

COMPARATIVE GENETIC ANALYSIS OF FHB-RESISTANT GERMPLASM FOR WHEAT IMPROVEMENT

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OBJECTIVES

To examine the difference of genetic constitution for resistance among FHB-resistant wheat germplasms by using the molecular markers.

INTRODUCTION

Previous studies indicate that resistance to FHB varies not only among wheat cultivars but also among some of their wild relatives. No accession, however, has yet been identified to be completely immune to FHB among the Gramineae. It was also demonstrated that resistant wheat germplasm could be divided into three gene pools: winter wheats from Eastern Europe, spring wheats from China and Japan, and spring wheats from Brazil and Italy (Snijders, 1990). Repeated screening of the genetic resources led to the identification of several resistant cultivars of spring wheat, such as Sumai 3 and Ning 7840 from the Chinese gene pool in the early 1990's. On another front, Shinchunaga, Nobeokabouzu-komugi and Nyubai were also identified as resistant cultivars to FHB from the Japanese gene pool (Nishikado, 1958; Gocho, 1985; Feadak *et al.*, 1997). Among them, Nobeokabouzu-komugi is highly resistant to FHB (Gocho, 1985; Miedaner, 1997). The genetic constitutions of sources for resistance to FHB originating from different gene pools, however, have not yet been elucidated. It is essential to study the genetics of the resistance to FHB, including the identification of the genes for different types of the resistance to FHB in several gene pools, so that different genes can be combined to improve the overall resistance of wheat. The objectives of our studies were to examine the difference of genetic constitution of resistance to FHB among the resistant wheat germplasms.

MATERIALS AND METHODS

Comparative QTL analysis for different types of resistance - This study was conducted to identify the number, the position, and the magnitude of QTLs for the resistance to initial infection of FHB (Type I) and fungal spread within plant tissues (Type II), and tolerance to Fusarium mycotoxins in wheat with DNA markers. Two populations of double haploid lines (DHLs) derived from the F₁ crosses of Sumai 3 (VR)/Gamenya (VS) and Nobeokabouzu-komugi (VR)/Sumai 3 were evaluated on the genetic constitution for the component of FHB resistance.

Screening of chromosome regions associated with FHB resistance in Sumai 3 with its susceptible NILs by using SSR and AFLP markers - The plant materials used in this study were Sumai 3 and its four susceptible NILs. The NILs were derived from a cross between Sumai 3 and Chuan980, a susceptible cultivar, followed by seven backcrosses with Sumai 3 and screening for FHB susceptibility in each generation by artificial inoculation with *F. graminearum*. SSR and AFLP analyses were applied to screen the DNA polymorphism between Sumai 3 and its four NILs.

Genetic variation of accessions within FHB resistance wheat cultivars revealed by SSR markers - We also revealed the genetic variation within accessions of Frontana (Brazil, USA, Canada and Japan) and Sumai 3 (China, USA, Canada, Iran, Austria and Japan) that had been sent to CIMMYT by using 242 SSR markers that encompass the whole of the wheat genome.

RESULTS AND DISCUSSION

Comparative QTL analysis for different types of resistance – Three and two genomic regions were significantly associated with Type I and Type II resistance, respectively. One of the QTLs on chromosome 2DS showed negative effect on both Type I and Type II resistance, which meaning Sumai 3 not only contain resistance genes but also have susceptible gene. The results suggested that the genetic constitutions for Type I and II resistance are not identical. We also examined the difference of the genetic constitution for resistance to FHB between Sumai 3 and Nobeokabouzu-komugi to find unique resistance genes in Japanese germplasm. From the cross combination of both highly resistant cultivars, transgressive segregants with the reaction of moderately resistant to FHB were detected. It is suggested that the unique configurations of resistance genes are causing the skewed distribution of the resistance in this cross. The genetic mode of the resistance indicated that three resistance genes to FHB were different between Nobeokabouzu-komugi and Sumai 3. Consequently, it is suggested that Nobeokabouzu-komugi harbours three dominant genes for the resistance, of which two are unique and another gene is identical with the one of Sumai 3 (Ban and Inagaki, 2001).

Screening of chromosome regions associated with FHB resistance in Sumai 3 with its susceptible NILs by using SSR and AFLP markers – The detected polymorphic markers were mapped using a mapping population of 118 DHLs of Sumai 3 and Gamenya. Eighty-eight SSRs markers and 107 AFLP primer combinations that produced approximately 900 AFLP markers were analyzed. Of these markers, nine (four SSR and five AFLP markers) showed polymorphism between Sumai 3 and its four NILs. The band patterns of these markers were not identical for the four NILs, indicating that the genetic constitutions of the four NILs were different with regard to susceptibility to FHB. Seven of the nine polymorphic markers were mapped on a region of chromosome 3BS where the resistance QTLs have been consistently detected in the populations including Sumai 3 or its derivatives. The remaining two markers were located on chromosome 2AL or 2DL. By using the NILs for FHB resistance, it is revealed that a critical region for Type II resistance to FBH located on chromosome 3BS in Sumai 3, and Sumai 3 may have other genes that affect the FHB resistance. The success for development of the susceptible NILs to FHB and the results obtained in this study demonstrated that some quantitative traits could be genetically analyzed like qualitative traits.

