of what is known about pathogen survival and sporulation on residues, tillage and crop rotation were recommended as means of reducing inoculum (Khonga and Sutton 1988). However, in Saskatchewan, zero till did not result in fields with higher levels of FHB compared with conventional till, while minimum till generated more severely diseased fields (Fernandez et al. 2001). Significant differences were found in disease incidence and severity and in DON content of grain in a Minnesota study that examined the effects on disease levels of moldboard plow (~10% residue retained), chisel plow (~30% residue retained), and zero till (~65% residue retained) (Dill-Macky and Jones 2000). However, while statistically significant, the differences were small. Disease incidences in moldboard plow, chisel plow, and zero-till plots were 64%, 72%, and 71%, respectively; disease severities, 16%, 20%, and 21%, respectively; and DON levels, 8.1, 10.6, and 11.1 ppm, respectively. The results of a 3-year tillage study in Ontario were inconclusive, with observations that *F. graminearum* persists on debris under both till and zero-till conditions, and that other factors such as rotation and cultivar susceptibility are likely to be more important than tillage practice (Miller et al. 1998).

Conclusions as to the effects of rotations are somewhat similar. Where differences were found, levels of disease on wheat following crops other than cereals or maize were significantly different, but small (Dill-Macky and Jones 2000). For example, in wheat planted into fields with corn, wheat, and soybean residues, FHB incidences were 75%, 67%, and 64%, respectively; disease severities, 23%, 18%, and 16%, respectively; and DON levels, 13.5, 9.2, and 6.9 ppm, respectively. Ahmed et al. (2002) found that FHB was higher in wheat in canola–wheat and pea–wheat rotations than in wheat–wheat and wheat–oat rotations, but disease levels were low, and results were not conclusive as the experiment had been conducted for a single year. Other studies have not demonstrated differences due to rotations in FHB levels (Fernandez et al. 2001), and even when wheat follows corn as part of the rotation, a report of a 3-year survey of 230 wheat fields in Kentucky concluded that the principal factor in FHB development is the weather (Hershman 2000).

