

Special Report

University of Minnesota Small Grains Research Initiative Update

New UM Wheat Variety Released as 'RB07' in January 2007

The objectives of accelerated breeding of disease-tolerant wheat at the U of M are to:

1) Develop high yielding, hard spring wheat germplasm and varieties with improved resistance to FHB, other diseases, and acceptable agronomic and end-use characteristics.

2) Investigate and implement new selection strategies for Fusarium head blight resistance

using both marker and field-based approaches.

The experimental line MN99436-6 was released as 'RB07' in January 2007. Named after former USDA-ARS Research Geneticist and wheat breeder Robert Busch, RB07 is an early, high-yielding semi-dwarf with good straw strength and moderate resistance to Fusarium head blight.

Two other advanced experimental lines have



A sample of RB07, UM's new wheat variety

high grain yield, good grain quality, resis-

tance to leaf rust and improved resistance

to FHB, comparable to Alsen. Data from the last three years have indicated that U of M releases and variety candidates have improved levels of scab resistance (Table 1).

Our project continues to identify other lines with high levels of scab resistance. Five scab resistant lines were entered into a regional scab nursery in both 2005 and 2006. A U of M experimental line had the lowest DON and visual scabby kernel rating of the 43 entries (representing 8 breeding programs) in the 2005 nursery. Unfortunately, these highly resistant lines have other characteristics that make them undesirable variety candidates, such as low yield, excessive height, or weak straw. Nevertheless, they are used as parents by our program and others in the region as we continue to incorporate the highest levels of scab resistance into agronomically acceptable varieties.

During 2006, FHB nurseries were estab-

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UM wheat breeder Jim Anderson demonstrating the marking of rows for scab inoculation at anthesis time.

Characterizing New Source of FHB Resistance from Australia

USDA-ARS wheat geneticist David Garvin and U of M plant pathologist Ruth Dill-Macky are characterizing a new source of FHB resistance in wheat that comes from a geographic region where one might least expect to find it - Australia.

FHB is not a serious disease on wheat in Australia, and thus selection for resistance to FHB has not been a focus of wheat breeding programs there. Several years ago, Garvin found that an Australian wheat line he was using for research on acid soils exhibited high levels of FHB resistance. Since then,

he and Dill-Macky have collaborated on research into the FHB resistance of this wheat line.

First, Dill-Macky's program confirmed the FHB resistance of this wheat line. Indeed, in greenhouse studies the line being investigated exhibits FHB resistance that can approach that found in Alsen. Garvin found that neither pedigree information nor molecular marker data pointed to a likely origin of the FHB resistance present in this line, and thus the two researchers believe that the resistance may be different than that found in Chinese germplasm such as

Sumai 3.

They are now completing genetic studies of FHB resistance in this line, and are undertaking prebreeding research to introduce the resistance into hard red spring wheat. Ultimately, they hope that this Australian wheat line will provide additional FHB resistance genes that hard red spring wheat breeding programs can employ to further protect this crop against FHB.

USDA-ARS wheat geneticist Dr. David Garvin (garvi007@umn.edu) works in cooperation with U of M crop scientists



This Australian wheat genotype is a promising source of novel FHB resistance genes that can be introduced into hard red spring wheat.

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lished at Crookston, Morris, and St. Paul. These nurseries were inoculated and misted to enhance disease and involve collaboration with agronomists at Crookston and Morris, and personnel from the Plant Pathology Department. The nursery at Crookston produced excellent data, but scab levels were low in the Morris and St. Paul FHB nurseries, probably due to continually high temperatures. More than 2,000 wheat lines were characterized for their FHB resistance in these field nurseries.

Data on FHB severity (spread of disease symptoms within the

Table 1. Comparative Performance of Recent U of MN Wheat Varieties and Experimental Lines.

Variety	Release Year	Days to Heading	Height (cm)	Straw Strength	Test Weight (Lb./Bu.)		Protein (%)		Baking Quality
					2006	2 yr.	2006	2 yr.	
Oklee	2003	53.7	75	medium	61.3	60.5	14.7	14.9	low-med.
Ulen	2005	53.8	82	medium	61.1	59.8	14.7	15.0	med.
Ada	2006	56.0	77	m. strong	62.0	61.0	14.3	14.6	med.-high
RB07	2007	53.9	76	m. strong	60.8	59.7	14.7	14.9	med.-high
MN Exp. 1	Experimental	57.8	76	m. strong	61.9	61.0	14.5	14.8	med.-high
MN Exp. 2	Experimental	55.9	81	medium	61.8	60.6	14.3	14.6	med.-high
Mean (~25 varieties)		55.7	78.8		61.3	60.0	14.3	14.3	
No. Trials		7	7	20	7	13	7	13	6
LSD (0.05)									

¹ 1-9 scale where 1 = most resistant, 9 = most susceptible

spike) was collected for all materials in the Crookston and St. Paul nurseries. At least 50 spikes of grain were harvested from the Crookston nursery and

selected materials in the St. Paul nursery. These samples were tested for vomitoxin and/or visual scabby kernel (VSK) assessment. FHB resistance ratings of named

varieties were reported in Prairie Grains magazine, Minnesota Varietal Trials Results, the 2007 Small Grains Update tour and field days at Crookston and Morris.

Beginning in 2006, we changed our FHB rating from the R-S scale for spike disease symptoms and 1-5 scale for kernels to a single 1-9 scale in which 1 = most resistant

Field and Greenhouse Evaluation of Breeding Lines for Resistance to Major Foliar Diseases

The use of resistance in the host plant is the most economic and environmentally friendly method for controlling most plant diseases. University of Minnesota plant pathologists Ruth Dill-Macky and Brian Steffenson, have been working at the St. Paul campus to assist the plant breeding programs led by Jim Anderson (wheat) and Kevin Smith (barley) to improve the resistance of wheat and barley to multiple diseases important to Minnesota.

These plant pathologists screen material in

St. Paul, and at other locations in Minnesota, for their response to the foliar diseases of wheat and barley such as tan spot and Septoria tritici blotch (STB) of wheat, and net blotch, Septoria speckled leaf blotch (SSLB), spot blotch and stem rust of barley.

The breeding efforts aimed at improving FHB resistance led to the introduction of many new wheat and barley lines into the breeding program. While this was essential to improve the FHB resistance, susceptibility to other diseases

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Researchers at the U of M spray wheat and barley lines with *Fusarium inoculum* (fungal spores suspended in water) to analyze disease tolerance. Plant pathologists also screen material for their response to other foliar diseases of wheat and barley such as tan spot as well as leaf and stem diseases.