Genetic variation of accessions within FHB resistance wheat cultivars revealed by SSR markers - In the case of Sumai 3, there was no difference in band pattern in any SSR markers examined among the Chinese (CHN), US (USA), Canadian (CAN) and Iranian (IRN) accessions; they were an identical genotype. Sumai 3-AUT showed polymorphism for 32 markers (13.2%) on 11 chromosomes. Some of them were linked on chromosomal regions. It is suggested that Sumai 3-AUT also derived from an original Chinese accession following outcross and selection. All Sumai 3 accessions had a high level resistance to FHB, while Sumai 3 AUT had higher levels of resistance. We can conclude that additional resistance genes to FHB should exist on the chromosome regions identified by aberrant types of SSR markers in Sumai 3-AUT. It was conclude that we need to pay attention to the source and genotype of such accessions when discussing the results of QTL analysis and using them in breeding programs with marker assisted selection. (see more detail in our poster presented in 2003 NFHBF)

Inheritance of resistance to FHB in wheat has been studied extensively over the last five decades. Various studies have determined the mode of inheritance and numbers of genes involved in resistance depending on the materials and methods used. However, lacking of knowledge about the genetic constitutions of different sources for resistance to FHB has hampered significant progress in the breeding of FHB-resistant wheat cultivars for a long time. Different types of genetic resistance to FHB in common wheat have been described. We can find many reports of QTL analyses for Type II resistance derived from Chinese germplasm (mainly Sumai 3). Further studies on the genetic basis of relationship between the characteristics of FHB and resistance mechanisms in wheat should be required to develop FHB-resistant wheat. We are tracing the genetic constitution for different types of resistance to FHB in Japanese wheat breeding systems combining the information of DNA markers and pedigree analysis (Fig. 1). The information obtained in these studies might provide a better understanding of the genetic resistance to FHB, and thereby enhance the resistance levels in wheat through introgression or pyramiding of several resistance genes.

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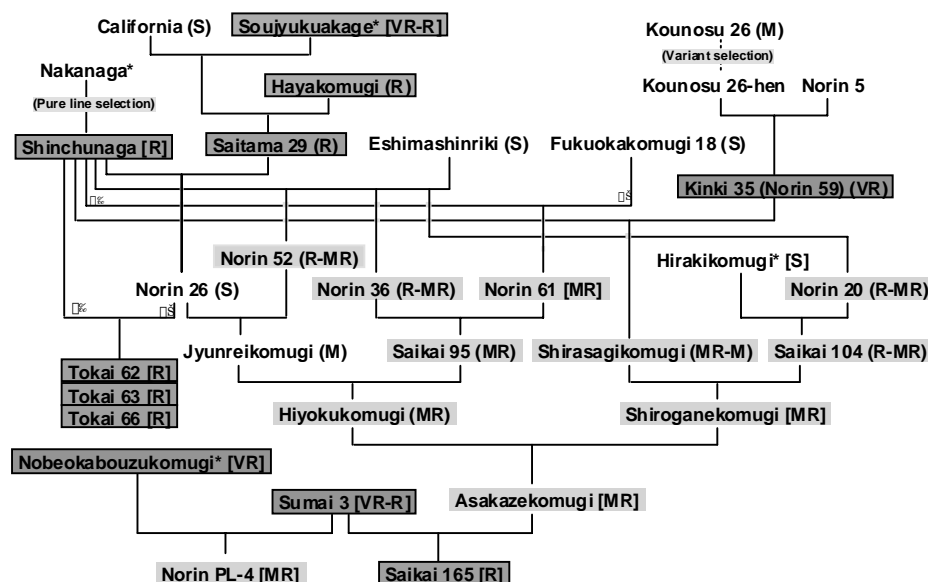


Fig. 1. Pedigrees of FHB-resistance cultivars in improved Japanese wheat

Each resistance level to FHB examined is following with parentheses, and previously reported ones (Yoshida *et al.* 1993) are with bracket. Cultivars in meshed boxes are selected as FHB-resistance cultivars. * Local variety.

GENETIC VARIATION OF ACCESSIONS WITHIN FUSARIUM HEAD BLIGHT RESISTANCE WHEAT CULTIVARS REVEALED BY SSR MARKERS

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ABSTRACT

Fusarium head blight (FHB) is one of the most destructive diseases of wheat. Repeated screening of genetic resources has led to the identification of several resistant cultivars of spring wheat, such as Frontana from Brazil, Sumai 3 from China and Nobeokabouzu-komugi from Japan. It is known, however, that several morphological and ecological variations with different responses to FHB exist within global accessions of Frontana and Sumai 3 (Nishio et al. 2002), and different sources of Sumai 3 have been identified by DNA markers (Bai et al. 2003). In this study, we revealed the genetic variation within accessions of Frontana (Brazil, USA, Canada and Japan) and Sumai 3 (China, USA, Canada, Iran, Austria and Japan) that had been sent to CIMMYT by using 242 SSR markers that encompass the whole wheat genome. Frontana-USA and -CAN were identical with, or variants of, the original Brazilian accession. In the case of Sumai 3, the US, Canadian and Iranian accessions were the same genotype as the Chinese one. Sumai 3-JIR might be a derivative from them. The Austrian accession was considered a derivative of an original Chinese accession following outcrossing and selection with additional resistance genes for FHB. The results of genetic variation within the accessions of Frontana and Sumai 3 reveal that we need to pay attention to the source and genotype of such accessions when discussing the results of QTL analysis and using them in breeding programs with marker assisted selection. (This poster was presented at the 10th International Wheat Genetic Symposium, Paestum, Italy, 1-6 September 2003.)

