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A Unified Effort to Fight an Enemy of Wheat and Barley: **Fusarium Head Blight**

Marcia McMullen, North Dakota State University, Fargo, ND

Gary Bergstrom, Cornell University, Ithaca, NY ♦ Erick De Wolf, Kansas State University, Manhattan, KS Ruth Dill-Macky, University of Minnesota, St. Paul, MN & Don Hershman, University of Kentucky, Princeton, KY Greg Shaner, Purdue University, West Lafayette, IN ♦ Dave Van Sanford, University of Kentucky, Lexington, KY

Wheat (Triticum aestivum, T. turgidum) and barley (Hordeum vulgare) are critical food and feed crops around the world. Wheat is grown on more land area worldwide than any other crop (30,53). In the United States, production of wheat and barley contributes to domestic food and feed use, and contributes to the export market and balance of trade. In the United States, wheat (all classes) currently is grown on approximately 20 to 25 million hectares per year, providing about 10% (50 to 68 Tg = million metric tons) of the world's wheat production (30). Per capita consumption of wheat in the United States exceeds that of any other food staple, and wheat is a national staple in many other countries. Barley is currently produced on approximately 1.2 million hectares per year in the United States, and this provides about 4% (5 Tg) of the world's barley production. Domestic barley production is critical to sustain the malting and brewing industry in the United States and is an important livestock feed (30,100).

Despite the importance of these crops, planted hectares of wheat and barley in the United States have declined drastically since the early 1990s. U.S. wheat plantings were about 29 million hectares in 1992 compared with 21.4 million in 2010. U.S. barley hectares were 2.8 million in 1992 compared with 1 million in 2010 (100). These historically important cereal crops are under siege, in part because of policies related to the support of agricultural commodities and biofuel production, because of food fads or diets, and partly because of a very challenging plant disease. The reduction of wheat and barley payments in the 1996 U.S. farm bill, the introduction and adoption of biotech corn (Zea mays) and soybean (Glycine max) in the early 2000s, which made corn and soybean easier to grow, ethanol use, which increased demand for corn, and food trends promoting low carbohydrate diets, all contributed to reduced American wheat consumption (V. Peterson, U.S. Wheat Associates, and D. Green, Wheat Foods Council, personal com-

Corresponding author: Marcia McMullen, North Dakota State University, Fargo, ND; E-mail: Marcia.Mcmullen@ndsu.edu

munications). In addition, a fungal disease, Fusarium head blight (FHB or scab), resulted in billions of dollars of wheat and barley yield and quality loss in the 1990s and early 2000s (77,79,89). The reduced yields and reduced market prices for FHB-infected grain made other crops more attractive to growers.

Fifteen years ago, Plant Disease published a feature article titled "Scab of wheat and barley: A re-emerging disease of devastating impact" (79). That article described the series of severe FHB epidemics that occurred in the United States and Canada, primarily from 1991 through 1996, with emphasis on the unparalleled economic and sociological impacts caused by the 1993 FHB epidemic in spring grains in the Northern Great Plains region. Earlier publications had dealt with the scope and damage caused by this disease in the United States, Canada, Europe, and China (4-6,26,40,94,119,127,136). Reviews published after 1997 further described this disease and its impact on North American grain production in the 1990s (7,39,77,115,121,122,126,146).

This feature article reviews the disease and documents the information on U.S. FHB epidemics since 1997. The primary goal of this article is to summarize a sustained, coordinated, and collaborative research program that was put in place shortly after the 1993 epidemic, a program intended to quickly lead to improved management strategies and outreach implementation. This program serves as a model to deal with other emerging plant disease threats.

Fusarium Head Blight Disease Cycle, Symptoms, and Impact on Grain Yield and Quality

Fusarium graminearum is the dominant fungal species causing FHB in North America (34,117). F. graminearum also is one of several causal agents of ear, stalk, and root rot of corn. The fungus persists on residue of small grains and corn, and prolonged moist weather during the growing season favors growth and sporulation of the fungus on crop residue. Spores (primarily ascospores) are windblown or water-splashed onto spikes of wheat and barley. Wheat is susceptible to infection from the flowering (anthesis) stage up through the soft dough stage of kernel development. In North America, the barley plant flowers in the leaf sheath (boot), and barley heads become most susceptible to FHB once the heads are out of the leaf sheath and exposed to F. graminearum spores. Infection at these growth stages is favored by prolonged wet weather and high humidity.

All or portions of infected wheat heads prematurely whiten (Fig. 1A), and barley heads have brown discolored kernels (Fig. 1B). Yield losses occur from failed kernel development or because infected kernels are shriveled, discolored, and light in test weight (Fig. 1C). The disease destroys grain yield and quality late in the crop's growth cycle, at the time when non-diseased wheat and barley grain heads normally are developing plump, sound kernels. Instead of a bountiful crop, yields may be reduced by as much as 80% (5). Market price is severely reduced when grain has low test weight and contains damaged kernels (scabby kernels are classed as damaged in U.S. Grain Grades) and contains fungal toxins (mycotoxins). Food grade grain may be reduced to feed grade because of this disease, or the grain may have no food or feed value at all. The predominant toxin associated with FHB infections in the United States is deoxynivalenol (DON) (34). This mycotoxin causes feed refusal or poor weight gain in animals and may cause immunological and teratogenic problems in humans (25). The U.S. Food and Drug Administration (131) has established guidelines for DON levels in human and animal feed, but many food and beverage industries self-imposed even greater restrictions.

Frequency and Magnitude of Epidemics Since 1997

The highly variable occurrence and intensity of FHB among years, geographical regions, crops, and grain market classes is evident when assessing U.S. outbreaks since 1996. The 1997 feature article (79) discussed the episodic nature of historic FHB epidemics and characterized FHB as a "re-emerging disease" for the period 1991 to 1996. In subsequent years, losses resulting from FHB have continued to cause major economic problems in one or more wheat classes and barley in most years, but some years are clearly more problematic than others (Fig. 2).

For example, Nganje et al. (89) conducted an economic analysis of losses attributable to FHB for the period 1993 to 2001, for nine states in the northern Great Plains and central United States (Illinois, Indiana, Kentucky, Michigan, Missouri, Minnesota, Ohio, South Dakota, and North Dakota). The authors determined that the cumulative direct economic loss attributable to FHB in wheat and barley for the entire period was US \$2.491 billion, with \$1.074 billion (43.1%) of the total being lost between 1998 and 2001. Annual losses varied greatly: total direct production losses were 18.7, 15.1, and 12.6% in 1998, 1995, and 1993, respectively. Losses were much lower in 1996 (6.8%), 2000 (6.4%), and 2001 (7.7%). The study also looked at secondary (indirect) losses and determined that for each U.S. dollar lost by the producer as a result of FHB, an additional \$2.08 is lost as other economic factors (e.g., retail trade, household income, tax revenue, employment) are adversely impacted. The authors estimated that combined direct and secondary economic losses between 1993 and 2001 were \$7.67 billion, with \$2.59 billion (29.9%) being lost during the 1998 to 2001 period. Across all nine states, total direct and secondary losses were 18.7% (\$1.44 billion), 15.1% (\$1.16 billion), and 12.6% (\$963 million) in 1998, 1995, and 1993, respectively (89).

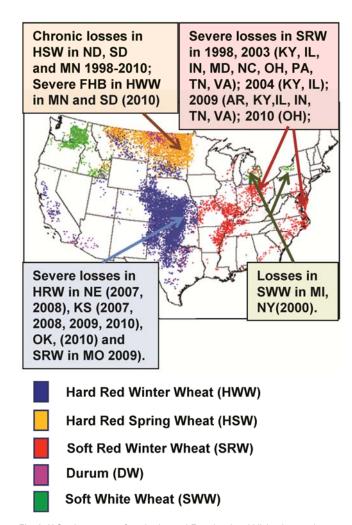


Fig. 2. U.S. wheat areas of production and Fusarium head blight-damaged areas, 1998 to 2010. Each dot = 5,000 acres at the county level, as estimated by Economic Research Service, USDA.



Fig. 1. Fusarium head blight symptoms. A, Wheat head infection with bleached spikelets. B, Six-row barley head infection. C, Infected durum wheat kernels showing pink and white discolorations. Durum kernel photo courtesy of Jim Miller (USDA).

In 2003, a regional epidemic occurred that involved much of the soft red winter wheat grown in the United States, but especially crops grown in Kentucky, Maryland, North Carolina, Pennsylvania, Illinois, Indiana, Ohio, Tennessee, and Virginia. Cowger and Sutton (18) documented the impact of this epidemic for 62 counties across the southeastern states of Georgia, Maryland, North Carolina, South Carolina, and Virginia. They estimated that 40 of these counties, across Maryland, North Carolina, and Virginia, experienced very damaging levels of FHB, resulting in reduced wheat yields of 28.3, 52, and 54.2%, respectively, with a total dollar loss estimated at \$13.6 million. By comparison, losses in 22 counties in South Carolina and Georgia were negligible. The authors also suggested that several million additional dollars were lost by millers in the region due to increased shipping costs (resulting from sourcing wheat from distant locations), the considerable time and expense associated with deoxynivalenol (DON) testing, and additional handling expenses (related to grain cleaning and blending).