Pre-Harvest Sprouting	Disease Reactions ¹			Grain Yield (% of Trial Mean) Statewide Trial			Grain Yield (% of Trial Mean) On-Farm Trial		
	Leaf Rust	Other Leaf Diseases	Scab	2006	2 yr.	3 yr.	2006	2 yr.	3 yr.
Res.	4	4	5	95	101	101	104	104	102
Mod. Sus.	3	5	6	107	107	108	105	105	104
Res.	2	3	6	97	100	101	98	100	-
Res.	2	4	5	106	106	107	105	111	110
Res.	3	3	4	100	101	103	95	101	102
Res.	2	3	4	100	109	107	102	-	-
				71	62	66	65	64	72
6				7	14	20	4	7	12
				8.3	9.2	7.0	13.5		

and 9 = most susceptible.

DNA Marker Screening

Our DNA marker screening efforts were

two-fold during the past year:

- 1) Large-scale screening of segregating lines that are supported by the U.S. Wheat and Barley Scab Initiative and

USDA-CSREES funded WheatCAP project; and

- 2) Parental characterization that we do primarily in-house and is supported by the Minnesota Small Grains

Initiative.

All parents that are used in crossing (60-70 per year) were screened for the presence of critical DNA markers (and linked genes). This

includes two genes for FHB resistance, a gene for tan spot resistance, high grain protein, high molecular weight glutenins, and semi-dwarfing genes.

One result of the parental screening is that we learned which of our elite breeding materials contained important genes, thereby directing future DNA marker screening of crosses. This database also helps us decide which crosses to make to be sure that the resulting progeny contain all the desired genes.

– Dr James A. Anderson, wheat breeder, ander319@umn.edu

Mapping Leaf Disease Resistance in Barley

Our Small Grains Initiative grant is directed toward implementing marker-assisted selection (MAS) to improve disease resistance in barley. While Fusarium head blight (FHB) remains the highest priority in that effort, this year's report will focus on progress toward MAS in two leaf diseases.

After FHB, net blotch and Septoria speckled leaf blotch are the two most important diseases for barley in Minnesota. Under conducive conditions, both diseases can cause substantial yield losses.

The UM Barley Breeding Program currently screens for resistance to these diseases using seedling assays in the greenhouse and field nurseries. This work is done in collaboration with Ruth Dill-Macky, Brian Steffenson, and Charla Hollingsworth in the Department of Plant Pathology.

In parallel with our breeding effort, we have conducted several genetic studies to map the position of resistance genes for these diseases. Once we have mapped the position of resistance genes to particular segments of chromosomes, we can

use DNA markers to select for the genes via MAS.

The advantages of using MAS to conduct selection is that it does not require field or greenhouse screening (which can sometimes fail), it can be done at a very early stage of the breeding program (saving time and resources), and we can select for resistance to several diseases in the same individual plant (multi-tasking).

Technician Charlie Gustus and undergraduate student Summer Kluck initiated this project to evaluate a population that was

created from crossing one parent that was resistant to net blotch, and another parent that was resistant to Septoria speckled leaf blotch. Each line of the population along with the parents was evaluated in three separate greenhouse experiments for each disease and also for set of molecular markers.

Analysis of the disease and marker data revealed that there was a major gene for resistance to each disease. Interestingly, both of these genes were located in the same region of barley chromosome 6. When geneticists con-

duct mapping studies, it is not uncommon to identify genes that are close together or linked. This case was problematic, because the genes are said to be linked in repulsion (see sidebar Repulsion Phase Linkage).

What this means is that the resistance gene for net blotch was very close to the susceptible gene for Septoria speckled leaf blotch in one parent, and that the reverse was true for the other parent. In order for these two linked genes to be separated so that the desirable resistance genes for each disease can be present

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previously controlled effectively through host resistance (e.g. leaf rust and stem rust) has been diluted in the Minnesota breeding programs by the addition of this new material.

To ensure that cultivars susceptible to any of the common diseases in Minnesota are not inadvertently released for commercial production, it is essential that all advanced breeding lines be rigorously screened for resistance to all the major diseases that occur in the region. For this reason, field and greenhouse evaluation of advanced breeding lines from the wheat and barley improvement programs for resistance to the major foliar diseases is

an ongoing activity for these plant pathologists.

The screening conducted in 2006 included:

Fusarium Head Blight (FHB) - wheat and barley. Screening was conducted at three Minnesota locations (St Paul, Morris and Crookston). Each year as much as 400 liters of Fusarium inoculum (fungal spores suspended in water) is produced for use in the inoculated and irrigated nurseries at St Paul and Morris. Dryland nurseries are also established for barley at St Paul and Crookston. These nurseries are inoculated but not irrigated and provide additional information on disease development under conditions more like

those of commercial crops. The pathology group also assisted in the greenhouse evaluations of lines, although fewer lines are being screened now compared to past years as the breeding programs have shifted their screening emphasis to the field nurseries. Identification of resistant material has enabled the breeding programs to make significant progress in breeding for FHB resistance.

Net Blotch - barley. Approximately 1,000 barley entries are tested annually as seedlings for their reaction to the net blotch pathogen in the greenhouses on the St. Paul campus. Approximately 40% of the lines tested exhibited

resistance and were advanced in the breeding program.

Septoria speckled leaf blotch (SSLB) - barley. Breeding lines were evaluated in the greenhouse as seedlings at St. Paul. Of the entries tested, approximately 50% appeared resistant. Resistant lines with good agronomic characteristics are being advanced in the breeding program.

Spot blotch - barley. Entries were planted for spot blotch evaluation at St. Paul with over 90% of the entries tested exhibiting resistant reactions.

The evaluation of wheat and barley breeding lines for multiple disease resistance is a collaborative effort between Dill-Macky and Steffenson in St.

Paul and Char Hollingsworth at the Northwest Research and Outreach Center, Crookston. As the pathology and breeding groups work collaboratively on many nurseries in the Red River Valley, this report contains details of nurseries conducted cooperatively at multiple locations throughout the state.

This work facilitates the development of wheat and barley cultivars with multiple disease resistance and will ultimately increase the sustainability of the production of small grains in Minnesota.

- Dr Ruth Dill-Macky, ruthdm@umn.edu and Dr Brian Steffenson, bsteffen@umn.edu plant pathologists, University of Minnesota

in an individual, there would need to be a recombination event between the two genes. This event, called crossing over, is essentially a breakage, swapping, and reconnection of chromosome segments. These recombination events occur naturally, but the closer two genes are together, the less likely there will be a recombination event between them.

So why is this a problem? If two resistance genes were not linked, then our friend Gregor Mendel would predict that half of the progeny in the population would be resistant to one disease and half resistant to the other. That would mean that about 25% of the progeny would be resistant to both diseases, which is the objective of our breeding program. Since these genes were linked in repulsion, less than 5% progeny were resistant to both diseases.

es. This creates a problem since we would like to select among dozens or even a hundred disease resistant lines to identify those that were also high yielding and have favorable malting quality.