IMPORTANCE OF FUSARIUM HEAD BLIGHT IN RUSSIA AND THE SEARCH FOR NEW SOURCES OF GENETIC RESISTANCE IN WHEAT AND BARLEY

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Russia is large country occupying over 17 million km² and very diverse climatic conditions. Cereal crops are cultivated in the European (North Caucasus, the Central and Volga regions, North-Western region) and Asian regions (Siberia and the Far East) of the country. Wheat and barley are significant components of the agricultural economy of Russia. Winter and spring wheat are grown on over 23-25 million hectares with an average annual production of 30.9-50.6 million tons (average for 1999-2002). Winter and spring barley are grown on 9.8-10.3 million hectares with an average yield of 10.9-19.5 million tons.

The first mention of Fusarium head blight (FHB) within the territory of Russia was from the Far East. The Far East region of cereal production is typically very damp and warm during the summer due to the influences of Sea of Japan and Pacific Ocean. As early as the 18th century, FHB was known as a problem of cereals in the Far East (Palchevsky, 1891; Voronin, 1890). From 1882 until about 1914, FHB epidemics occurred almost every year in the region. The use of seeds and straw contaminated with mycotoxins produced by various *Fusarium* species caused numerous cases of food poisoning in people and animals. Initially, the symptoms observed in people ingesting this tainted grain resembled alcohol intoxication and was often referred to as “intoxicating bread” syndrome. The research of several Russian mycologists revealed that the fungus *Gibberella saubinetii* Sacc. (now *G. zae* or *F. graminearum*) was the principal causal organism of FHB (Jaczewski, 1904; Naumov, 1913, 1916). FHB was a persistent problem in the Far East during the first half of the 20th century (Abramov, 1938; Naumov, 1940) and continues to be today. High severities of FHB are reported nearly every year in the region. Mycological analyses of seed samples from 1998-2002 have shown a high level of FHB-infected wheat and barley seed (from 23-32%). The most frequently isolated pathogens were *F. graminearum*, *F. avenaceum*, and *F. poae*.

Another major FHB outbreak within the territory of Russia occurred in the Altai region and Bashkirij (south of Siberia) in 1932-1945. Food shortages during this time forced rural people to consume inferior grain that was left out in the field under snow during the winter. After ingesting this grain, many people suffered the serious disease of alimentary toxic aleukia. Extensive research led by A. Sarkisov revealed that the disease was due to the ingestion of cereals contaminated with T-2 toxin produced by fungus *F. sporotrichioides* (Sarkisov, 1954). In recent years, the level of Fusarium infected grains has been relatively low (0-10%). The principal pathogens found on grain in this region are *F. poae* and *F. sporotrichioides* (Levitin et al., 2000).

Nearly one hundred years after the first major epidemic was reported in the Russian Far East, FHB became one of the most important fungal diseases in the North Caucasus region. There, FHB epidemics occurred in 1985, 1987, 1988, 1992, 1993, 1997, 1998, 2000, and 2002. In the North Caucasus, maize and winter wheat and winter barley are the main crops and are often cultivated in continuous rotation with each other. Favorable weather conditions, coupled intensive agricultural practices have led to a dramatic increase in

FHB severity. Since cereals in the North Caucasus comprise nearly one third of the total cereal production in Russia, the severity of FHB epidemics was of great concern and research efforts to combat the disease were initiated. *F. graminearum* (*G. zeae*) is the most important FHB pathogen in this region and was responsible for widespread mycotoxin contamination problems. For example, in 1992, analysis of wheat grain from the Krasnodar district showed that DON was present in 100% of the examined samples with concentrations ranging from 0.15-10.5 ppm. In 57% of samples, the level of DON exceeded the permissible level for human consumption (1 ppm). Zearalenone was observed in 68% of the samples in concentrations ranging from 0.01-1.4 ppm (Lvova et al., 1997).

The NorthWest region (near Baltic Sea) is characterized by a damp climate and moderate summer daytime temperatures. In past years, FHB was reported on cereal crops in the region, but was never considered a significant problem (Naumov, 1940). A study of seed infection from recent years revealed significant levels of FHB. In 2000, FHB seed infection averaged 16% (maximum 23%) and 22% (maximum 24%) for spring barley and spring wheat, respectively. In 2002, the average FHB infection level for both barley and wheat seed was about 6% with a maximum of 15%. The 2003 season was very wet and all harvested grain was infected by FHB. The average level of grain infection by *Fusarium* species was 16% for barley (maximum 32%) and 12% for wheat (maximum 20%). The dominant species isolated from seed were *F. poae*, *F. sporotrichioides*, *F. avenaceum*. In this area, symptomatic kernels are rarely observed, except in warm and moist seasons like in 2003. More often asymptomatic kernels are found to carry infections of various *Fusarium* species. Analyses of trichothecene toxins conducted with Finnish colleagues in 2002 revealed principal toxin in this region is nivalenol (0,2-3.7ppm), most likely produced by *F. poae* (Yli-Mattila et al. 2002).