The period 2007 to 2008 highlights the episodic nature of FHB and the potential for the disease to strike in consecutive years on a smaller scale. For example, during 2007 and 2008, FHB was a minor problem across most of the United States (24,52); however, serious disease outbreaks occurred both years in parts of Nebraska and Kansas. In 2007, FHB damaged about one-third of the wheat grown in Nebraska and was considered by local experts to be the worst outbreak in Nebraska in 22 years (81). The greatest damage occurred in eastern, south-central, and southwestern Nebraska, where there were reports of DON levels being high enough to incur elevator dockages of up to \$0.036/kg (=\$1.00/bu), with some loads being rejected. That same year, above-average rainfall triggered above normal levels of FHB (10% incidence; incidence = % tillers showing FHB symptoms) in eastern and central Kansas. In 2008, FHB was again severe in south-central and eastern Nebraska, as well as other parts of the state, especially in irrigated fields (24,140). Losses of up to 20% were estimated for some fields, and overall statewide yield loss was estimated at 2.3% (valued at \$13.3 million). In the most severely affected fields, DON was as high as 18 mg/kg (mg/kg = ppm), and discounts at the point of sale were as high as \$0.18/kg (=\$5.00/bu). In Kansas, FHB was particularly severe during 2008 in the eastern third of the state, with losses estimated at 17.6, 15.8, and 8.75% for the northeast, east-central, and southeast reporting districts, respectively (24). Statewide losses were estimated at 1.9% (426 Gg or 7.1 million bushels), valued at \$57 million.

In 2009, FHB was epidemic in parts of several mid-south and southeastern states, including Arkansas, Kentucky, Maryland, Missouri, North Carolina, Georgia, Illinois, Indiana, Virginia, and Tennessee (116,133). No formal loss estimates were developed for the FHB epidemic in this region, but anecdotal reports of FHB incidence of 50% or higher, unacceptably high DON levels, and poor seed quality were widespread (109). In western Kentucky, for example, a miller related that the average DON was 2.89 mg/kg (ppm) for 1,000 loads of wheat received during 2009. That compared with an average of less than 0.5 mg/kg (ppm) in 2007 and 2008 (47).

A review of FHB occurrence across states in 2010 (66) indicated that FHB was at low levels in many states, but the disease was severe in parts of Ohio where FHB incidences reached 60% and DON levels were 18 mg/kg (ppm) in some fields. A survey of 145 fields in 32 Ohio counties revealed that 30% of them had FHB incidence levels above 25%. FHB also was a problem for the fourth straight year in parts of Kansas, where the FHB index [(incidence × head severity)/100] ranged from 2 to 10% in affected districts. The overall impact of the disease in Kansas was estimated at 90 Gg (3.3 million bushels), valued at \$13 million. FHB was also severe in 2010 in parts of Oklahoma, as well as in winter wheat grown in South Dakota and Minnesota. In Minnesota, FHB indexes approaching 20% were common in fields that were not sprayed with a fungicide to suppress FHB. Similarly, in 2011, FHB had regional impacts, with severe losses in some states (67).

In summary, FHB and DON continue to cause significant economic losses to both wheat and barley in wet years and locations in the United States, despite advances made in managing FHB over the last decade. Still, an argument has been made (133), supported by considerable observation and experience, that losses would have been much greater if not for advances made in managing FHB and DON. Research, much of it conducted since 1993, made these advances possible, and allows farmers to make FHB management decisions that greatly improve the outcome when conditions favor FHB (63,74).

Establishment and Funding of the U.S. Wheat and Barley Scab Initiative (USWBSI)

Regional discussions of FHB epidemics in the 1990s (Minnesota, 1993; North Dakota, 1994; Manitoba, 1996; North Dakota, 1996; Michigan, 1997) revealed two things—that the disease was not occurring in just one region or grain class, and that sustained funding for research on FHB was difficult to obtain (142). At a meeting organized by Michigan State University, held in Chicago's airport with financial support from the Agricultural Experiment Station Directors, discussion of the disease occurrence in Michigan and other states led participants to propose a mechanism to seek funding to support this research (3). Subsequently, scientists from the north-central region presented a cooperative proposal to Representative Marcy Kaptur from Ohio in March 1997 for securing federal funding for FHB research. The meeting led to a decision to secure political support for a federally funded U.S. Wheat and Barley Scab Initiative (USWBSI). The first funding (\$200,000) was derived from federal year-end funds and was allocated to FHB researchers late in 1997. By June 1998, \$200,000 was added, and by October of that year, the federal Agricultural Appropriations conference committee added \$3 million. The FY2000 federal agricultural appropriations bill brought the total funding to \$4.3 million. In FY2001, the U.S. Congress increased Agricultural Research Service (ARS) funding for FHB research by \$1.2 million, half of which was allocated to the USWBSI. An additional increment in FY2004 brought funding to \$5.2 million, where it has remained, except for small budget reductions imposed by the United States Department of Agriculture (USDA)-ARS. Funds appropriated by Congress to the ARS for FHB research are disbursed through grants administered by the USWBSI.

The goal of the USWBSI (http://www.scabusa.org/mission.html) is "to develop, as quickly as possible, effective control measures that minimize the threat of Fusarium head blight (scab), including the reduction of mycotoxins, to the producers, processors, and consumers of wheat and barley". To accomplish this goal, the USWBSI distributes research funds appropriated by the U.S. Congress, through USDA-ARS, to FHB researchers at public institutions in the United States.

In the early to mid-1990s, nearly all funds used to support FHB research came primarily from local commodity boards or councils, formula funding allocated to Land Grant institutions, or industry. Since 1999, USWBSI-facilitated USDA-ARS funding has been awarded to support 1,628 research projects involving 174 scientists across multiple institutions, grain classes, and states, for a total of \$61.9 million. USWBSI-facilitated grants are the main source of funding for FHB research programs in the United States (personal communication with 39 leading FHB scientists in the United States). However, state or commodity funding, other competitive grant sources, and noncompetitive industry grants continue to be important funding sources. Similarly, multi-state regional small grain disease committees, such as NCERA-184 and WERA-97, as well as the Western Wheat Workers, Mid-South Association of Wheat Scientists, Eastern Wheat Workers, and Southern Small Grain Workers, often provide avenues (but usually minimal funding, if any) for scientists to plan, develop, and conduct coordinated research projects that address FHB. Moreover, programs at state universities often have multi-disciplinary wheat or small grain groups that facilitate and promote FHB research programs and activities conducted at the state level. The costs associated with the infrastructure needed to conduct essential FHB research are usually borne by the Land Grant University or other institution and include

building and equipment costs, salaries for faculty and support staff, and many other costs necessary to support research programs. These "in kind" contributions are substantial and necessary to augment FHB grants from any funding source.

Although the investment in FHB research has been substantial, advances made in managing FHB in recent years (as will be discussed throughout this article) suggest that the investment in FHB research is small compared to the long-term economic benefits that have been or will be reaped as a result of greatly improved FHB and DON management. Return on investment for agricultural research is high. For example, Fuglie and Heisey (33) report an average rate of return on federal–state investment in agricultural research of 43.5%, based on an analysis of 18 peer-reviewed studies.

USWBSI funding has supported scientists working on pathogen biology and genetics; cultivar development and host resistance for five winter and spring grain classes; gene discovery and genetically engineered resistance; food safety, toxicology, and utilization; and management strategies in addition to host resistance, with outreach components for each research area. New information in some of these areas has led to improved disease management which has benefited producers and the milling, baking, and brewing industries; other areas are leading to greater understanding of the interaction between pathogen and host, which will lead to better or new management strategies in the future.

F. graminearum Taxonomy and Trichothecene Genotypes: Implications for Management

Major changes in species concepts regarding F. graminearum have occurred during the past 15 years, and these changes have generated debate and indeed considerable controversy among Fusarium researchers. It is clear, however, from examining the historical literature, that this is just the latest chapter in the development of our understanding of this challenging taxon. F. graminearum is also referred to as Gibberella zeae, a name denoting the sexual stage in the life cycle of this fungus. In response to an international nomenclature agreement for naming fungi (45), the elimination of dual names for fungi is proposed. Fusarium is expected to be conserved as the sole name for the fungal genus, and the usage of Gibberella is expected to be discontinued. One of the most recent chapters in the history of F. graminearum taxonomy divided isolates of F. graminearum from around the world into nine distinct phylogenetic lineages, each with strong geographic associations (91), with nine phylogenetic species proposed, based on concordance of single nucleotide polymorphisms in the mating type locus and seven other genes. Two further phylogenetic species were introduced subsequently (125). In this scheme, F. graminearum lineage 7, recognized as the lineage that predominates as the head blight pathogen of wheat and barley in North America, retains the designation of F. graminearum sensu stricto. Because isolates of lineage 7 were able to mate with isolates of other lineages under laboratory conditions and produce progeny with hybrid genotypes, the distinction of phylogenetic species has been questioned (12,64,65). It was recognized, however, that the physical separation of lineage 7 isolates from other lineages remains a significant barrier to inter-lineage gene flow. If other lineages move into North America by natural or human conveyance, direct gene flow leading to hybrid strains would likely occur. F. graminearum lineage 6 (F. asiaticum) has been reported on wheat in two parishes of Louisiana (36). Other proposed species separated from F. graminearum sensu lata include: F. acaciae-mearnsii, F. austroamericanum, F. asiaticum, F. boothii, F. brasilicum, F. cortaderiae, F. gerlachii, F. meridionale, F. mesoamericanum, and F. vorosii (91,125). Phylogenetic subdivision of the anamorph may be important to agriculture, particularly if taxonomic differences are linked to differences in pathogen virulence, host range, ecological adaptation, or mycotoxin profile. A high degree of genotypic and phenotypic variation exists within the lineages of F. graminearum sensu lato (this is particularly true for lineage 7); however, inter-lineage distinctions in pathogen biology and ecology are not obvious. The occurrence in certain countries and regions, but not in

others, of biological species can create the potential for disruption of world grain commerce through quarantine and non-tariff trade barriers (65). Therefore, some scientists feel that adoption of the species level nomenclature changes proposed for *F. graminearum* is premature (65).