This is where using marker-assisted selection comes in handy. Screening hundreds of lines in the field or greenhouse for both diseases would be very laborious. Instead, we can isolate DNA from each line and screen them for two DNA markers (one on each side of the linked genes). We can then use the marker data to identify plants where the rare recombination event has placed the two resistance genes in an individual.

Once we have identified individuals containing both resistance genes, there will be a low frequency that this linkage will be broken, making it easier

to identify progeny of future crosses that contain both genes, and are agronomically acceptable.

One thing that makes the DNA markers screening fast and inexpensive is the establishment of USDA Regional Genotyping Labs to help breeders implement MAS. We work with the lab in Fargo, N.D. under the direction of Shiaoan Chao. We grow plants for about two weeks, snip off a half inch piece of leaf tissue from each plant, place it into a small plastic plate that can hold 96 leaf

samples, and ship them to Fargo. In about 6-8 weeks, Dr. Chao emails a spreadsheet with the results and we can select the individuals that we want to advance in the breeding program.

The identification of these two genes for resistance to net blotch and Septoria speckled leaf blotch should allow us to quickly move them into our breeding program. Since all of our current barley varieties are susceptible to these diseases, this will be an important first step to improve resistance.

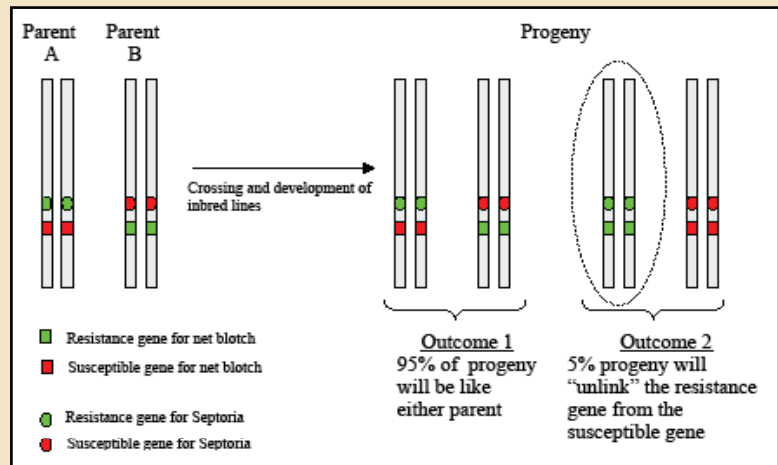
Because the patho-

gen may overcome these resistance genes, it will be necessary to continue to identify new genes to combine with existing genes. Several breeding lines with both genes will be entered into our first year yield trials this year, and crosses made last fall will generate more lines to be screened using MAS this summer. Our ultimate goal is to combine resistances for these two diseases with lines in our program that have improved resistance to FHB.

– Dr Kevin Smith, barley breeder, smith376@umn.edu



Separating Resistance Genes from Susceptible Genes



This graphic courtesy U of M barley breeder Dr Kevin Smith helps illustrate the challenge of breeding stronger disease tolerance in new lines, in this example, net blotch and Septoria in barley. The two parents A and B are said to be in 'repulsion phase linkage,' because for parent A, the desirable gene for resistance to net blotch is linked to the susceptible gene for Septoria. Likewise for Parent B, the desirable gene for resistance to Septoria is linked to the susceptible gene for net blotch. The vertical rectangles represent the pair of chromosomes of each individual, and the circles and squares represent the genes for the two diseases. If these genes were unlinked (on different chromosomes), half of the progeny would be resistant to each disease and 25% of the progeny would be resistant to both diseases. In this case, where the genes are linked or close together, only rare recombinants would result in linkage of the two resistance (or susceptible) genes together. In breeding for disease resistance we would select those individuals with resistance genes for both diseases (shown circled).

Mapping New Genes for Leaf Rust Resistance in Wheat Cultivars

Leam rust occurs annually on wheat in Minnesota, causing significant yield losses in susceptible cultivars such as Oxen and Reeder. New races that can attack leaf rust resistant wheat cultivars are constantly emerging. In fact, many different leaf rust races are found in the U.S., over 50 each year. As a result, it is critical that new genes for leaf rust resistance be characterized and added to wheat breeding germplasm.

Jim Kolmer, a plant pathologist at the USDA-ARS Cereal Disease Laboratory, St. Paul, has been working with U of M wheat breeder Jim Anderson to characterize new genes for leaf rust resistance in wheat, and to improve the leaf rust resistance in advanced breeding lines. The goal is having wheat cultivars that have very good leaf rust resistance, high yield, good quality and agronomic traits combined with FHB resistance.

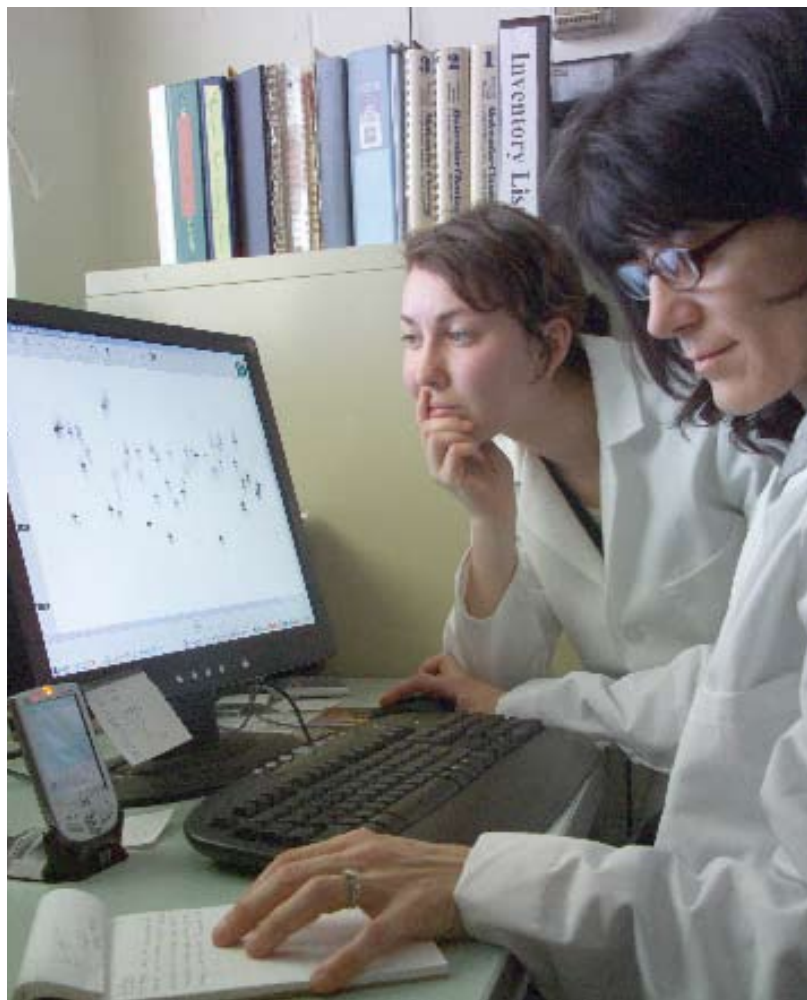
Wheat lines with new genes for leaf rust resistance that were originally derived from durum wheat, einkorn wheat, and an accession of common bread wheat, were crossed with the leaf rust susceptible wheat Thatcher, and the segregating progenies were tested for leaf rust resistance.