Disease resistance is one of the best means of combating FHB in wheat and barley. In the past, the breeding programs for cereals in the Central, North-West regions, and Siberia never focused on FHB resistance. This led to the release of many susceptible cultivars, which were planted over a large area. In Russia, the most active breeding program focusing on FHB resistance is at the Krasnodar Research Institute of Agriculture (North-Caucasus). This is an area of winter cereal production and recently released winter wheat cultivars such as Krasnodarskaya 6, Yuna, Delta, Demetra, Kolos, Leda, Rufa, Eho, Basianka appear to have tolerance to toxin accumulation (Anpilogova et al., 1996; Ablova, Gritcai, 2001; Kolesnikov et al., 2001; Ribalkin et al., 2000). To breed for FHB resistance, breeders are making crosses among ecogeographically diverse lines and making early generation selections of individuals. Successive crosses are complex involving highly resistant in Krasnodar region Nung Ta 173 (China), Lee (USA), Frontana (Brazil), WSP96.6, Livius (Austria), Kincso, Ringo Sztar (Hungary) and local varieties (Ribalkin et al., 2000).

To broaden resistance to FHB, efforts are being made to identify new resistance sources. The N. I. Vavilov Institute of Plant Industry (VIR) in Russia houses one of the largest and most diverse collections of cereal genetic resources in the world. The wheat collection contains more than 44,000 accessions. Approximately two-thirds of the collected accessions (27,832) include bread wheat germplasm originating from 85 countries. Wild and primitive wheat accessions number 2,867 and goat grass (*Aegilops* L.) accessions number 3,847. A considerable part of the wheat collection was obtained from 1907 to 1940 and are mostly landraces or old varieties. The barley collection comprises 20,197 accessions of cultivated barley: 39% are landraces, 46% are cultivars, 8% are breeding lines, 6% are mutants and genetic stocks and 1% is wild species. In 1947, the number of accessions in the collection amounted to 9000, representing 38 countries besides Western Europe (Kovaleva, 1999; Mitrofanova, 2003; Terenteva, 2001). Estimation of the degree of biodiversity for disease resistance in the genetic resources of cultivated plants and their wild relatives is being documented in joint projects between VIR and VIZR.

Evaluation of wheat and barley accessions from VIR collection identified a group of landraces and old local cultivars of wheat and barley with relatively high levels of FHB resistance (Gagkaeva et al., 2002). All these samples were collected from 1915-1936 in the Far East territory where environmental conditions are favorable for FHB infection.

Two hundred fifty-two accessions comprising 26 species of *Triticum* L. with different ploidy levels were evaluated for FHB resistance in the field. No correlation was found between ploidy level and FHB resistance. However, some feature of plants may be associated with resistance. For example *T. durum*, *T. aethiopicum*, and *T. turanicum* have a high frequency of florets that undergo open flowering and are susceptible to FHB. Likewise, *T. urartu* has a prolonged flowering period and is susceptible to FHB. *T. timopheevii*, *T. persicum*, *T. ispahanicum*, and *T. karamyshevii* originated from regions with high moisture and were generally resistance to FHB. *T. vavilovii*, *T. turanicum*, *T. dicoccoides*, *T. sphaerococcum* originated from dry regions of Middle Asia and were highly susceptible to FHB. The most resistant wild accessions were *T. timopheevii*, *T. karamyshevii*, and *T. militinae* (from Georgia), *T. persicum* (from Dagestan), *T. dicoccum* (from Germany), *T. spelta* (from Switzerland). A wide diversity for resistance was detected in *T. aestivum* accessions (Gagkaeva et al., 1993)

Aegilops species are of particular interest because they carry genes for resistance to many fungal pathogens that may be introgressed into common wheat. *Aegilops* accessions belonging to 9 different species and several ploidy levels (*Ae. tauschii*, *Ae. triuncialis*, *Ae. cylindrica*, *Ae. juvenalis*, *Ae. vavilovii*, *Ae. ovata*, *Ae. crassa*, *Ae. kotchui*, *Ae. bicornis*) were evaluated for reaction to FHB. *Ae. tauschii* was most resistant to *F. graminearum*. Of 56 samples belonging to this species 19.6% were highly resistant. All tested samples of *Ae. triuncialis* and *Ae. ovata* were highly susceptible (Gagkaeva, Navruzbekov, 1991). The most of resistant *Ae. tauschii* germplasm originated from Afghanistan. One of them is used in crossing with wheat at the Crop Breeding Institute (Harbin, China) (Lianfa et al., 2000). The wild accessions (*T. militinae*, *Ae. squarosa*, *Ae. sharonensis*, *Ae. umbellulata*, *Ae. speltoides*, *Ae. glaucum*, *S. cereale*) are potential sources of resistance to the disease and toxin accumulation and are being utilized for breeding purposes at the Krasnodar Research Institute of Agriculture (Kolesnikov et al., 2001). The combining of different resistance genes from diverse sources will broaden the effectiveness of FHB resistance in released cultivars.