Isolates of F. graminearum have been further differentiated by trichothecene chemotypes (chemical phenotypes). The NIV chemotype produces nivalenol, whereas the 3-ADON and 15-ADON chemotypes produce deoxynivalenol (DON) and smaller quantities of 3-acetyldeoxynivalenol and 15-acetyldeoxynivalenol, respectively. Chemotype is only assignable by growing the isolate on a substrate and identifying the trichothecene(s) produced. Recently, polymerase chain reactions (PCR) that amplify the TRI3 and TRI12 genes have been utilized to identify trichothecene genotypes corresponding to putative chemotypes ("3-ADON chemotype", "15-ADON chemotype", and "NIV chemotype") (125,137). For each primer set, a PCR amplicon of characteristic size is associated with each of the trichothecene genotypes. The "15-ADON chemotype" of F. graminearum sensu stricto appears to predominate across most of the United States and Canada. Ward et al. (138) documented a cline across Canada of the "3-ADON chemotype", with the highest proportion in the eastern Maritime Provinces and the lowest in the western Prairie Provinces, and documented a dramatic increase in the "3-ADON chemotype" in western Canada between surveys conducted in 1998 and 2004. A similar increasing cline of "3-ADON chemotypes" relative to "15-ADON chemotypes" was shown along the eastern United States, from North Carolina to New York (113). The apparently recent shift from the "15-ADON chemotype" to the "3-ADON chemotype" as the predominant putative chemotype in wheat may be driven by selection in agricultural systems, climate change, or other factors, although there is insufficient evidence to support any hypothesis at this time. Cohorts of "3-ADON chemotypes" have been reported to produce more total trichothecene toxins, grow faster in culture, and sporulate more profusely than the "15-ADON chemotype" (102,138). Puri and Zhong (102) reported that the severity of FHB incited by the "3-ADON chemotype" was greater, compared to severity incited by the "15-ADON chemotype", when examined on one susceptible and one moderately resistant wheat cultivar but not on another moderately resistant cultivar. Some evidence for the increased aggressiveness of the "3-ADON chemotype" has been presented, but changed virulence toward wheat or barley cultivars that carry genes for resistance to FHB has not been clearly demonstrated. Gale et al. (35) inoculated wheat and barley lines in the field in Minnesota with a bulk of isolates representative of each of the antecedent ("15-ADON chemotype") and emerging ("3-ADON chemotype") midwestern populations. However, the results were inconclusive despite a trend in which the emergent population induced higher levels of DON than the antecedent

Gale et al. (36) reported that "NIV chemotypes" of *F. gramine-arum* sensu stricto and *F. asiaticum* predominated over "DON chemotypes" in a survey of *Fusarium* in wheat in southern Louisiana; they also noted "NIV chemotypes" among a small sampling of isolates from Arkansas, Missouri, and North Carolina. Schmale et al. (113) reported that 4% of the isolates of *F. graminearum* sensu stricto collected in North Carolina were of the "NIV chemotype" and found a single isolate of the "NIV chemotype" from each of *F. graminearum* and of *F. cerealis* in New York. Puri and Zhong (102) also found "NIV chemotypes" in North Dakota. Horevaj et al. (51) reported that winter wheat lines developed for resistance to "DON chemotypes" had even higher levels of resistance to "NIV chemotypes" of *F. graminearum*, suggesting that host resistance is not chemotype-specific.

Continued vigilance and investigation of changes in the biology and genetics of head blight pathogen populations is clearly warranted. Changing climate, agricultural practices, and the employment of FHB control measures may affect the community of FHB pathogens on wheat and barley (148). But, at this juncture, there is no strong indication that integrated pest management strategies

including host resistance, chemical, or cultural control tactics need to respond specifically to shifts in the pathogen populations.

Germplasm Evaluation and Cultivar Development

The USWBSI's breeding effort comprises public breeding programs in 3 states in the spring wheat region, 14 states in the soft winter region, 4 states in the hard winter wheat region, 2 public barley breeding programs, and 1 public durum breeding program. Representatives of these breeding programs gathered initially at the first National FHB Forum in Saint Paul, MN in November 1997. This meeting served as a venue for information exchange about which resistance genes and parents were effective, which traits were most informative, and the FHB screening methods that were most useful. Breeders from private wheat and barley breeding programs also have been deeply involved in informational exchanges and FHB breeding strategy discussions, although their programs are not funded by the USWBSI.

The initial phase of breeding for FHB resistance in the USWBSI emphasized finding new resistance sources. Spring wheat breeders had already begun this process (124), but winter wheat programs were not actively screening new material for FHB resistance at the time (6). Numerous exotic accessions were screened in greenhouses or irrigated, inoculated field nurseries. At the same time, breeders recognized the need to screen adapted material, and created uniform scab nurseries, which were established at multiple locations and were inoculated and mist-irrigated. Despite extensive screening of various germplasm collections, the exotic material did not provide a higher level of resistance than was found among the adapted resistance sources, with the exception of a limited number of Asian accessions including, notably, the Chinese spring wheat 'Sumai 3'. Over time, the breeding focus shifted from finding resistance genes to incorporating resistance into adapted cultivars that seemed to be broadly effective. Differences were evident in the level and frequency of resistance already available in adapted germplasm among wheat market classes. For example, FHB resistance was much more abundant in the existing, adapted soft red winter wheat (SRWW) germplasm than in the adapted hard red spring wheat (HRSW) germplasm.

In barley and durum, the situation was entirely different than in wheat, and it remains so to this day. In those crops, sources of FHB resistance are rare, and researchers continue to screen international germplasm collections in hope of finding new resistance sources. Some success has occurred in the form of the partially resistant durum 'Divide' (North Dakota State University [NDSU]; released in 2006, now grown on an average of 27% of North Dakota hectares [100]) and the newly released barley 'Quest' (University of Minnesota [UMN]; http://www.scabusa.org/pdfs/Quest-Release _PrairieGrains_April10.pdf), but FHB resistance remains an intransigent problem for barley and durum breeders. The resistance in 'Quest' barley is derived from exotic barley cultivars that trace back to China and Switzerland (K. P. Smith, UMN barley breeder, personal communication). The resistance in 'Divide' was of a transgressive nature, exceeding the resistance of either of its moderately susceptible adapted parents (E. Elias, NDSU durum breeder, personal communication). Improvement in resistance to FHB and DON accumulation also has been recently achieved in winter barley (61).

As initial inheritance studies and uniform nursery reports were published, breeding efforts involving 18 states intensified, with breeders crossing to the best resistance sources they could find. Within the USWBSI, breeding programs have extended collaborative efforts beyond participation in uniform screening nurseries, through joint mapping studies, evaluation of recurrent selection populations at many locations, and release of doubled haploid lines (http://www.scabusa.org/research_vdhr). Individual breeding programs, however, have chosen their own approach to breeding resistant cultivars. In general, wheat breeders have followed two pathways toward resistance: (i) incorporation of exotic resistance genes such as the widely used quantitative trait locus (QTL) Fhb1, which was introduced through crosses with 'Sumai 3' (82,123),

and (ii) utilization of FHB resistance from adapted wheat germplasm (75).

Use of exotic QTL resistance. Most, if not all, of the USWBSI wheat breeding programs have used *Fhb*1 in their cultivar development efforts. Breeders have used backcrosses and doubled haploids, along with traditional forward-breeding methods, in conjunction with phenotypic and marker assisted selection (MAS). Most breeding programs are currently using MAS either in their own labs or in cooperation with the USDA-ARS Regional Small Grains Genotyping Labs (134) for the characterization and selection of parents and pure lines, backcrossing, and population enrichment for *Fhb*1 (11). In addition to *Fhb*1, programs are incorporating and pyramiding FHB resistance QTL located on wheat chromosomes 1B, 2B, 2D, 3A, 3BSc, 4B, 5A, and 6B as well as from wheat relatives including *Qfhs.ndsu-3AS* from *T. dicoccoides* and *Qfhs.pur-7EL* from tall wheatgrass (37,73).