The wheat lines with

the resistance genes and Thatcher were tested to determine which chromosome-specific DNA markers showed differences between the resistant lines and Thatcher. More than 25 markers have been found that showed differences between the resistant and susceptible wheat lines. These markers will be used to determine which of the 42 chromosomes carry the new genes for leaf rust resistance. The gene from einkorn wheat has been mapped to the long arm of chromosome 3A.

Kolmer and Anderson will soon be working on mapping new genes for leaf rust resistance from wheat landraces that were grown in the early 20th century in South America. The landraces are highly resistant to leaf rust and also carry new leaf rust resistance genes. Once the chromosome locations of all these new genes are determined, tightly linked DNA markers for the genes can be developed to assist in selecting wheat breeding lines with these genes.

The wheat improvement project at the University of Minnesota also tests all preliminary and advanced breeding lines for leaf rust resistance. Preliminary lines are tested in field plots in St. Paul that have been inoculated with the most common leaf



Researchers at the U of M are working on mapping new genes for leaf rust resistance.

rust races in the spring wheat area of Minnesota, North Dakota and South Dakota.

Breeding lines that show good resistance in this test should also have high levels of resistance in plots and farm fields. Advanced breeding lines are also tested with a number of leaf rust races individually in greenhouse tests to characterize their leaf rust resistance genes.

New genes for leaf rust resistance are also being added to the wheat project. The leaf rust resistance genes *Lr21*, *Lr22a*, *Lr46*, *Lr47*, and *Lr52*, have been crossed into the wheat germplasm by testing for rust resistance and by using DNA markers. Wheat lines that have one of these genes combined with the resistance genes already present in the breed-

ing lines and cultivars are highly resistant to leaf rust. Recent U of M released cultivars Oklee (2003), Ulen (2005), Ada (2006), and RB07 (2007) have better leaf rust leaf resistance compared to previously grown cultivars such as HJ98, Ingot, and Oxen.

— Dr James Kolmer, research plant pathologist, USDA-ARS Cereal Disease Laboratory, St. Paul

Identifying genes and mechanisms that provide resistance to scab

My laboratory is using genomics technologies to identify genes and mechanisms that provide resistance to barley and wheat scab. We are using Affymetrix GeneChip technologies, which provide the ability to monitor the expression of 22,000 and 61,000 genes in barley and wheat, respectively.

We have conducted a variety of experiments with this technology. We used this technology to examine gene expression in barley during *Fusarium graminearum* infection. We detected the expression of 467 genes that were significantly induced during infection. We also conducted an experiment to identify genes that respond to the accumulation of trichothecenes. Trichothecenes, such



Gary Muehlbauer and his research team have developed transgenic wheat lines, including lines related to Alsen, carrying a variety of potential scab resistance genes.

as deoxynivalenol, are produced by *F. graminearum* during infection and reduce the quality of barley and wheat grain.

We identified 69 barley genes that responded to the accumulation of trichothecenes. We also conducted experiments to examine the gene expression differences during infection of resistance and susceptible wheat and barley genotypes. In these experiments, we identified a set of genes that are differentially expressed in the resistance or susceptible genotypes. Taken together, we have identified a large set of genes that have the potential to be involved in scab resistance. Currently, we are establishing assays to test the efficacy of these genes to

provide scab resistance.

We also used the gene expression data to identify markers that are closely linked to regions in the barley genome that contain scab resistance. We mapped two genes near a scab resistance gene on barley chromosome 3H. We developed a collaboration with Dr. Andy Kleinhofs (Washington State University) for mapping markers to a region providing resistance on barley chromosome 2H. We provided Dr. Kleinhofs with a large set of genes for mapping.

My laboratory is also interested in identifying *F. graminearum* genes that are specific to infection and may be targets of control measures. In collaboration with Dr. Corby

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Evaluating Grain Samples for DON and Other Mycotoxins

Mycotoxin analysis plays an important role in fighting Fusarium Head Blight (FHB), a devastating disease for all classes of wheat and barley. The Mycotoxin Diagnostic Laboratory in the Department of Plant Pathology has been providing rapid and reliable mycotoxin analysis services to FHB research projects using gas chromatography-mass spectrometry (GC-MS) since 1994.

Deoxynivalenol (DON) is the toxin subject to most analysis, although our laboratory also provides analytical services for other DON related toxins such as 3-acetyl-DON, 15-acetyl-DON, and nivalenol as well as zearalenone, a mycotoxin also produced by *Fusarium* fungi.

From August 2005 to June 2006, our laboratory analyzed 12,013 samples submitted by 15 FHB research groups from six states: Minne-

sota, Michigan, Virginia, Kansas, Indiana and Utah. For 2006/2007, a survey among FHB research projects conducted in Minnesota indicated that a total of about 12,500 samples would need to be analyzed for mycotoxins. We have finished mycotoxin analyses for ~9,000 samples by the end of January.

A method for analyzing ergosterol, a chemical marker for measur-

ing fungal biomass in wheat and barley, was finalized and published in the *J. Agric. Food Chem.* 2006, 54, 4121-4125 during the 2005/2006 project period. The ergosterol analysis service has been provided to the FHB researchers.

By analyzing mycotoxins, our laboratory provided support to barley and wheat breeding programs to develop resistant varieties, and

to researchers to study disease mechanisms and to develop effective and economical chemical and biological disease controls. Mycotoxin results provided by our laboratory give FHB researchers a means to evaluate the effectiveness of their efforts in fighting Fusarium Head Blight.

- Dr Yanhong Dong,
U of M mycotoxin lab manager, dongx001@umn.edu

Spring Wheat and Barley Disease Screening Nurseries at Crookston

2006 is the twelfth year that inoculated and misted disease screening nurseries of spring wheat and barley have been grown at Crookston, Minn. The continued objective is screening of spring wheat and barley lines for the respective U of M breeding programs in cooperation with the Plant Pathology Department.

Spring wheat is screened for resistance to fusarium head blight caused by *Fusarium graminearum* and septoria tritici blotch caused by *Septoria tritici*. Spring barley is also screened for resistance to Fusarium head blight caused by *Fusarium graminearum* as well as septoria speckled leaf blotch caused by *Septoria passerinii* and net blotch caused by *Pyrenophora teres*. Approximately

10,000 misted rows of nursery were grown at the Northwest Research and Outreach Center in 2006. Additionally, 1,920 rows of barley were screened for resistance to net blotch near Stephen, MN.