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HAPLOTYPE DIVERSITY AT FUSARIUM HEAD BLIGHT RESISTANCE QTLs IN WHEAT

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ABSTRACT

Fusarium head blight (FHB) reduces grain yield and quality in common and durum wheat. Host FHB resistance is an effective control measure that is achieved by stacking multiple FHB resistance genes. Resistance gene stacking would be facilitated if breeders knew which FHB resistance sources carry different resistance genes. A diverse collection of FHB resistant and susceptible wheat lines was characterized with microsatellite markers linked to known FHB resistance quantitative trait loci (QTLs) on chromosomes 2DL, 3BS (distal to the centromere), 3BSc (proximal to the centromere), 4B, 5AS, and 6BS identified in Maringa, Sumai 3, and Wuhan 1. Putative Sumai 3 QTLs were commonly observed in advanced breeding lines, whereas putative Maringa and Wuhan 1 QTLs were relatively rare. The microsatellite data suggested that the 3BS, 3BSc, and 5AS QTLs in the Brazilian cv. Maringa were derived not from Frontana, as previously thought. Maringa appeared to be closely related to Asian germplasm at the 3BS, 3BSc, and 5AS QTL regions. Other Brazilian wheat lines did not appear closely related to other FHB resistance sources. These Brazilian wheats may have novel FHB resistance that will be useful for stacking with FHB resistance derived from Asian germplasm.

MOLECULAR GENETIC DIVERSITY OF GEOGRAPHICALLY DIVERSE SCAB RESISTANT WHEAT LINES

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ABSTRACT

Fusarium graminearum Schwabe (teleomorph *Gibberella zeae* (Schwein.), also known as scab, is an increasingly important problem in wheat and barley globally because of the emphasis on conservation tillage, the lack of effective cultural and/or fungicide control, and the lack of effective sources of genetic resistance. Yield losses in spring and soft red winter wheat regions of the US alone have exceeded \$4 billion in the last decade. Host plant resistance is considered the most practical and effective means of control but breeding has been hindered by a lack of effective resistance genes and by the complexity of the resistance in identified sources. No source of complete resistance is known, and current sources provide only partial resistance, therefore, the identification of different sources of resistance and their incorporation into adapted wheat varieties is critical to the continued improvement of Fusarium head blight resistance in winter wheat. Research funded by the National Wheat and Barley Scab Initiative (USWBSI) has led to the systematic evaluation of scab resistance of accessions contained in the National Small Grains Collection at Aberdeen, Idaho, and, through a collaborative effort with CIMMYT, has led to the introduction of germplasm containing potentially different sources of resistance from scab programs globally. A group of 191 lines, with varying levels of resistance, have been assembled from globally diverse geographic regions. They likely contain genes for scab resistances that differ from those derived from the Chinese line "Sumai 3", which is currently, the most widely used source of resistance. The material includes lines from CIMMYT (38), Romania (7), China (17), Argentina (40), Brazil (12), Japan (12), Hungary (6), Italy (3), South Korea (1) and the United States (55). These lines have been evaluated with 10 different AFLP primer pair combinations resulting in over 50 bands per primer pair. Cluster analysis was performed using Phylip Version 3.6 to assess genetic diversity among the material and to identify genetically different sources of scab resistance that can be used for further studies. Relationships among germplasm will be discussed as will their potential for carrying novel genes for scab resistance.

IDENTIFICATION OF NOVEL SOURCES OF FUSARIUM HEAD BLIGHT RESISTANCE FROM WHEAT-ALIEN SPECIES DERIVATIVES

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ABSTRACT

Sources of resistance to Fusarium head blight (FHB) are limited in wheat. Identification of novel sources is vital for enhancing resistance of wheat to this disease. We have evaluated 284 wheat lines derived from crosses between wheat and its relatives for FHB resistance. Materials were evaluated in the greenhouse using the point inoculation method and the percent of infected spikelets was measured. Approximately 20 spikes were inoculated for each of the wheat lines. Of the 284 lines evaluated, 100 were resistant (<15% infected spikelets), 108 were moderately resistant (15-50% infected spikelets), and 76 were susceptible (>50% infected spikelets). Resistant lines include synthetic common wheat lines, wheat-alien species amphiploids, addition lines, and other wheat-alien species derivatives. Further evaluation is being conducted to confirm these results. Cytogenetic characterization is in progress to understand chromosome constitutions of wheat lines with high levels of resistance. Following an initial chromosome count, fluorescence *in situ* hybridization (FISH) is performed to determine the amount of alien chromatin present in each resistant line. FISH patterns of mitotic chromosomes indicate that 4 of the most resistant lines carry 14 *Thinopyrum ponticum* chromosomes and 42 wheat chromosomes. Additional crosses are being made to localize resistance genes, to minimize alien chromatin, and to pyramid FHB resistance genes.

REACTION OF *AEGILOPS SHARONENSIS* TO FUSARIUM HEAD BLIGHT

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ABSTRACT

Fusarium head blight (FHB), caused by *Fusarium graminearum* is a serious disease of wheat in many production areas. The deployment of resistant cultivars is one of the best means for controlling this disease. To obtain broad-based resistance in wheat, it is important to combine into cultivars diverse alleles for FHB resistance. Wild relatives are rich sources of resistance alleles for wheat. The diploid wheat relative *Aegilops sharonensis* ($2n=2x=14$, genome S¹S¹) is native to the coastal areas of Israel and Lebanon and is known to be a rich source of resistance to diseases such as leaf rust, stripe rust, powdery mildew, and Karnal bunt. However, few data are available on the reaction of this species to FHB. Thus, the objective of this study was to evaluate the reaction of a large collection of *Ae. sharonensis* accessions to FHB. Eighty-two accessions originating from nine sites within the coastal plain of Israel were tested. The spray inoculation method was used to assess resistance to initial infection, and the single floret inoculation method was used to assess resistance to spread. A high level of diversity was observed in *Ae. sharonensis* for reaction to FHB as infection levels ranged from 0-100% for both inoculation methods. Eleven accessions exhibited a very high level of resistance (0% infection) with both inoculation methods. These accessions were from two different sites (Ashdod and Ben Zakai) in Israel. Accessions with putative resistance will be evaluated again in the greenhouse in 2003-04 and also in the field. The results suggest that potentially useful sources of FHB resistance may be present in *Ae. sharonensis*.