Use of resistance from adapted sources. All wheat breeders in the USWBSI routinely screen their own breeding lines, adapted cultivars, and colleagues' breeding lines through cooperative nurseries in search of FHB resistance in the adapted gene pool. DNA markers have not been associated with most of this type of resistance; thus breeders must rely on extensive phenotypic evaluation. Typically, this is done in inoculated, mist-irrigated screening nurseries and through greenhouse testing using point-inoculation. Inoculum used in field nurseries is in the form of macroconidial inoculum spray applied or 'grain spawn' (F. graminearum-colonized corn or wheat kernels), which is spread throughout the nursery several weeks prior to flowering. Promising lines are reevaluated a second and third time, often through the USWBSI uniform screening nurseries at multiple locations. If the resistant FHB phenotype is stable, these lines are used as parents in single or three-way crosses with other adapted lines that have acceptable agronomic, disease, and quality profiles. The goal of this effort is to incrementally add favorable scab resistance alleles to breeding lines that are on track for cultivar release.

FHB traits and resistance. The two most important types of resistance, referred to as 'Type I' (resistance to initial infection) and 'Type II' (resistance to spread within the spike), were first described by Schroeder and Christensen (114). From the outset, most wheat breeding programs focused on Type II resistance, and this trait continues to receive considerable attention, whether the emphasis is on using MAS for the selection of Fhb1 or greenhouse screening for the selection of putative native resistant types. Type I resistance, although present in some cultivars, remains largely elusive. In part, this is due to a low frequency of the resistance, and in part it can be attributed to difficulties in screening for this type of resistance. In recent years, because of economic penalties and food safety concerns associated with high DON levels, there has been an increased focus on resistance traits expressed in kernels, specifically Fusarium damaged kernels (FDK; visually scabby kernels, VSK) and DON. Although independent resistance to DON has been postulated (83), most wheat breeders concentrate on reducing FHB development in the crop. Thus, the usual array of traits measured in field nurseries includes FHB incidence (percentage of spikes exhibiting symptoms), FHB severity (percentage of symptomatic spikelets in diseased spikes), FHB index [(incidence \times severity)/100], ISK [(incidence, severity, and kernel damage) = $(0.3 \times \text{incidence} + 0.3 \times \text{severity} + 0.4 \times \text{FDK})]$, and DON (µg/g).

Four mycotoxin-testing labs are funded through the USWBSI to quantify DON concentration in FHB nursery samples. This activity has become more important with time in terms of number of samples tested and resources allocated. In Fiscal Year 2010 (FY2010), for example, the four labs handled a total of 63,416 DON samples at a cost of \$639,714, in contrast to FY1999, when these labs handled 9,720 samples at a cost of \$190,244 (S. M. Canty, USWBSI Networking Office, *personal communication*).

Cultivars released with *Fhb1* **resistance.** *Fhb1* resistance is widely used in the spring wheat region, where scab resistance is considered to be a "must have" trait by growers. Anderson et al. (2) reported that *Fhb1* resistance was present in wheat cultivars that

covered 40% of the 2011 hectarage in Minnesota, North Dakota, and South Dakota. The frequency of susceptible cultivars has declined from 76% in 1999 to 31% in 2011. Cultivar surveys are still conducted in the spring wheat region; in other areas that lack surveys it is difficult to assess the impact of a given resistance source. Although Fhb1 is widely used in the spring wheat region, Pumphrey et al. (101) estimated that this QTL conferred an average reduction of 27% in FHB-damaged kernels in spring wheat, underscoring that FHB resistance is a quantitatively inherited trait, and although Fhb1 is a major locus, it alone does not confer effective resistance. In the SRWW region, where scab also is a chronic threat, most of the moderately resistant cultivars that have been released contain FHB resistance from adapted sources. Fhb1 has not been extensively used in this region because in soft wheat backgrounds this gene is often associated with undesirable traits including low yield, and susceptibility to other major diseases including leaf rust (caused by Puccinia triticina), stripe rust (caused by Puccinia striiformis), wheat soilborne mosaic, and glume blotch (caused by Stagonospora nodorum). A backcrossing program can be used to eliminate most of the donor parent genes except for Fhb1 and other desirable QTL for FHB resistance through MAS, but the recurrent parent must also have a high level of FHB resistance, because any other FHB resistance in the donor parent that is not linked to Fhb1 will be selected against.

Since the USWBSI's inception, only the first round of parent building and cultivar release has occurred. Breeding programs have increased the frequency of FHB resistance alleles in their cultivar development populations. In the Uniform FHB Nurseries, productive lines with good end-use quality combined with FHB resistance are now appearing at greater frequencies (Fig. 3). Although progress has been steady, the incremental nature of this progress underscores the intransigence of FHB. We can expect continued improvement in degree of resistance for the mid- and long-term, yet challenges remain (7). In the winter wheat region, one of the biggest challenges is to get growers to use resistant cultivars. Perception of a yield penalty associated with FHB resistance exists among growers. If there is little or no FHB for several years, the focus of a farmer will shift away from FHB resistance in favor of new, high-yielding cultivars. In the spring wheat region, on the other hand, cultivars with the best available FHB resistance predominate. For example, the cultivars most commonly grown in North Dakota and Minnesota (>50% of the state hectarage) have at least moderate FHB resistance. 'Alsen', the first spring wheat cultivar with Fhb1, was released in in 2000. By 2003, 'Alsen' occupied 37.4% of total wheat hectarage in North Dakota, and 67.7% of the wheat hectarage in a district of North Dakota historically impacted by the disease (100). Based on hectarage grown and yield and



Fig. 3. Variation in susceptibility to Fusarium head blight between breeding lines of soft red winter wheat, Logan County nursery, Kentucky; moderately resistant on left, susceptible on right.

quality improvements achieved by 'Alsen' wheat, an estimated \$30 to \$50 million improved economic return was realized by North Dakota wheat producers in 2002 and 2003 alone.

When the USWBSI was created in 1997, breeders assumed that it was just a matter of time until resistant cultivars would solve the problem of FHB. This has not proved to be the case. It is now widely agreed that resistant cultivars must be coupled with other management strategies to withstand moderate to severe FHB epidemics.

Long-Term Genetic Improvement

It is impossible to know how emerging approaches and technologies might accelerate the development of cultivars resistant to FHB. Although commercial interest in transgenic wheat has increased over the past two years, transgenic wheat and barley lines developed by USWBSI researchers over the past decade have not demonstrated FHB resistance levels superior to those obtained through conventional breeding (R. Dill-Macky, unpublished). Other approaches, such as whole genome selection for FHB resistance, are being explored; yet we do not know how effective they will be. The search goes on for additional resistance QTL through collaborative mapping studies. Additional resistance genes selected through MAS, and deployed in homozygous lines by doubled haploid technology, should expedite the process of releasing resistant cultivars. The importance of these approaches does not eliminate the absolute, never-ending requirement for accurate evaluation of phenotypes over multiple years and locations in the field. This requirement will dictate the pace of development of resistant cultivars.

Cultural, Chemical, and Biological **Management Strategies**

Cultural. Most cultural strategies for control of FHB are based on avoiding or limiting the exposure of cereal spikes to spores during flowering and early grain fill. Following pathogenic colonization of susceptible plants, F. graminearum survives saprophytically on residues of corn, small grain cereals, and numerous other plant species and produces both macroconidia and ascospores on these substrates (97,127,139,147). Crop rotation, i.e., planting of wheat or barley following a crop that is not a host of F. graminearum, is a principal means to avoid exposure to inoculum produced on cereal residues (94,97). Tillage operations that bury infested cereal residues below the soil surface also may be employed to reduce exposure of wheat and barley spikes to spores (98). Burning of infected cereal residues reduces inoculum levels (106) but is not desirable in many environments. Residues of wheat cultivars resistant to FHB are less heavily colonized by F. graminearum than residues of susceptible cultivars, and therefore result in less inoculum potential during subsequent growing seasons (105-107). Mechanical chopping of residues may hasten the rate of decomposition of Fusarium-infested host residues, and biological control agents, fungicides, and soil amendments applied directly to residues (including green manures, bentonite clay, urea, and spent lime) may also reduce the level of colonization by Fusarium species and thus the inoculum potential of residues, but none of these treatments has been demonstrated to provide sufficient control to be effective against FHB (R. Dill-Macky, unpublished; 99).

The impact of inoculum reduction/avoidance strategies such as crop rotation and tillage may be considered for FHB management in individual cereal fields and over broader regions of cereal production. Ascospores released during the spring and summer, from perithecia that develop on crop residues, provide the primary inoculum for FHB epidemics (31,117,127). Conidia are generally dispersed short distances (meters) from debris by rain splash (95). Ascospores are dispersed in a gradient away from the inoculum source (20,57,120), but also may be aerially transported in a viable state over kilometers or even greater distances in the planetary boundary layer of the atmosphere (71) and may be deposited on distant cereal spikes by precipitation or gravitational settling (112). As a consequence, wheat and barley plants in fields without cereal

residue may also develop FHB. The management of Fusariuminfested residue by tillage would therefore likely have the greatest impact if practiced over broad production regions. Indeed, the historical pattern of epidemics indicates that the only period when FHB was of minor importance was from the end of World War II until the mid-1980s (122). This period spans the years from the introduction of tractors with sufficient power to efficiently pull a plow that could invert the top layer of soil, until the time when moldboard plowing was largely abandoned in favor of reduced tillage systems. Current soil conservation strategies (17) rely on reduced tillage to mitigate soil erosion due to wind and water, and it is not feasible to change this practice for the control of FHB. It is also very difficult to affect change in regional hectarage and sequence of rotational crops such as corn in cereal production areas. Therefore, we are left to consider the contributions of cultural measures in individual cereal fields to integrated management of FHB.