Three different methods of inoculation are used in the nurseries. Spores are sprayed on the two septoria nurseries commencing at the two leaf stage and repeated at weekly intervals until flag leaf emergence. Infected straw is spread over the net blotch nursery at the three to four leaf stage. The FHB nursery is inoculated at the five leaf stage by spreading about 50 pounds per acre of corn seed which has been sterilized and infected with *Fusarium graminearum*. A second 50 pound application is made 10 to 14 days later. The screening nurs-



eries have increased in size substantially through the years. As such, more efficient methods of conducting the nurseries facilitate the increased number of rows. This past year the planting crew was reduced from three people to one by using a tray system of planting. The application of inoculum was mecha-

nized in the Fusarium and Septoria nurseries requiring only one person for the applications. An irrigation system which required only ¼ the number of irrigation sprinklers as previously needed was installed. An electronic switch was also developed and installed, which turns the misting system off during periods of

rainfall or dew, thereby allowing prolonged daily periods of damp crop canopy while concurrently minimizing the application of water with the irrigation system.

– Galen Thompson, Northwest Research and Outreach Center, Crookston, thomp169@umn.edu

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Kistler (USDA-ARS, St. Paul, MN), we examined the gene expression patterns of the *F. graminearum* genes during barley infection. We detected the expression of over 7,000 fungal genes during infection. We also identified the expression of 431 fungal genes that were specific to barley infection. This work provides the basis for future studies aimed at understanding genes that are essential

for infection and may possibly lead to specific control measures.

Developing transgenic wheat with resistance to scab

My laboratory has developed a large set of transgenic wheat lines carrying a variety of potential scab resistance genes. We have identified many lines that exhibit reduced scab severity compared to non transgenic controls in multiple greenhouse

screens. We conducted field screens of our best transgenic wheat lines in the summers of 2004, 2005 and 2006 (collaboration with Dr. R. Dill Macky, U of M). From the field screens, we have identified eight lines that exhibit significant reductions in scab severity.

We crossed five transgenic wheat lines that exhibited reductions in scab severity in the field to the partially resistant cv. Alsen. Our goal is

to increase the level of resistance in Alsen. An initial screen indicates that these lines exhibit reduced severity similar to Alsen. Currently, we are conducting further testing to determine if there are differences between Alsen and the Alsen lines carrying the transgenes.

Recently, we developed lines carrying a wheat lipid transfer protein (LTP), wheat glutathione-S-transferase (GST) and a wheat

oxalate oxidase gene. We identified lines carrying the LTP and GST transgenes that exhibited a reduction in disease severity compared to the non transgenic controls. Currently, we are screening the lines carrying the oxalate oxidase gene in the greenhouse.

– Dr Gary J. Muehlbauer, UM Department of Agronomy and Plant Genetics, muehl003@umn.edu

Red River Valley On-Farm Yield Trials

The 'Red River Valley On-Farm Yield Trials' have been conducted each year since 1996. The objectives of the Red River Valley On-Farm Yield Trials are to:

- Provide yield trial information and varietal comparisons in addition to the state yield trials conducted in Morris, Crookston, Stephen, and Roseau.
- Serve as demonstration plots for new releases for producers in the region.

The 2006 Red River Valley On-Farm Yield

Trials were grown in five locations throughout the region and included 25 hard red spring wheat varieties and 6 six-row malting barley varieties. The locations, cooperators, and planting dates are summarized in Table 1. Conditions were dry for most of the season. Oklee suffered the most severe drought stress and as a consequence was harvested in mid-July. The drought also caused a very uneven stand and variable growth in Perley. Very

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Table 1. Location of the 2006 Red River Valley On-Farm Yield Trials

Location	Cooperator	Planting Date	Harvest Date Barley	Harvest Date Wheat
Foxhome	Dave Hasbargen	April 24	July 20	August 2
Perley	Brian Hest	April 25	July 20	August 4
Oklee	Ray Swenson	April 18	July 18	July 19
Strathcona	Jim Kukowski	April 27	July 18	August 7
Humboldt	Gerald Olsonowski	May 12	August 1	August 10

Table 2. Grain yield expressed as a percentage of the trial mean across all locations 2006 and multi-year (2004-2006) comparisons and agronomic characteristics of cultivars entered in the Red River Valley On-Farm Yield Trials.

Cultivar	Across All Locations						
	Grain Yield			1-Year Data			
	1 year	2 year	3 year	Plant Height	Lodging ¹	Test Weight	Protein
	—— (% of mean) ——			(inches)	(1-9)	(lb/bu)	(%)
Ada	97.2	97.6	-	28.0	8.4	60.8	14.8
Alsen	96.6	94.5	95.8	30.3	8.5	59.5	14.9
Bakker	91.8	-	-	30.3	9.0	54.6	15.5
Banton	110.0	100.4	-	31.1	9.0	61.1	14.9
Bigg Red	96.1	-	-	33.0	8.1	59.6	14.4
Briggs	110.9	104.7	101.5	31.5	7.5	60.4	14.7
Fire Ball	91.9	-	-	28.0	8.6	57.6	16.1
Freyr	98.1	101.5	99.6	32.3	8.1	59.2	14.3
Glenn	103.5	102.7	-	32.3	8.6	60.3	15.2
Granger	107.6	105.2	106.2	33.0	8.0	60.2	14.7
Granite	94.2	87.1	92.4	29.1	9.0	57.2	16.1
Howard	106.0	-	-	31.5	8.0	58.6	14.6
Kelby	100.9	-	-	26.4	8.5	60.4	15.0
Knudson	107.8	106.8	105.0	28.1	8.4	60.2	14.2
Marshall ²	83.8	-	-	26.0	8.8	55.3	15.2
Oklee	102.7	101.9	99.0	29.0	8.3	60.0	14.9
Oxen	94.9	93.4	95.6	29.8	8.4	59.4	15.0
Polaris	87.3	93.5	100.0	31.1	9.0	53.5	14.8
Reeder	97.3	93.0	95.0	31.8	8.4	57.4	14.9
Rush	90.3	-	-	28.9	9.0	60.9	15.3
Steele-ND	109.4	105.0	100.8	32.0	8.4	59.2	14.9
Traverse	109.6	-	-	32.5	8.6	57.8	14.1
Trooper	98.5	98.3	100.5	25.4	9.0	57.5	14.5
Ulen	106.0	104.2	101.9	31.1	8.6	59.4	14.7
Walworth	102.6	103.3	99.7	30.3	8.3	59.1	14.7
C.V.	13.6	13.5	11.4	7.8	8.7	3.8	4.3
LSD (5%)	13.5	10.1	6.5	2.3	0.7	2.2	0.6
Mean	64.9	64.8	74.7	29.9	8.5	59.0	14.9

¹ 1=flat and 9 =erect

²Historical check



U of M small grains specialist Jochum Wiersma

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little, if any, lodging or disease pressure was observed last summer.