RELATION BETWEEN TYPE II AND TYPE I RESISTANCE TO *FUSARIUM GRAMINEARUM* IN WHEAT

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OBJECTIVES

The purpose of these experiments was to evaluate germplasm for both type I and type II resistance to *Fusarium graminearum* and to explore the relation between the two types of resistance.

INTRODUCTION

Effective control of Fusarium head blight (FHB) in the field with genetic resistance may require cultivars that have at least resistance to both primary infection (type I resistance) and resistance to spread of the fungus through the spike after primary infection (type II resistance). Although these two types of resistance are conceptually distinguishable, it is not known to what extent the same genes influence both.

Greenhouse screening of material in breeding programs or for genetic studies usually employs the point inoculation method, with subsequent measurement of the spread of blight symptoms in the spike. This measures type II resistance. Type I resistance is assessed by spraying the entire head with a spore suspension, with the goal of exposing all florets to inoculum. Evaluation of wheat lines in the field probably reveals information about both type I and type II resistance, although the relative contribution of each type to the phenotype cannot be distinguished

In previous work, we selected lines for stable expression of type II resistance from several wheat accessions (Shaner and Buechley 1999). Here, we report the results of both spray and point inoculation of these selections. We also evaluated recombinant inbred lines from a cross between wheat cultivars Clark (susceptible) and Chowkang (resistant) for type II resistance (Buechley and Shaner 1999). We evaluated these lines for type I resistance. Results from these experiments allow us to compare the correlation between these two types of resistance.

MATERIALS AND METHODS

We evaluated 32 selections and cultivars (hereafter referred to as selections) simultaneously for type II and type I resistance. Most of the selections were from accessions that showed some degree of type II resistance in initial screenings. We tested selections in the fall of 2002 and again in the spring of 2003. Seedlings were vernalized and then transplanted to the greenhouse. Selections were evaluated for type II resistance by point inoculation. When flowering had progressed to the top of the spike (GS 65), we injected 10 μ L of a suspension of macroconidia (10⁴ spores/ml) of *F. graminearum* into a well-developed floret near the top of the spike. We used spray inoculation to test for type I resistance. When anthers were extruded on all florets of a spike (GS 67), we sprayed the spike with the same suspension of spores used for point inoculation. Plants to be inoculated were set out in a row, with their heads oriented such that spikelets on both sides of the spike would receive direct spray. The sprayer was passed down the line of plants at a speed such that each plant received about a 1-s burst of spray. After inoculation by either method, inoculated head was enclosed in a clear polyethylene bag. For several years we had used 5

cm × 10 cm, clear polyethylene bags, which could be stapled closed around the peduncle. The bags were left in place for 48 h. Within 3 h after placing a bag over a head, its interior would become clouded with condensed water, indicating a saturated atmosphere surrounding the inoculated head. In the fall of 2002 we used self-closing “Ziploc type” bags. However, these could not be tightly closed around the peduncle without risking severing the head. As a result, moisture did not condense on the interior of the bag, suggesting that the atmosphere surrounding the head was not as humid as when the other bags were used. For the experiment conducted in the spring of 2003, we reverted to the bags that could be stapled shut around the peduncle. Severity of head blight was measured by counting the blighted spikelets on each head (Shaner and Buechley 2001). This was done at 5-d intervals beginning 5 d after inoculation.

We conducted similar experiments with recombinant inbred lines from a cross between Chokwang and Clark. Chokwang is moderately resistant to FHB and Clark is susceptible. This population was tested for type II resistance by point inoculation in 1999 and 2000. In 2003, the same population was evaluated for type I resistance after spray inoculation.

RESULTS

Germplasm selections. Most lines showed some resistance and a few had a high degree of resistance to head blight. In each experiment there was a moderate but significant correlation between type I and type II resistance ($r = 0.39$, $P = 0.03$ for the fall; $r = 0.68$, $P = 0.0000$ for the spring). For data averaged over the two experiments, the correlation was even greater ($r = 0.75$, $P = 0.0000$; see Fig. 1). The line in Fig. 1 is not a regression, but represents a perfect agreement between the two types of resistance. The preponderance of points below this line indicates that most selections had a greater degree of type II resistance than type I resistance. Between the two experiments, expression of type II resistance was reasonably consistent ($r = 0.63$, $P = 0.0002$), but, the expression of type I resistance was inconsistent between experiments ($r = -0.04$, $P = 0.83$). The poor correlation between expression of type I resistance between the two experiments was largely the result of several selections that had a low severity in the fall experiment, but a high severity in the spring experiment.

In each experiment, a few selections had some degree of type II resistance, but very little type I resistance. A few selections showed the opposite trend: some degree of type I resistance, but not much type II resistance. No line showed either of these traits consistently in both experiments, probably a consequence of the inconsistency in expression of type I resistance.