Evidence for the impact of tillage or crop rotation on FHB reduction in individual cereal fields or experimental plots is varied (8,9,28,62,85,97,129). In a small-plot field study undertaken in Minnesota to examine the development of FHB in spring wheat following previous crops of corn, wheat, or soybean under three tillage practices, FHB severity was less following moldboard plowing than following either chisel plowing or no-till treatments, and FHB severity was less in wheat following soybean than in either wheat following wheat or wheat following corn (28). Local sources of inoculum within the field contributed most of the inoculum load in this environment (28), and this study corroborated other studies in which epidemics of FHB were associated with wheat-corn rotations (62,129). Crop rotation or management of infected residue within individual wheat and barley fields may result in up to 30% reductions in FHB and DON. Studies in cereal growing environments where corn predominates suggest that spores from regional atmospheric sources result in greater FHB development and DON contamination than spores from within-field cereal debris (8,9). Therefore, in environments where atmospheric spore loads are high, there must be greater reliance on genetic and chemical control of FHB.

Some cereal producers stagger planting dates or plant cultivars differing in maturity to achieve different flowering dates across their cereal hectarage and thereby reduce the risk that their entire crop would encounter weather conditions at flowering and early grain fill favorable for *Fusarium* infection (M. McMullen, *personal communication*). These practices are most important where high-yielding cultivars with moderate resistance to FHB are not yet available.

Cultural practices may also be employed at or following the harvest of grain. Cereal producers have responded to the presence of

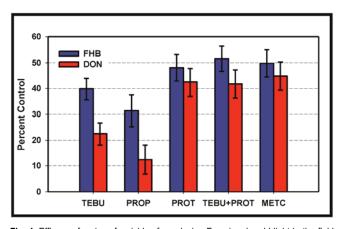


Fig. 4. Efficacy of various fungicides for reducing Fusarium head blight in the field and suppressing deoxynivalenol content in harvested grain, expressed as percent control compared to untreated wheat. FHB = Fusarium head blight index; DON = deoxynivalenol; TEBU = tebuconazole; PROP = propiconazole; PROT = prothioconazole; TEBU + PROT = tebuconazole plus prothioconazole; METC = metconazole (96).

FHB in their wheat crops by increasing the fan speed in their combines to reduce the fraction of *Fusarium*-damaged kernels in the harvested crop. Salgado et al. (108) documented that fan speeds and airflows higher than standard combine configurations resulted in consistently lower FDK and DON levels in winter wheat. *Fusarium*-damaged kernels can also be removed after harvest using seed cleaning equipment, such as gravity separators that sort the grain based on specific gravity. These practices reduce total grain quantity in the cleaned samples, but the expense of running a large harvest over a gravity table often is offset by the improved price received for the clean grain. These cleaning techniques needs to be used judiciously based on an assessment of FHB and DON levels, grain prices, and cost of practices.

Fungicides. In the 1997 feature article (79), limited text was devoted to managing FHB and DON using fungicides. This is an area that has changed radically since 1997. In 1997, most plant pathologists were skeptical that fungicides could be used to successfully manage FHB and DON. At that time, propiconazole (Tilt 3.6E, Syngenta Crop Protection) was the only "modern" fungicide labeled and marketed extensively for use on wheat in the United States; however, that product showed little potential for managing FHB (76,88). In addition, fungicide efficacy tests of other potential products had yielded inconsistent results, with low levels of disease control relative to their efficacy against other diseases (68,80, 84,143).

Attitudes regarding the use of fungicides to manage FHB began to shift in the late 1990s as more favorable research findings came to light, especially involving tebuconazole (Folicur 3.6F, Bayer CropScience) applied at or near early anthesis (13,56,72,80,128). Based on favorable research findings, as well as the imminent threat of another FHB epidemic during 1997, the state of North Dakota sought, and was granted, a Crisis Exemption, under Section 18 of the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA; http://www.epa.gov/agriculture/lfra.html), which allowed the application of tebuconazole (up to 30 days prior to harvest) for FHB and DON control. (The period from anthesis in wheat until grain harvest generally is greater than 30 days in most years in most locations in the United States.) Also in 1997, the newly formed Fungicide Technology Initiative within the USWBSI created a mechanism for developing, funding, and implementing multi-state "Uniform Fungicide Trials" (UFT) (76). Additional encouraging results with tebuconazole in the UFTs (78) fueled more interest in the use of tebuconazole to manage FHB and DON. As a result, six additional states (Illinois, Kentucky, Michigan, Minnesota, Montana, and South Dakota) were granted Section 18s allowing the use of tebuconazole in one or more years from 1998 to 2008. Data generated by UFTs were instrumental in justifying the need for tebuconazole in state Section 18 requests (46). Section 18 emergency exemptions are granted by the U.S. Environmental Protection Agency (EPA), the U.S. federal agency that approves pesticide registrations under the FIFRA act.

No studies have been conducted to determine the economic benefit of tebuconazole Section 18s across years and states. However, it is estimated that the application of tebuconazole in North Dakota to wheat and barley in 2006 resulted in estimated savings of \$47 million and \$3 million, respectively (M. P. McMullen, *unpublished data*).

Data from the UFTs suggested that other demethylation inhibitor (DMI) fungicides (i.e., prothioconazole, metconazole, and the combination of prothioconazole and tebuconazole) provided superior control of FHB and DON compared to tebuconazole (16). Paul et al. (96) subsequently conducted a multivariate meta-analysis of over 100 UFTs and concluded (Fig. 4) that the combination of prothioconazole and tebuconazole was the most efficacious fungicide for suppressing FHB (52% control compared to the nontreated check), followed by metconazole (50%), prothioconazole (48%), tebuconazole (40%), and propiconazole (32%). For DON suppression, metconazole was the most effective product (45% suppression), followed by prothioconazole alone (43%) or when mixed with tebuconazole (42%), tebuconazole (23%), and propiconazole

(12%). Fungicides were significantly more efficacious in spring wheat compared to winter wheat at suppressing both FHB (50% control across fungicides in spring wheat compared to 37% in winter wheat) and DON (40% control in spring wheat compared to 27% in winter wheat). It has been suggested (46,96) that reduced fungicide performance in winter wheat is related to longer anthesis periods in winter wheat compared to spring wheat.

In late 2006, Proline 480 SC (prothioconazole, Bayer Crop-Science) was approved by the EPA under Section 3 (full federal registration) of FIFRA for use on wheat; however, the manufacturer marketed that product to only a limited extent for wheat in the United States. In the spring of 2008, EPA approved Section 3 label registrations for the use of additional DMI fungicides on wheat. These included: Folicur (tebuconazole) and various generic tebuconazole products; Prosaro 421 SC (prothioconazole plus tebuconazole, Bayer CropScience); and Caramba 0.75 SL (metconazole, BASF Corporation). In recent years, these fungicides have been economically applied to wheat in many states for suppression of FHB and DON, as well as for the control of other foliar and head diseases caused by fungi (104,141). At the time of this writing, there are no new fungicides being developed that show superior performance against FHB and DON compared to fungicides already available (14). Currently labeled and recommended fungicides for use in managing FHB and DON in the United States are all DMIs (16). Although various quinone outside inhibitor (QoI) fungicides or fungicide combinations that contain a DMI and a QoI are labeled for use on wheat in the United States, none of them is used for FHB and DON suppression. This is because use of a QoI is frequently associated with greater DON concentration in grain compared to nontreated wheat (86,87,103). Because of this increase in levels of DON, QoI fungicides are not used for managing FHB because DON contamination of grain is such an overriding consideration in terms of global food safety (87).

Determining if the risk of FHB is great enough to justify applying a fungicide and achieving excellent coverage of heads with fungicides in a timely manner remain significant challenges for FHB management with fungicides. Recent advances in FHB modeling and disease prediction have helped growers evaluate the risk of disease during the growing season and thus determine the need for fungicides (25). Similar advances in application technology during the same period have also helped improve the efficacy of fungicide treatments (36). Despite these advances, the timely application of fungicides remains a challenge for producers because the period for application is short (generally being limited to the anthesis period) and periods of high disease risk often coincide with wet weather, which hinders spraying operations. These constraints have prompted several recent studies focusing on how early or late into anthesis fungicides can be applied and still be effective for suppressing FHB (14,15). Results suggest that similar FHB suppression levels can often be achieved when fungicides are applied just before the start of anthesis (Feeke's stage 10.5), at beginning anthesis (stage 10.51), and in some situations, 5 days into anthesis (10.51 + 5 days). However, current fungicide labels have a 30-day preharvest interval, which dictates how late fungicides can be legally applied for FHB suppression, regardless of biological activity and effectiveness of post-Feeke's stage 10.51 applications.