In addition to the named HRSW varieties, the Red River Valley On-Farm Yield Trials are used by the University of Minnesota's spring wheat and barley breeding programs for testing of candidate varieties.

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Table 3. Grain yield expressed as a percentage of the trial mean across locations for 2006 and multi-year (2004-2006) comparisons and agronomic characteristics of cultivars entered in the Red River Valley On-Farm Yield Trials.

Cultivar	Across All Locations							
	Grain Yield			Plant Height*	Lodging*	3-Year Data		
	1 year	2 year	3 year			Plump	Test Weight	Protein
———— (% of mean) ————			(inches)	(1-9)**	(%)	(lb/bu)	(%)	
Drummond	103.8	104.6	102.1	31.6	8.8	80.6	44.9	13.5
Lacey	99.8	100.7	103.5	29.8	8.3	80.3	45.5	13.8
Legacy	88.2	91.9	96.6	30.3	7.5	69.6	41.7	13.4
Robust	94.2	93.6	93.2	31.3	7.9	77.0	44.7	13.9
Stellar	105.2	100.3	-	30.7	8.8	81.3	44.5	13.4
Tradition	101.7	101.1	99.7	31.0	7.9	79.9	45.2	13.4
CV	8.5	7.9	7.7	5.2	8.6	8.2	2.7	3.3
LSD (5%)	10.7	8.5	7.2	2.1	1.2	6.1	1.0	0.4
Mean	107.9	103.3	109.8	30.7	8.3	76.9	44.4	13.5

* 2 year data (2006) ** 1=flat and 9=erect

Small Grains Outreach and Communications

The Small Grains Update, in its tenth consecutive year, is jointly organized with the Minnesota Association of Wheat Growers (MAWG). The update is comprised of 9 half-day meetings across the northwestern part of the state in the third week of January. The series was expanded to the south with the addition of Morris as the ninth location. The attendance once again exceeded 700 growers this past winter.

The 'Best of the Best' series of seminars was held for the third time this past winter, organized cooperatively with the MAWG, NDSU, and grain groups in N.D. The event focused on the most advanced management approaches to HRSW and the latest research results.

The 'Southern Wheat Tour' series was focused on the southern part of the state. The Center for

Small Grains Production and Management has built a solid foundation for small grains production clinics south of I-94. Doug Holen, regional extension educator in Fergus Falls, has been instrumental in this development. Locations this

past winter included the cities of Benson, Dawson, Kilkenny, and Hutchinson. Attendance continues to grow, especially at the meetings in west central part of the State. The programming effort was expanded with two scouting clinics in the

southeastern part of the state in the month of July.

I continued to address timely production issues with eight articles in the Minnesota Crop eNews and contributions to Prairie Grains. I co-authored the 'Winter Wheat in Minnesota'

extension bulletin, and updated 6 HRSW variety fact sheets. Four new HRSW variety fact sheets were developed for 'Ada,' 'Freyr,' 'Granite,' and 'Trooper.'

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On-Farm Disease Management Trials of Spring Wheat in the Red River Valley

During 2006, data were collected from two on-farm locations located near Oklee and Foxhome, MN (cooperators: Ray & Barbara Swenson and Dave & Matt Hasbargen). Small plots of spring wheat varieties were planted during April into soybean residues. Twelve wheat varieties (Ada, Alsen, Banton, Bigg Red, Briggs, Freyr, Glenn, Knudson, Oklee, SteeleND, Ulen and Walworth) were tested to determine if yield and quality responses from six disease management strategies would complement or compete with disease resistance levels in each variety. For example, if a variety had little resistance against a disease, application of fungicide to protect its yield potential would be logical. For a variety with greater resistance, an application of fungicide may or may not provide protection over-and-above the level that the variety's disease resistance would accomplish anyway. We calculated economic analyses for each variety/disease treatment combination from representative grain samples that were graded by Mid-Valley Grain Cooperative in Crookston. For reporting purposes, fictitious grain sales were made based on samples to determine the esti-

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Table 1. One-year data ranking variety and treatment combinations based on dollars/A revenue returned (1=best rank, 72=lowest rank).

Rank	Variety	Trtmt ¹	Protein	Test Wt	Yield	Prem vs Disc ²	Cash Price	Gross \$/ac	Fung. Appl. Cost \$/ac	Estimated Return
1	Steele ND	SD	14.2	61.6	70.4	0.01	\$4.67	\$328.77	\$3.84	\$324.93
2	Ulen	SD	14.5	61.6	70.0	0.02	\$4.68	\$327.60	\$3.84	\$323.76
3	Briggs	SD	14.8	61.5	69.1	0.04	\$4.70	\$324.77	\$3.84	\$320.93
4	Steele ND	H-F	14.2	61.0	72.0	0.01	\$4.67	\$336.01	\$17.08	\$318.93
5	Walworth	SD	14.5	59.8	68.6	0.02	\$4.68	\$321.05	\$3.84	\$317.21
6	Ada	H-F	14.4	62.3	70.5	0.02	\$4.68	\$329.94	\$17.08	\$312.86
7	Oklee	H-F	14.6	61.8	69.6	0.03	\$4.69	\$326.42	\$17.08	\$309.34
8	Knudson	SD	14.4	61.1	66.6	0.02	\$4.68	\$311.45	\$3.84	\$307.61
9	Walworth	NONE	14.4	59.5	65.5	0.02	\$4.68	\$306.54	\$0.00	\$306.54
10	Briggs	H-F	14.3	61.7	69.2	0.01	\$4.67	\$323.16	\$17.08	\$306.08
11	Walworth	H-F	14.6	59.3	68.8	0.03	\$4.69	\$322.67	\$17.08	\$305.59
12	Ulen	SD-F	14.8	61.5	68.2	0.04	\$4.70	\$320.54	\$16.03	\$304.51
13	Walworth	SD-F	14.2	60.0	67.7	0.04	\$4.70	\$317.96	\$16.03	\$301.93
14	Oklee	SD	15.1	61.4	64.8	0.05	\$4.71	\$305.21	\$3.84	\$301.37
15	Knudson	H-F	14.5	61.3	68.0	0.02	\$4.68	\$318.01	\$17.08	\$300.93
16	Ulen	H-F	14.6	60.5	67.4	0.03	\$4.69	\$316.11	\$17.08	\$299.03
17	Walworth	F	14.7	59.0	66.4	0.03	\$4.69	\$311.18	\$12.19	\$298.99
18	Steele ND	NONE	14.5	60.2	63.8	0.02	\$4.68	\$298.58	\$0.00	\$298.58
19	Knudson	NONE	14.4	61.3	63.6	0.02	\$4.68	\$297.41	\$0.00	\$297.41
20	Banton	SD	14.5	63.0	64.4	0.02	\$4.68	\$301.16	\$3.84	\$297.32
21	Steele ND	F	14.7	60.4	65.9	0.03	\$4.69	\$309.07	\$12.19	\$296.88
22	Briggs	NONE	14.7	60.8	63.2	0.03	\$4.69	\$296.41	\$0.00	\$296.41
23	Steele ND	SD-H-F	14.4	60.7	67.7	0.02	\$4.68	\$316.84	\$20.92	\$295.92
24	Bigg Red	H-F	13.7	62.9	67.7	-0.04	\$4.62	\$312.77	\$17.08	\$295.69
25	Knudson	F	14.4	61.5	65.6	0.02	\$4.68	\$306.77	\$12.19	\$294.58
26	Freyr	H-F	14.2	61.1	66.7	0.01	\$4.67	\$311.26	\$17.08	\$294.18
27	Bigg Red	SD-H-F	14.4	62.6	67.2	0.02	\$4.68	\$314.50	\$20.92	\$293.58
28	Ulen	F	14.8	60.7	65.0	0.04	\$4.70	\$305.27	\$12.19	\$293.08
29	Banton	H-F	14.4	62.9	66.2	0.02	\$4.68	\$309.58	\$17.08	\$292.50
30	Briggs	F	14.5	61.6	65.0	0.02	\$4.68	\$303.97	\$12.19	\$291.78
31	Bigg Red	SD	13.8	62.7	63.7	-0.02	\$4.64	\$295.57	\$3.84	\$291.73
32	Ada	SD-F	14.5	62.0	65.7	0.02	\$4.68	\$307.48	\$16.03	\$291.45
33	Walworth	SD-H-F	14.7	58.6	66.6	0.03	\$4.69	\$312.12	\$20.92	\$291.20
34	Glenn	SD	15.1	62.3	62.5	0.05	\$4.71	\$294.14	\$3.84	\$290.30
35	Oklee	F	14.9	61.6	64.3	0.04	\$4.70	\$301.98	\$12.19	\$289.79
36	Oklee	NONE	15.1	61.6	61.5	0.05	\$4.71	\$289.67	\$0.00	\$289.67
37	Oklee	SD-F	14.8	61.5	64.8	0.04	\$4.70	\$304.56	\$16.03	\$288.53
38	Briggs	SD-H-F	14.7	61.2	65.9	0.03	\$4.69	\$308.84	\$20.92	\$287.92
39	Oklee	SD-H-F	14.5	61.2	65.8	0.02	\$4.68	\$307.94	\$20.92	\$287.02
40	Ulen	NONE	14.8	60.4	61.0	0.04	\$4.70	\$286.47	\$0.00	\$286.47