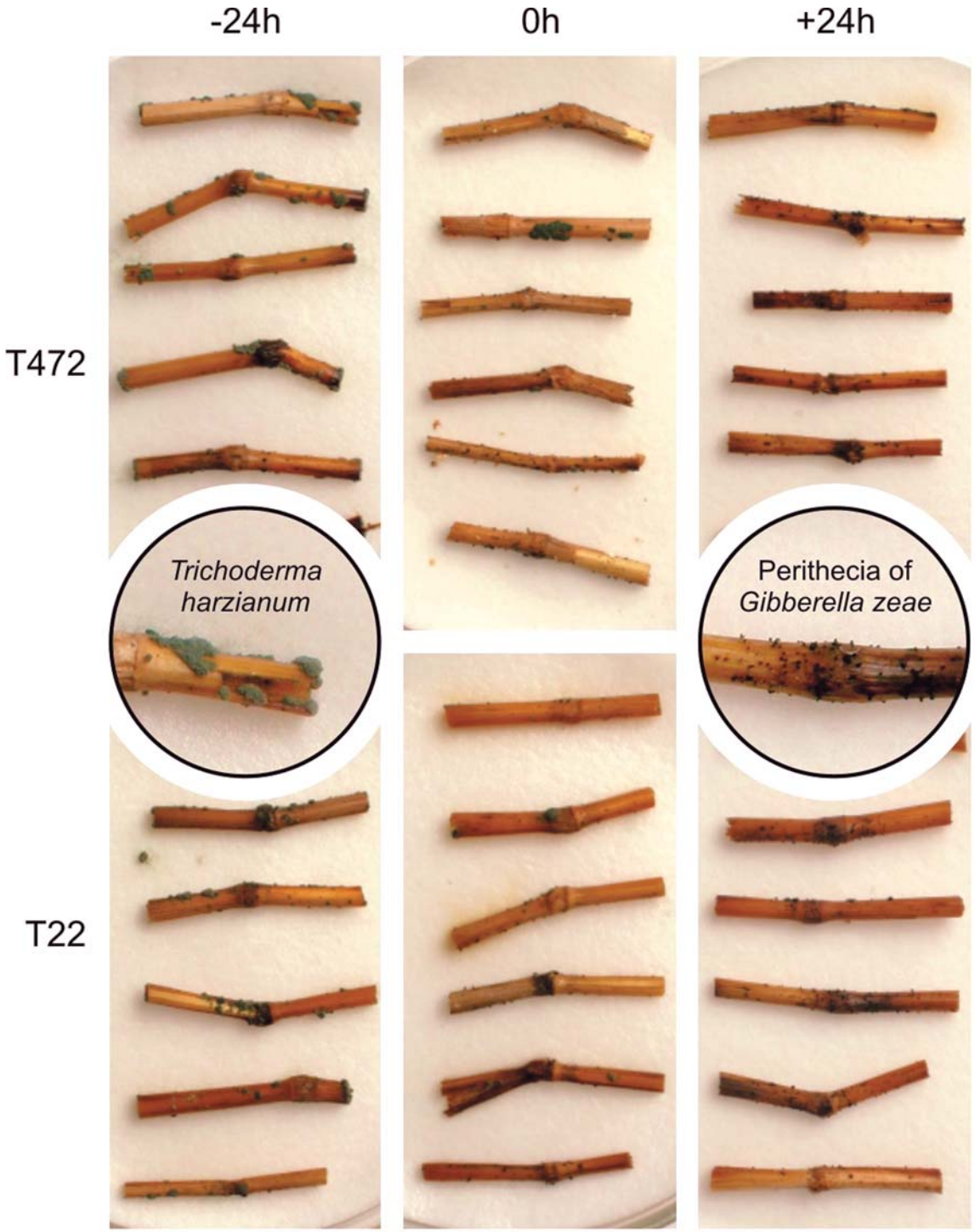
Interactions with other microorganisms in the rhizosphere and on the head also govern the epidemiology of *F. graminearum*. These interactions, naturally occurring or caused by artificial inoculation, may reduce the inoculum. For example, an antagonistic bacterium or fungus may be applied to the head at flowering (the most susceptible period of the host to the pathogen), or a hyperparasitic fungus may naturally colonize *Fusarium*-infested stubble in soil (Cook and Baker 1983). Biological pesticides are an attractive alternative when the window of protection is narrow. Their use will reduce the risk of emergence of fungicide-resistant strains that may develop with continuous use of fungicides (Campbell 1989). The more specific a fungicide is, the greater the likelihood that a resistance develops, and this applies as well to the most widely used fungicide against *Fusarium*, Folicur®. As biocontrol agents are living organisms, they may need specific or optimal conditions, similar to the requirements of the pathogen, to be effective (Fernando 2003). These epidemiological conditions may include, but are not limited to, temperature, relative humidity, soil moisture, leaf wetness, solar radiation, and wind. As the wheat head has a more open habitat, it is subject to harsher environmental conditions (Windels and Lindow 1985).

Biological control: target areas

Application to the head

Application of biocontrol agents at anthesis may achieve pathogen control by aborting, curtailing, or delaying germination of *F. graminearum* spores in the infection court of the head (Fernando 2001). These biocontrol agents may be effective both in reducing FHB incidence and severity and in reducing DON levels. Three bacterial strains, H-08, S-01, and L-01, that were isolated from wheat head, stem, and leaf, respectively, caused significant inhibition of *F. graminearum* (Fernando et al. 2002). *Bacillus subtilis* (Ehrenberg) Cohn strain H-08 reduced disease incidence and severity and maintained high population levels on the head after inoculation under controlled conditions. *Lysobacter enzymogenes* Christensen & Cook strain C3, a gram-negative bacterium, reduced disease incidence (type-I resistance) and spread (type-II resistance) when applied to spikelets of the wheat head (Jochum and Yuen 2002). When strain C3 was subjected to heat treatment (70 °C for 20 min) and sprayed onto spikelets that were then inoculated with *F. graminearum* spores 1 day later, disease reduction was not significantly different from that observed under a treatment with live bacteria, indicating induced resistance in the host by strain C3 (Yuen et al. 2003). It was also found that the effectiveness was dependent on host genotype. C3 was effective in controlling FHB on 8 of 11 cultivars. The National Center for Agricultural Utilization Research, Agricultural Research Service, US Department of Agriculture, Peoria, Illinois, has several biocontrol agents under consideration for commercial development (Schisler et al. 2002) and is actively working on formulations with three bacteria (*Bacillus*

Fig. 1. Perithecial development of *Gibberella zeae* on autoclaved wheat straw residue inoculated 24 h before (–24 h), 24 h after (+24 h), or coinoculated (0 h) with *Trichoderma harzianum*, strains T472 and T22.



spp.) and three yeasts (*Cryptococcus* spp.) (Schisler et al. 2001). Anther-colonizing organisms capable of utilizing tartaric acid, a compound that is poorly metabolized by *G. zeae* and which could be added to formulations of biocontrol agents, reduced FHB (Khan et al. 2001). Cornell University researchers also have initiated a study identifying bioprotectants effective in controlling *G. zeae* (Loper and Stockwell 2000). Their approach targets spray applications at anthesis, seed application, and crop residue treatment with bioprotectants.