Suppression of FHB and DON in malting barley with fungicides has received modest attention over the past 13 years. Several states in the Northern Great Plains region have included barley in UFTs since 1998. Progress, however, has been slow compared to wheat because of the difficulty in achieving the brewing industry's DON standard of <0.5 µg/g for malting barley (10). Nonetheless, management of FHB and DON in malting barley involves the same fungicides as used for wheat (56), albeit the timing of application is slightly different (full head emergence for barley rather than early anthesis) because anthesis in barley occurs when the head is still in the leaf sheath (boot). Early full head emergence in spring barley generally occurs at least 30 days prior to harvest. Like wheat, success in managing FHB and DON in malting barley (and feed-grade barley, when economical) is highly dependent on the use of all available management tactics as part of an integrated management strategy (10).

Fungicide application technology. Fungicide application methods for foliar disease management proved ineffective against FHB. Specifically, applications targeting foliar diseases direct spray downward in order to maximize coverage of foliage. Targeting foliar disease results in little fungicide being deposited at the infection sites located on the vertically oriented spikes. Additionally, fungicides used for FHB management (DMIs) are only "locally" systemic, and thus primarily effective at the site of contact, so good coverage of the spike is essential.

In the late 1990s, plant pathologists and agricultural engineers at North Dakota State University and Michigan State University began examining a number of spray application variables that could affect deposition and spread of fungicide on grain spikes (56,78,93,132). The variables examined for ground equipment included: nozzle type and configuration on the spray boom; droplet size; speed during application; spray pressure; liters of water per hectare; and use of adjuvants. Similar studies were also being conducted in Canada (50). Variables with aerial equipment also were

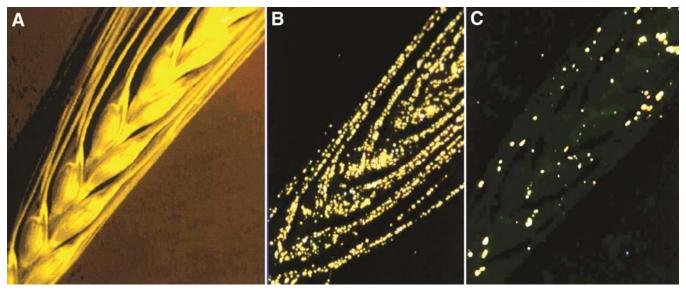


Fig. 5. A, Incandescent light image of a wheat head. B, Fluorescent dye image of spray coverage after wheat head was sprayed using an XR800 angled spray nozzle. C, Fluorescent dye image of spray coverage after wheat head was sprayed using a Turbo drop TF01 nozzle.

studied, primarily looking at nozzle configuration, droplet size, spray pressure, and water volume (32,48).

Initial application studies were carried out mostly in field research plots, with tractor-mounted or hand-held sprayers, and application speeds of 6.4 to 9.6 km/h (4 to 6 mph); or in a greenhouse equipped with a specially designed track sprayer. Studies used food grade dyes or UV dyes and fluorescent light detection systems to determine extent of coverage of spray materials delivered under various conditions (Fig. 5A to C). Results from these early studies indicated that, for ground equipment, dual XR8001 flat fan spray nozzles (Fig. 6A) angled 30 degrees from the horizontal, delivering droplet sizes between 300 to 350 µm (microns), sprayed at 140 liters/ha (=10 gpa), and using a nonionic surfactant as an adjuvant, were optimal conditions for maximum fungicide coverage of the spikes (132). Subsequent studies in North Dakota determined that similar coverage (and disease control) could be achieved by commercial sprayers traveling at 16 km/h (=10 mph) or greater, delivering fungicide in 140 liters/ha (=10 gpa), using a single flat fan nozzle, angled at 30 degrees from the horizontal or less (Fig. 6B), and droplets 300 to 350 µm (microns) in diameter (41,42). Based on research studies with aerial application equipment, the recommendations were also to use a 300 to 350 µm size spray drop, but with a minimum spray pressure of 0.21 MPa (=30 psi), using 47 liters/ha (=5 gpa), and applying at a distance of 2.4 to 3 m (=8 to 10 ft) or 3 to 3.6 m (=10 to 12 ft) above the canopy for smaller (slower) and larger (faster) aircraft, respectively

Despite advances made in fungicide application technology over the past decade, using fungicides to manage FHB and DON will likely always be hampered by a variety of challenges that either result in imperfect timing of application or inadequate coverage. Wet fields pose perhaps the greatest challenge in scheduling proper fungicide applications. Other challenges include uneven heading in fields, a short period of flowering during which applications must be made to be most effective, low spray volumes and fast ground speeds, uneven terrain, or irregular field shapes with obstacles that encourage uneven spray application. These challenges will remain no matter how advanced spray equipment becomes. Application of biological agents to spikes poses similar challenges.

Prospects for biological control. The incomplete efficacy of cultivar resistance, cultural practices, and foliar fungicides warrants research to develop and deploy additional tools for integrated management of FHB. Biological control could play an especially important role in protecting against FHB in organic cereal production where fungicides cannot be used. Biological control has been explored by investigators around the world as a possible weapon



Fig. 6. A, Hand-held sprayer used for research studies with various nozzle configurations, forward/backward XR8001 flat fan illustrated, 276 kPa (40 psi), 168 liters/ha (18 gpa) at ~6.4 km/h (4 mph) (41,42,93). **B,** For commercial ground application of fungicides with a tractor-mounted sprayer at 16 km/h (10 mph) and 94 liters/ha (10 gpa), a single forward nozzle gives almost as much coverage and disease control as forward/backward nozzles used at slower speeds. The nozzle illustrated is a forward flat fan nozzle angled toward the grain head using a single swivel nozzle adapter (42).

against FHB (38,54,58-60,70,92,110,111,135,149), although to date no biological control method is in widespread use against the disease. USWBSI-associated scientists have conducted laboratory, greenhouse, and field research with gram positive bacteria (Bacillus amyloliquefaciens and B. subtilis) (19,59,60,69,70,110), gram negative bacteria (Lysobacter enzymogenes) (55), and yeasts (Cryptococcus nodaensis and C. flavescens) (59,60,110,111) as potential biological control agents against F. graminearum. The main target for biological control agents has been initial infection of cereal florets by the pathogen. Significant reductions in both disease and mycotoxin contamination have been documented consistently in greenhouse experiments and occasionally in the field. Biological control agents may also prove useful for application to cereal residues to limit the inter-season survival of F. graminearum and reduce the potential for spore production. Important modes of action by different biological control agents on cereal spikes include competition for nutrients (Cryptococcus), induction of localized resistance (Lysobacter), and production of antifungal metabolites (Bacillus). In uniform field tests conducted by USWBSI investigators to assess the efficacy of biological control agents alone and combined with DMI fungicides in wheat and barley, biological control agents, by themselves, have seldom shown consistent or sufficient control of FHB and DON, but in several tests, these agents have enhanced the protection afforded by DMI fungicides (43,55,151). Biological control agents could yet make a large contribution to integrated management of FHB and DON if they can be enhanced to provide sufficient protection of florets past full anthesis when DMI fungicides can no longer be legally applied. Improved control with already identified biological control agents may result from advances in formulation, application technology, or the use of genetic enhancement or exogenous stimulants to increase colonization and metabolic activity of these agents on cereal spikes. Biological control strategies of the future might also utilize small peptides of microbial origin, such as mating pheromones derived from F. graminearum, to protect cereal florets from infection by the pathogen (150).

Fusarium Head Blight Forecasting

Prediction models for FHB. FHB epidemics are sporadic, and it is common for a region to experience severe epidemics for two or more years followed by several years of relatively little disease. The sporadic nature of FHB epidemics means that growers must decide each year whether fungicides are needed to suppress the development of FHB. Incorrectly evaluating the risk of disease could result in severe yield losses and extensive DON contamination of harvested grain in years when FHB epidemics occur, or unnecessary input costs when the disease is absent. This decision is further complicated by large fluctuations in grain prices and the brief period for application of fungicides for suppressing FHB, which is typically before any symptoms of disease appear. Until recently, growers lacked a means to make reasonable FHB risk assessment, which hindered the use of fungicides to suppress FHB and DON. One of the goals of the USWBSI was to develop a predictive model that could help growers better evaluate disease

Prior to the development of FHB prediction models, wheat producers relied on qualitative reports of weather conditions associated with past FHB epidemics and personal experience to determine if a fungicide application was needed. Producers would be watching for periods of rainy, humid weather during anthesis when the plants were most vulnerable to infection. The association of wet weather with outbreaks of FHB is well documented in accounts of both historic and recent epidemics of FHB (1,4,5,79) and is mentioned in most general descriptions of the disease (27,90). With the advent of disease prediction models, producers were given access to tools that could help them quantify the risk of disease and the need for fungicide applications. Advanced notification of an FHB epidemic could also help the agriculture industry and food processers prepare for the potential of grain damaged by FHB, thus further reducing the impact of the epidemic.

Work on the FHB prediction models began in 1999, and benefited greatly from the cooperative approach fostered by the US-WBSI. Researchers from several institutions combined historical data from the three major market classes of wheat (hard red spring, hard red winter, and soft red winter) and very different production environments. By working together, the cooperating researchers accomplished in a few years what would have taken a single institution many years to accomplish.