RILs. We evaluated type II resistance in a population of recombinant inbred lines (RILs), derived from a cross between wheat cultivars Chokwang and Clark. The correlation between experiments for number of blighted spikelets 22 d after inoculation was 0.505. There was transgressive segregation for resistance. We evaluated this same population for type I resistance. Family mean severities at 20 days after inoculation were normally distributed and ranged from 2 to 17 blighted spikelets (Fig. 2). Chokwang averaged 10 blighted spikelets; Clark averaged 15. Of 77 RILs, 52% had a lower severity than Chokwang. There was no significant correlation ($r = 0.17$) between type I and type II resistance in this population.

DISCUSSION

For the germplasm selections, the correlation between head blight ratings for the two methods of inoculation was significant, but low, suggesting that type I and type II resistance are not entirely under control of the same genes. The correlation was even lower for the RILs derived from Clark × Chokwang. The germplasm selections were

from cultivars that were identified elsewhere as having resistance, or from areas where FHB has long been a problem. It is possible that these cultivars were subjected to selection in the field, where both type I and type II resistance would contribute to a low overall severity of FHB. Even though we performed our reselection work using point inoculation, if these lines possessed genes that conferred type I resistance, they would likely have been retained in the selected plants. The situation was different for the RILs derived from Clark × Chokwang. If genes that condition type I and type II resistance were mostly different, then one would not expect a correlation between the two types of resistance in the RILs. This is what we found. Among the RILs there was considerable transgressive segregation for type I resistance. Chokwang had only a moderate degree of type I resistance (Fig. 2). Although Clark was susceptible when sprayed, not all heads were completely blighted, and possibly it contributes genes that enhance type I resistance when combined with genes from Chokwang. Tamburic-Ilicic et al. (2002) also found transgressive segregation for greater resistance when plants were spray-inoculated.

Part of the variation between experiments with the germplasm selections may have been the result of different methods of bagging heads to provide high humidity after inoculation. The self-closing bag we used in the fall did not seem to retain moisture as well as the bags we had used in earlier tests. In the spring experiment, we resumed use of the original bags and severity of blight was higher than in the fall.

Our findings of a poor correlation between type I and II resistance agree with those of McKendry et al. (2002) and Tamburic-Ilicic et al. (2002). McKendry et al. evaluated severity 21 d after point inoculation and at both 10 and 21 d after spray inoculation. Although not explicitly discussed by them, the earlier evaluation (10 d) of symptoms after spray inoculation would be expected to give a clearer indication of type I resistance than the later evaluation (21 d). Type II resistance could confound the assessment of type I resistance when ratings are deferred until 21 d after infection. If a line had type I resistance, but little type II resistance, it would have a low severity early (10 d), but subsequent spread of the fungus from only one or a few primary infections would result in severe head blight by 21 d, so by that time it would appear to be susceptible. A line with both type I and II resistance would still have a low severity by 21 d, but it would be difficult to determine the relative contribution of each type of resistance to the final severity. We considered this possibility in our analyses and did compare severity at 10 d after spray inoculation with severity at 20 d after point inoculation. There seemed to be little difference compared to what we saw in the comparison of severities at 20 d after either type of inoculation (the data presented in Figs. 1 and 2) We plan to further explore the effect of time of severity rating on the perceived degree of type I resistance.

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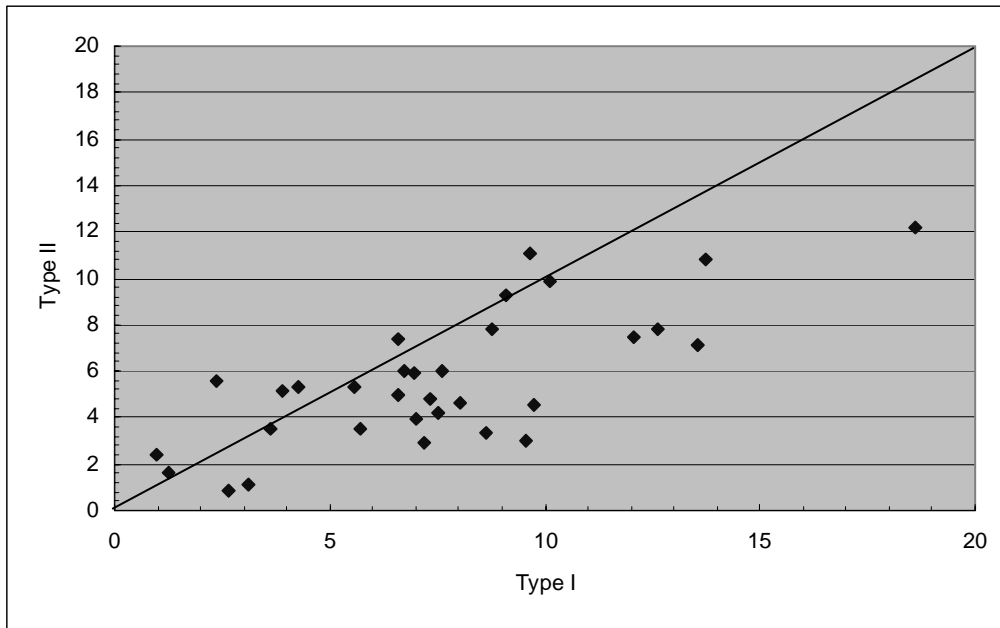


Fig. 1. Relation between type I and type II resistance to *Fusarium graminearum* in a group of wheat selections originally selected for consistent expression of type II resistance. Data are summarized over 2 experiments. The line depicts a perfect association between the 2 types of resistance, not the regression.