Residue management

Microorganisms are naturally active in controlling pathogen propagules on plant debris. This is one of the benefits of tillage, which provides for greater microbial contact and degradation of the pathogen. This takes the form of

mycoparasitism, antibiosis, or the production of volatile compounds that are inhibitory to the pathogen. In laboratory assays, we found several bacterial strains capable of producing volatile compounds that completely inhibited growth and germination of overwintering structures of several plant pathogens (Fernando et al. 2004). Using gas chromatography – mass spectrometry, we have identified these compounds as benzothiazole, cyclohexanol, *n*-decanal, dimethyl trisulfide, 2-ethyl 1-hexanol, and nonanal. These were completely inhibitory to survival and reproductive structures of *Sclerotinia sclerotiorum* (Lib.) de Bary (Fernando 2003) and will be tested against *Fusarium* spp. Some of these compounds are available commercially and are known to be used in pesticides. *Microsphaeropsis* sp. strain P130A, which attacks the perithecia of *Venturia inaequalis* (Cooke) Wint. causing apple scab, reduced the production of *G. zeae* perithecia when applied to straw and spikelet residue as a preplanting or postharvest application (Bujold et al. 2001). Use of *Trichoderma* spp. in stubble management was investigated by Inch and Gilbert (2003c). The latter were able to show a significant reduction in perithecial formation on autoclaved wheat straw pieces when *Trichoderma harzianum* Rifai was inoculated prior to, or coinoculated with, the pathogen (Fig. 1). Though the mechanism has not been studied, it is speculated that mycoparasitism and (or) enzymatic activity may be involved. *Trichoderma harzianum* was identified as an effective biocontrol agent against *F. graminearum* and *Cochliobolus sativus* (Ito & Kuribayashi) on wheat residue (Fernandez 1992). However, in residue management, more work is needed to optimize the efficacy of the biocontrol agent, including the dose, formulation, and timing of application. The same bacterial and fungal genera identified as being effective in studies of Fernando et al. (2002, 2004) and Inch and Gilbert (2003c) were found to be effective in Argentina (Dal-Bello et al. 2002), suggesting that common strains might be ubiquitously found colonizing the wheat plant. This is an important epidemiological aspect if we are to succeed in biological control of fusarium head blight. Early establishment of *F. subglutinans* may act as a biological control providing protection against invasion by more commonly toxigenic fusaria like *F. graminearum* (Cooney et al. 2001).

Limitations

Epidemiological factors limiting activity of biocontrol agents on the phyllosphere or spike

A relatively hostile environment on the phyllosphere and wheat head prevents optimizing a biocontrol agent that would be effective all the time. These environmental conditions range from a lack of free moisture, high UV radiation, and high temperature to a depleted food source. Addition of polymers and selection of strains that are capable of tolerating severe environmental conditions are being investigated (http://www.ag.auburn.edu/bci/foliar.htm). Until such polymers are developed, and bacteria that are tolerant of a harsh environment are found, long-term survival and multiplication of biocontrol agents on the phyllosphere or spike may be difficult. However, if the biocontrol agent is able to induce resistance in the host, like *Lysobacter enzymogenes* strain C3, its survival on the head will not be as critical.

Biological control: fermentation and formulation

To be successful in the marketplace, formulation technology must provide opportunities to enhance numerous characteristics of biocontrol agents, including shelf life, efficacy, growth and survival in the environment, and compatibility with agricultural practices and machinery (Loper and Stockwell 2000). For example, uridine was chosen as a formulation ingredient to stimulate *Bacillus subtilis* colonization of wheat heads (Ierulli et al. 2001), and osmolytes have been found to enhance shelf life of freeze-dried culture cells of *Enterobacter cloacae* (Jordan) Hormaeche and Edwards (Van Cauwenberge et al. 2001).

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