Special Report

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mated revenue from each variety/disease management treatment combination. The sales occurred in mid-November. Deoxynivalenol (DON or vom) levels were non detectable or well below the allowable limit of 2 ppm so discounts did not apply.

Varieties

The drier growing season resulted in few production issues related to disease, however having little disease development is unusual in the Valley. The Oklee location suffered from drought conditions with powdery mildew and leaf rust developing on susceptible varieties late in the season. The Foxhome location experienced more timely rains, but overall low levels of leaf and stripe rust, Septoria leaf blotch, powdery mildew, and leaf streak mosaic were noted at this location. Moderate bacterial leaf stripe disease pressure was noted at Foxhome. Bacterial leaf stripe is caused by a bacterial disease and leaf streak mosaic is caused by a virus, so neither are controlled by fungicide application.

Seven different varieties, (Steele ND, Ulen, Briggs, Walworth, Ada, Oklee, Knudson) represented the top 10 estimated revenue returns (Table 1).

There were significant differences between varieties at locations but not between management treatments. When averaged across both test sites, two disease

Table 1 (continued). One-year data ranking variety and treatment combinations based on dollars/A revenue returned (1=best rank, 72=lowest rank).

Rank	Variety	Trtmt ¹	Protein	Test Wt	Yield	Prem vs Disc ²	Cash Price	Gross \$/ac	Fung. Appl. Cost \$/ac	Estimated Return
41	Glenn	H-F	15.0	62.0	64.4	0.05	\$4.71	\$303.32	\$17.08	\$286.24
42	Steele ND	SD-F	14.3	61.2	64.4	0.01	\$4.67	\$300.75	\$16.03	\$284.72
43	Freyr	NONE	14.4	60.3	60.8	0.02	\$4.68	\$284.54	\$0.00	\$284.54
44	Banton	NONE	14.7	62.9	60.6	0.03	\$4.69	\$283.98	\$0.00	\$283.98
45	Freyr	F	14.4	61.2	63.3	0.02	\$4.68	\$296.01	\$12.19	\$283.82
46	Bigg Red	NONE	13.6	63.2	61.4	-0.04	\$4.62	\$283.44	\$0.00	\$283.44
47	Ada	SD	14.7	61.3	61.2	0.03	\$4.69	\$287.03	\$3.84	\$283.19
48	Ada	F	15.0	61.1	62.7	0.05	\$4.71	\$295.08	\$12.19	\$282.89
49	Freyr	SD-F	14.2	61.4	64.0	0.01	\$4.67	\$298.88	\$16.03	\$282.85
50	Ulen	SD-H-F	14.7	60.4	64.7	0.03	\$4.69	\$303.21	\$20.92	\$282.29
51	Freyr	SD	14.3	60.8	61.2	0.01	\$4.67	\$285.57	\$3.84	\$281.73
52	Ada	NONE	14.4	61.5	60.1	0.02	\$4.68	\$281.27	\$0.00	\$281.27
53	Banton	F	14.5	63.0	62.7	0.02	\$4.68	\$293.44	\$12.19	\$281.25
54	Alsen	SD	14.8	60.9	60.6	0.04	\$4.70	\$284.59	\$3.84	\$280.75
55	Glenn	NONE	15.3	61.5	59.4	0.06	\$4.72	\$280.37	\$0.00	\$280.37
56	Bigg Red	F	14.0	62.7	62.5	0.00	\$4.66	\$291.25	\$12.19	\$279.06
57	Knudson	SD-H-F	14.2	60.7	64.1	0.01	\$4.67	\$299.11	\$20.92	\$278.19
58	Freyr	SD-H-F	14.5	60.3	63.3	0.02	\$4.68	\$296.01	\$20.92	\$275.09
59	Ada	SD-H-F	14.3	61.1	63.4	0.01	\$4.67	\$295.84	\$20.92	\$274.92
60	Bigg Red	SD-F	14.6	62.4	61.8	0.03	\$4.69	\$289.84	\$16.03	\$273.81
61	Banton	SD-H-F	14.5	62.8	62.8	0.02	\$4.68	\$293.90	\$20.92	\$272.98
62	Alsen	SD-F	14.5	61.5	61.5	0.02	\$4.68	\$287.82	\$16.03	\$271.79
63	Banton	SD-F	14.5	63.1	61.5	0.02	\$4.68	\$287.82	\$16.03	\$271.79
64	Knudson	SD-F	14.5	60.7	61.5	0.02	\$4.68	\$287.82	\$16.03	\$271.79
65	Briggs	SD-F	14.7	61.1	61.2	0.03	\$4.69	\$286.79	\$16.03	\$270.76
66	Glenn	SD-F	14.8	61.3	60.7	0.04	\$4.70	\$285.29	\$16.03	\$269.26
67	Glenn	SD-H-F	14.9	60.9	61.4	0.04	\$4.70	\$288.35	\$20.92	\$267.43
68	Alsen	NONE	15.2	60.5	56.4	0.06	\$4.72	\$266.21	\$0.00	\$266.21
69	Glenn	F	14.5	62.1	59.4	0.02	\$4.68	\$277.99	\$12.19	\$265.80
70	Alsen	H-F	15.2	60.3	59.2	0.06	\$4.72	\$279.42	\$17.08	\$262.34
71	Alsen	F	14.9	60.5	57.5	0.04	\$4.70	\$270.02	\$12.19	\$257.83
72	Alsen	SD-H-F	15.0	60.9	57.5	0.05	\$4.71	\$270.83	\$20.92	\$249.91
	Mean		14.5	61.3	64.2	0.03	\$4.69	\$300.77	\$11.68	\$289.09