The initial models developed for wheat for use in the United States considered weather conditions during both the pre- and postanthesis time periods, which coincide with critical periods for inoculum production and infection by Fusarium, respectively. One of the first pre-anthesis models used the duration of rainfall (hours) and duration of temperatures between 15 and 30°C for the 7 days prior to anthesis (21). Other, more accurate post-anthesis models combined both temperature and relative humidity into a single variable. The simplest of these models used the duration of hours that relative humidity was >90% when temperatures were between 15 and 30°C for the 10 days after anthesis. The accuracy of the pre- and post-anthesis models was 70 and 84%, respectively, based on the data available at the time of development.

Several iterations of model development have occurred since the first generation models. Each of these iterations sought to incorporate new information generated by cooperative research efforts within the USWBSI, expand the geographical regions represented in the model, and account for new sources of variation. One important milestone in the modeling effort occurred in 2004 when variables representing influence of genetic resistance (available primarily in spring wheat at that time) on the risk of FHB epidemics were incorporated into the model along with the environmental variables (85).

Advances in the models used in the winter wheat production regions were facilitated by additional observational data but also by new research on the reproduction of F. graminearum. The research indicated that the fungus was capable of producing spores below the 15°C threshold used in the early prediction models (29,130). Adjusting the temperature range in these models helped to maintain prediction accuracy to near 70% for regions producing winter wheat (22,85).

The current models perform reasonably well, but there is still need for improvement. The accuracy of the current spring wheat model remains near 75%. The accuracy of the current winter wheat model is also similar to the 70% benchmark set during its development, based primarily on a strong specificity (ability to predict nonepidemics).

The data collected through the cooperative efforts of the US-WBSI continue to open new possibilities for model development by accounting for the influence of genetic resistance in winter wheat, and exploring the potential role of crop residues on disease risk (D. Shah, E. De Wolf, P. Paul, and L. Madden, unpublished). In recent years, the focus of the modeling effort was expanded to include DON levels as well as severity of FHB as seen in the field.

Deployment of the prediction models. Application of the prediction models began in 2003, but the deployment of the models was largely left to individual states, and ranged from descriptions of disease risk published in extension newsletters to statewide de-

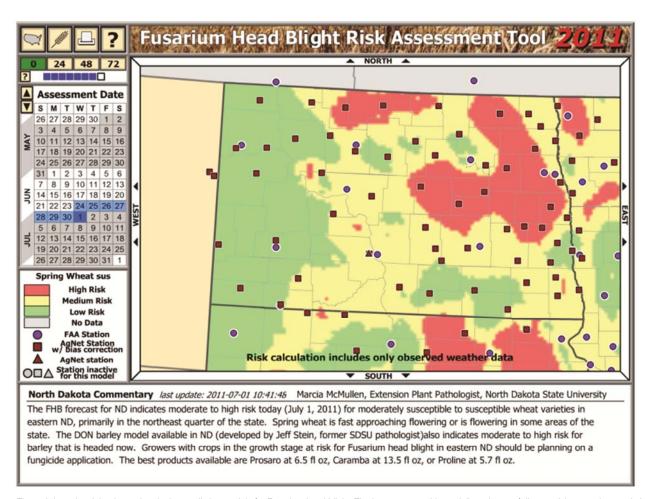


Fig. 7. The web-based tool that is used to deploy prediction models for Fusarium head blight. The base map provides a daily estimate of disease risk on a 5-km resolution in 30 states and is shown here zoomed in to North Dakota. Points on the map represent weather stations that are maintained by either the National Weather Service (blue circles) or the North Dakota Agriculture Weather Network (red squares). The text below the map is a commentary developed by a disease specialist for the selected state. A calendar on the left side of the map allows users to identify dates that are most relevant to the growth stage of the local crop. Selection of the weather station displays summaries of disease risk and weather observations for that location. The models and user interface were developed through cooperative effort between researchers Kansas State University, The Ohio State University, and The Pennsylvania State University.

ployments where automated summaries of disease risk within a state were summarized in tables and made available through extension websites. The NDSU Small Grain Disease Forecasting Model is one example of how the products of the USWBSI modeling effort have been successfully used by individual states. This webbased deployment of the prediction models can be accessed online at http://www.ag.ndsu.nodak.edu/cropdisease/.

Regional deployment of the models began in 2004 with a three-state effort including Pennsylvania, Ohio, and New York. This regional deployment of the models was greatly aided by a multi-disciplinary effort among plant pathologists, meteorologists, geographers, and GIS specialists working at The Pennsylvania State University and The Ohio State University. During the next two years, the model was deployed in 23 states that had experienced severe epidemics of FHB in recent years. The large-scale deployment of the models was enhanced by access to weather information provided by the National Weather Service and capitalized on investments by the federal government in atmospheric modeling.

This cooperative effort continued to expand, fueled in part by the availability of fungicides brought about by Section 18 labeling and eventually the full EPA approval of several DMI fungicides (see fungicide section). Currently, the FHB prediction models are used to develop daily estimates of disease risk for 30 states, making it one of the largest disease prediction efforts ever deployed. The current deployment of the models delivers the daily estimates of disease risk through a specialized web-based tool (www. wheatscab.psu.edu; Fig. 7). The tool provides information ranging from statewide maps of disease risk to 7-day summaries of risk level from specific weather stations. Text commentary describing the status of the crop, local weather, and risk of disease is also displayed along with the risk maps. This commentary is provided by cooperating disease specialists and is available for nearly all of the participating states.

Beginning in 2009, the USWBSI launched an effort to further improve communication of disease risk with "FHB Alerts". The FHB Alerts send the commentary developed for the disease prediction effort to e-mail lists, or as text messages sent to cellular phone users notifying them that the commentary has been updated. The information is also presented on a blog site maintained by the

USWBSI. This blog provides readers with detailed summaries of FHB risk and updates on emerging disease problems from throughout the United States in a single location (44).

Surveys of users of the prediction tools and the FHB Alerts were conducted in 2009 and 2011 (23). The surveys involved more than 1,000 participants and provided information about who is using the information, how it is being used to help manage FHB, and the



Fig. 9. Examples of Outreach activities of the U.S. Wheat and Barley Scab Initiative (USWBSI). **A,** Example of Initiative's Fusarium Focus newsletter. **B,** Home page of Scab Smart website (www.scabsmart.org). **C,** Front page of Scab Smart brochure.

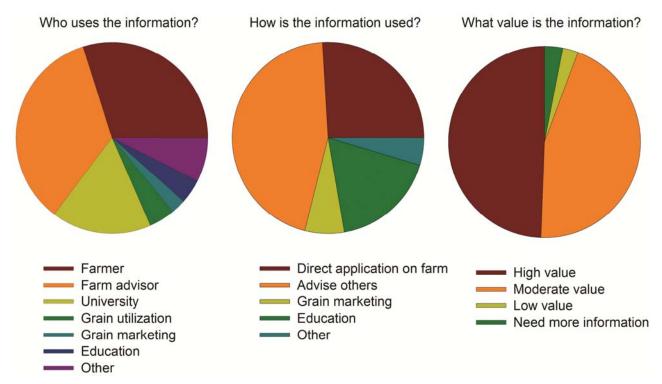


Fig. 8. Summary of survey results for the Fusarium head blight (FHB) prediction models and the FHB Alerts. The survey was conducted in 2009 and 2011 and included 1,486 users of the internet-based prediction tools and the FHB Alerts.

value of the information (Fig. 8). While direct measure of the economic impact of the FHB prediction models is unavailable, current estimates indicate that annual value of the information provided by the prediction models and the FHB Alerts exceeds \$47 million.

Integration of Management Strategies

Crop rotation, improved cultivar resistance, or improved fungicide efficacy and timing has benefited producers in years or locations with low disease pressure. However, when environment is highly favorable for infection, use of a single management strategy often fails to control the disease and hold DON to acceptable levels. To hold DON to manageable levels, 75% reduction in FHB index must be obtained when disease pressure is great (144). Use of the best available resistant cultivars and fungicides can provide this level of control, based on multivariate analysis of data over 40 trials across 12 states, conducted from 2007 through 2010 (144). A combination of the best resistance available and optimum fungicide use resulted in 76 and 71% reduction, respectively, for estimated mean percent control of FHB index and DON relative to an untreated susceptible check. The combination of fungicide application and resistance was additive in terms of percent control for FHB index and DON, and efficacy across environments was more stable for both FHB index and DON than for either approach (fungicide or resistance) used alone. Similar studies in the Czech Republic, with a combination of fungicide and cultivar resistance, showed up to 86.5% reduction in DON (118).

In the United States, a few studies also included a previous crop as a factor in addition to fungicide and cultivar response, and results showed that when the previous crop was not a host for F. graminearum, the FHB index was further reduced by 10% and DON by 15% over that achieved for use of a resistant cultivar plus an effective fungicide (145). In North Dakota and Minnesota, results of a survey of wheat growers indicated that 81% of respondents use a cultivar with improved resistance, 76% rotate wheat away from wheat or corn ground, 68% apply a fungicide, and more than 50% use all three strategies at once (74). The use of fungicides in this integrated approach is based on risk as indicated by the FHB forecasting model.

Major research accomplishments

Identification of additional sources of resistance that are being incorporated into breeding lines.

QTL identified and used in breeding programs.

MAS, double haploids widely used in breeding programs.

Cooperative screening nurseries established; resources shared; coordinated projects established within grain classes.