¹Fungicide treatment product, rate and timing: NONE= No fungicide treatment; SD= Dividend Extreme, 3 oz/100 lbs as a seed treatment; H-F= Headline, 3 fl oz/a at the 4-5 leaf stage and Folicur 4 fl oz/a at early flower; SD-H-F= Dividend Extreme, 3 oz/100 lbs as a seed treatment followed by Headline, 3 fl oz/a at the 4-5 leaf stage and Folicur 4 fl oz/a at early flower; SD-F= Dividend Extreme, 3 oz/100 lbs as a seed treatment and Folicur 4 fl oz/a at early flower; F= Folicur 4 fl oz/a at early flower. NOTE: Headline and Folicur treatments included 0.125% Induce, a nonionic surfactant.

²On 13 Nov., 2006, started with a base price of \$4.66 /bu. Protein premiums based up 1 per 1/5. Protein discounts based down 2 per 1/5.

management treatments resulted in greater estimated returns (Table 1). An application of Headline at the 4-5 leaf stage followed by Folicur at early flower increased

estimated revenues above the \$300/a level for six of the varieties tested, likewise a solitary fungicide application in the form of a seed treatment (without later

foliar or head fungicide applications) resulted in similar returns for a comparable number of varieties. However, these treatments were not statistically better

than other treatments tested. A varietal trend in the data showed increased revenue from a seed treatment compared to the cor-

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Incorporating FHB Resistance identified in Barley Line COMP 351

From the screening of a genetically diverse composite cross population of barley (CC XXX) for Fusarium head blight (FHB) reaction, a line (COMP 351) was selected that consistently exhibits low disease severity and DON. This line was shown to be different than other FHB resistance sources based on molecular

markers.

To effectively utilize the resistance in COMP 351, information is needed on the number, effect and chromosomal position of the resistance loci. Thus, a cross was made between COMP 351 and an advanced, but susceptible Minnesota breeding line (M98-102). In 2006, F6 families from the COMP



Research data generated by U of M plant pathologists helps the wheat and barley breeders to develop more effective strategies for incorporating disease resistance.



Tamas Szinyei checking on plants developed for characterizing the number, effect, and chromosomal location of FHB resistance in COMP 351, a line that consistently exhibits low disease severity and DON, and shown to be different than other FHB resistance sources based on molecular markers.

351/M98-102 population were planted in two replicates each at St. Paul and Crookston. Disease levels in the St. Paul nursery were very low as the susceptible parent M98-102 exhibited no higher than 2.2% infection. This nursery was not conducive for detecting differences in FHB resistance among families.

In contrast, the disease levels in Crookston were high with the susceptible parent exhibiting FHB severities from 26-27%. The resistance of COMP 351 was expressed well in this environment, as FHB severities never exceeded 4%. F6 families exhibited a

wide range of severities from 0.9% to 51.5% in replicate 1, and 0.4% to 25.6% in replicate 2. A high frequency of F6 families exhibited low FHB severities. In the Crookston nursery, 19 families were selected as having low disease severity and also heading dates comparable to Stander.

Once the DON assays are completed, we will select the best lines for crossing in the next generation. Our primary goal is to reduce the losses caused by FHB, including quality discounts due to DON contamination. This can be best achieved by developing barley cultivars with the high-

est level of resistance possible – i.e. incorporating resistance from COMP 351 as well as other sources of FHB resistance.

We anticipate that this research will lead to the identification of molecular markers closely linked with the most important loci conferring resistance to FHB and the accumulation of DON. This information will allow breeders to develop more effective strategies for incorporating resistance, thereby hastening the time needed to develop FHB resistant barley cultivars.

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responding varietal non treated control treatment.

Disease Management Treatments

When dollars returned per acre is considered exclusively, treatment results varied widely across varieties. Economically speaking varieties known for having good disease resistance packages, such as Glenn and Alsen, did not offer any needed benefits in the absence of disease. Several management strategies on these two varieties were ranked lowest in estimated revenue (Table 1). Protein premiums for most varieties ranged from \$0.01 to \$0.06/bushel while some discounts were assigned for reduced protein.

This project was funded by the MN Wheat Research and Promotion, AgriPro Wheat, Trigen Seed, WestBred and the Northwest Research and Outreach Center's Extension Plant Pathology Program. It was conducted with support from two grower cooperators, Dr. Yanhong Dong, Univ. of Minnesota Mycotoxin Laboratory; Jim Tholund and Rick Meine from Mid-Valley Grain Co-op; BASF; Bayer Crop-Science; and Syngenta.

– Charla Hollingsworth, Extension Plant Pathologist, Chris Motteberg, and Lorilie Atkinson, Plant Pathology Scientists, and Doug Holen, Regional Extension Educator

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More comprehensive research information may be found in the booklet, "2006 Wheat

Research Review." It is free to the public and may be requested by contacting the Minnesota Wheat Research and Promotion Council, 1-800-242-6118. More scab research information is also available on the World Wide Web, at the MWRPC web site, www.smallgrains.org, and the University of Minnesota Agricultural Experiment Station, www.maes.umn.edu. Research conducted at the U of M and other

research institutions under the U.S. Wheat and Barley Scab Initiative can be found on the Internet at: www.scabusa.org.

This report prepared by the Minnesota Wheat Research and Promotion Council and the Minnesota Association of Wheat Growers in cooperation with the University of Minnesota. Photos by David Hansen, Minnesota Agricultural Experiment Station.



Minnesota wheat and barley growers support research at the University of Minnesota, with investments through the wheat and barley checkoff allocated toward research on FHB and other yield and quality limiting factors.