Pathogen lineages and dominant chemotypes identified.

Elucidation of role of DON in pathogenicity.

Establishment of uniform, cooperative fungicide trials

Further understanding of environmental effects on disease.

Further understanding of spore dispersal and pathogen survival.

Establishment of high throughput genotyping centers and identification of useful genetic

Use of genomic, transcriptomic, and proteomic approaches to understand host pathogen interactions.

Adaptation of transformation systems for wheat cultivar development.

Impacts

Development and release of wheat cultivars resistant to FHB

Identification and registration of efficacious fungicides.

Improved fungicide application methods identified.

Accurate disease forecasting models deployed.

FHB alerts deployed and used.

Value of integrated strategies demonstrated.

Outreach network established.

Use of Scab Smart web site by growers and industry.

Continued Challenges

Incorporation of resistance into wheat, durum, and barley cultivars with superior agronomic traits and quality.

Identification and incorporation of more QTL for resistance.

Success with and acceptance of transgenic cultivars.

Monitoring changes in the biology of the pathogens: virulence, toxin production, sensitivity to fungicides.

Development of improved fungicides and biological control agents; improved application methods.

Better information delivery methods to reach more producers.

Fig. 10. Accomplishments, impacts, and continued challenges in managing Fusarium head blight (FHB).

Outreach

An important goal of the USWBSI has been to deliver research discoveries to producers and the agriculture industry that will allow them to make informed decisions. As stated earlier, the mission of the USWBSI is "to develop, as quickly as possible, effective control measures that minimize the threat of FHB, including the reduction of mycotoxins, to the producers, processors, and consumers of wheat and barley". Information has been disseminated through a variety of avenues:

Publications and other state outreach. Over the past decade, many states have produced and disseminated a variety of electronic and print extension publications about FHB and its management. Short videos on FHB have also been posted on the online network YouTube. State commentaries on FHB risk, generally written by extension specialists, have been made available to people through the FHB Risk Prediction Center, maintained by The Pennsylvania State University. Through FHB Alerts, farmers and others can sign up to receive instant notification by cell phone or e-mail when state or regional commentaries have been updated. State extension specialists also conduct field demonstrations and meetings to educate growers about FHB management strategies. These state-based publications and information sources are essential because they allow scientists in each state to tailor FHB information to meet the needs of that state's clientele. Information generated by USWBSI researchers is also an excellent resource for producers, commodity groups, and public policy makers.

ScabUSA website (http://www.scabusa.org). This website is an excellent resource, not only for research and extension scientists working on FHB, but also for producers, industry, and policy makers. The website allows users to access a wealth of information on FHB, including: information on all the research areas of the US-WBSI, summaries of research progress, publications on FHB, management tools for both growers and industry, information about the disease, newsletters, news releases, and more.

Fusarium Focus newsletter. The USWBI has published newsletters about the Initiative's activities since the spring of 1998 (Fig. 9A). All newsletters may be accessed under the news section of the website (http://www.scabusa.org). Since the fall of 2001, the newsletter has been published as the *Fusarium Focus*, with two to three issues per year. The newsletter contains annual summaries of the extent of FHB in the United States, highlights of annual FHB forums and other meetings, research results, and impacts.

Scab Smart website. The USWBSI supported the development of a website that provides scab management information for all small grain classes affected by this disease in the United States. The website, Scab Smart (Fig. 9B) (http://www.scabsmart.org), is intended as a quick guide to good management strategies. Scab Smart provides the latest information on: (i) cultivar responses for eight grain classes grown in the United States; (ii) fungicides registered; (iii) fungicide application timing and application technology; (iv) crop rotation strategies; (v) residue management; (vi) harvesting tips; (vii) scab forecasting; and (viii) seed treatment. The Scab Smart website also serves as a portal for links to additional information, provided on the USWBSI website or other local resources, on management strategies for FHB and DON. Scab Smart, launched on 24 September 2009, is continuously updated through the USWBSI network. A brochure to promote the Scab Smart website has been developed and distributed to potential users in each participating state (Fig. 9C).

Summary and Future Directions

Fusarium head blight is a difficult disease to manage. However, substantial progress in understanding the pathogen, the genetics of resistance, and epidemiology, and in developing successful strategies for FHB management have been achieved in the last 15 years (Fig. 10). More complete understanding of the pathogen and host mechanisms of resistance is certainly needed. Before creation of the USWBSI, funding for FHB research was often curtailed when environments became less favorable for the disease (142).

However, with recurring epidemics across various grain classes and regions across the United States in the past 15 years, and with increased international scrutiny of mycotoxin content in food, the sustained funding provided in part by the USWBSI has been critical for success in improving management solutions for this potentially ruinous disease.

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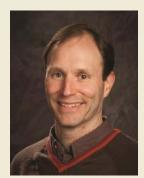
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Marcia McMullen



Gary Bergstrom



Erick De Wolf



Ruth Dill-Macky



Don Hershman



Greg Shaner



Dave Van Sanford

Dr. McMullen is a professor and extension plant pathologist at North Dakota State University, Fargo. She received her B.S. and M.S. degrees from Iowa State University, Ames, and her Ph.D. in plant pathology from North Dakota State University. She joined the faculty at North Dakota State University in 1984. She provides leadership for outreach education in North Dakota on management of cereal diseases and on Integrated Pest Management. Her applied research efforts have concentrated on management strategies for leaf and head diseases of wheat and barley. She has been active in the U.S. Wheat and Barley Scab Initiative since its inception and served for 8 years on its executive board.

Dr. Bergstrom is professor of plant pathology at Cornell University, where he has been a faculty member since 1981 with responsibilities for research and extension on the biology, epidemiology, and integrated management of field crop diseases in New York. He received degrees from Purdue University (B.S. in microbiology and M.S. in plant pathology) and the University of Kentucky (Ph.D. in plant pathology). Bergstrom is a fellow and past president of the American Phytopathological Society, as well as a recipient of the Distinguished Agricultural Alumni Award from Purdue University and the Excellence in Applied Research Award from Cornell's College of Agriculture and Life Sciences. He currently co-chairs Cornell's Integrated Field Crop, Soil, and Pest Management Program Work Team.

Dr. De Wolf is an associate professor in the Department of Plant Pathology at Kansas State University, where he serves as an extension plant pathologist specializing in diseases of wheat and other small grains. He received a Ph.D. in plant pathology from North Dakota State University in 2000, and was a postdoctoral researcher at The Ohio State University/OARDC in Wooster, OH. Dr. De Wolf held a faculty position at The Pennsylvania State University as an extension plant pathologist from 2001 to 2007, when he assumed his current position at Kansas State University. His research interests include plant disease epidemiology and disease management. He is particularly interested in the relationship of weather with disease epidemics and the development of disease forecasting systems.

Dr. Dill-Macky is a plant pathologist and professor in the Department of Plant Pathology at the University of Minnesota specializing in small grains. She earned her B.Sc. (Hons) and Ph.D. degrees in botany at The University of Queensland, Australia. She worked as a plant pathologist at the Queensland Wheat Research Institute, Toowoomba, Australia from 1984 to 1992, and as a re-

search associate at the Cereal Rust Laboratory, St. Paul, MN from 1992 to 1994. She joined the faculty at the University of Minnesota in 1994. Her applied program in small grains pathology focuses on disease management through the use of host resistance and cultural control practices. She has been active in the U.S. Wheat and Barley Scab Initiative since its inception and has served on the executive committee since 2000.

Dr. Hershman is an extension professor and plant pathologist in the University of Kentucky's Department of Plant Pathology. He earned a B.A. in biology at West State College in 1978, and M.S. and Ph.D. degrees in plant pathology at Rutgers University in 1981 and 1983, respectively. He joined the faculty at UK in 1984, housed at the Research and Education Center in Princeton. He has statewide extension and applied research responsibilities for small grains and soybean. In addition, he supervises the Plant Disease Diagnostic Laboratory located at the UKREC and is the current extension coordinator for the department. His research interests focus on chemical and nonchemical control of diseases of wheat and soybean, as well as soybean cyst nematode management.

Dr. Shaner is professor emeritus of botany and plant pathology at Purdue University. He spent his career at Purdue working on diseases of field crops: genetic resistance, epidemiology, and management with fungicides. During his last 15 years at Purdue, he was an extension specialist for field crop diseases. He also taught various courses in plant pathology, botany, and scientific writing. Since his retirement, Dr. Shaner volunteers with various urban forest organizations and a local land trust, gardens, and spends time with his grandchildren.

Dr. Van Sanford is professor and wheat breeder in the Plant and Soil Sciences Department at the University of Kentucky. He earned his B.S degree from Oregon State University, M.S. from Colorado State University, and Ph.D. from North Carolina State University. His program focuses mainly on the development of high-yielding, scab-resistant soft red winter wheat cultivars. He conducts research on the use of native and exotic scab resistance genes and their indirect impact on agronomic and end use quality traits. Dr. Van Sanford has authored or co-authored numerous refereed journal articles, abstracts and research and extension publications. He was Chair of the National Wheat Improvement Committee from 2000 to 2005, and since 2006 has served as co-chair of the U.S. Wheat and Barley Scab Initiative's Steering Committee and director of the initiative's networking and facilitation office.

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