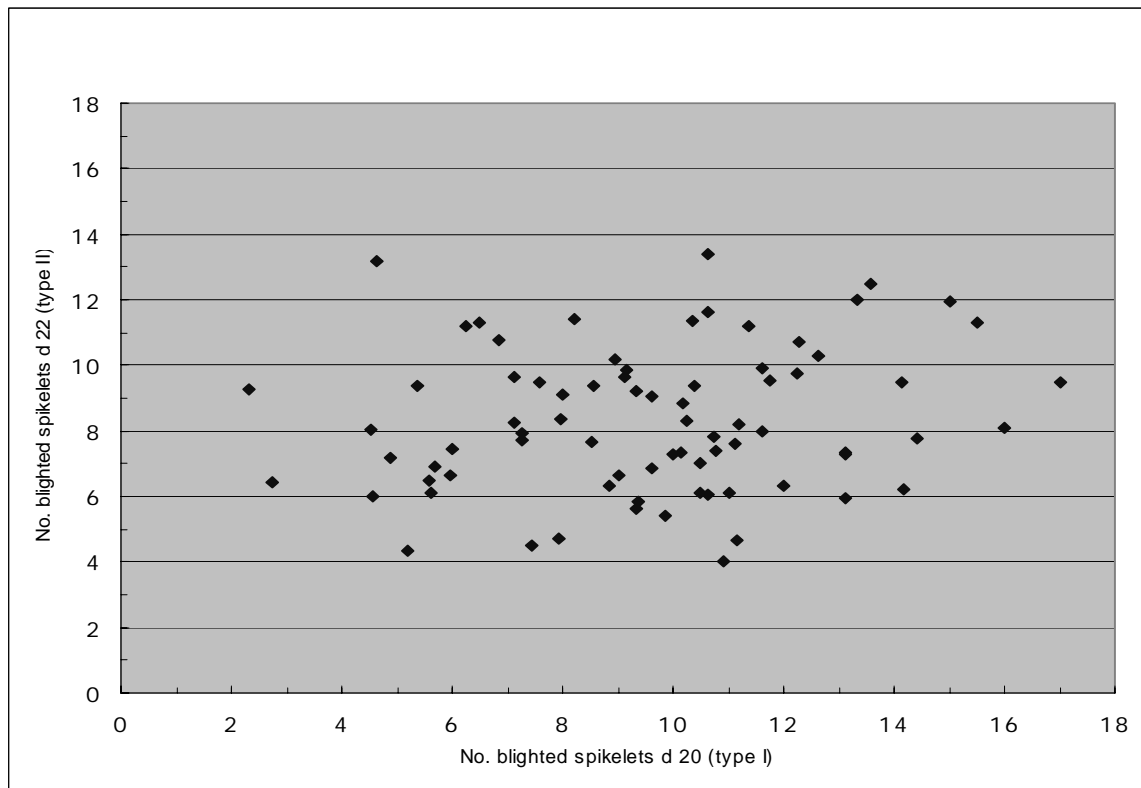


Fig. 2. Relation between type I and type II resistance to *Fusarium graminearum* in a group of recombinant inbred lines derived from a cross between cultivars Clark and Chokwang. Data for type II resistance are averages from 2 experiments; data for type I resistance are means from a single experiment. Clark averaged 11.4 blighted spikelets for point inoculation and 15.2 for spray inoculation; Chokwang averaged 5.0 blighted spikelets for point inoculation and 10.1 blighted spikelets for spray inoculation.

GENETIC CHARACTERIZATION OF FHB RESISTANCE SUPPRESSION CONDITIONED BY CHROMOSOME 2A OF *TRITICUM DICOCOIDES*

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ABSTRACT

Disomic substitution lines, LDN(DIC), prepared by replacing chromosomes of Langdon durum with those from wild emmer (*Triticum dicoccoides* (TDIC)) showed highly significant differences in response to Fusarium head blight (FHB) when challenge inoculated with *Fusarium graminearum* in the greenhouse (Stack et al. 2002. Crop Science 42:637-642). Several of the LDN(DIC) lines showed increased resistance to FHB. One line, LDN(DIC2A), was highly susceptible to FHB, just as is the TDIC accession that contributed the chromosomes to the substitution lines. In F-1 hybrids with other substitution lines the gene(s) on 2A behaves as a "susceptibility gene" that acts in an additive manner. In most F-1 hybrids involving LDN(DIC-2A), the FHB score was intermediate between the parents. The F1 hybrid between the resistant line LDN(DIC-3A) and LDN had a FHB score similar to the parent, suggesting that the 3A resistance is dominant. The F1 hybrid between Langdon and the LDN(DIC-2A) however, was intermediate, suggesting a quantitative inheritance. In populations derived from crosses of the LDN(DIC-2A) to an FHB resistant line, such as LDN(DIC-3A), the FHB resistance frequency distribution in the F-2 suggests that the gene(s) on chromosome 2A is epistatic to any resistance genes. The distribution of FHB severity values in the F-2 exhibited a trimodal distribution suggestive of a 1:2:1 segregation ratio that might be expected due to segregation of a single gene that acts additively. This supports the hypothesis that a single gene is present on chromosome 2A that not only increases FHB susceptibility, but also suppresses the action of the FHB resistance on chromosome 3A. (This poster was presented at the annual meeting of the American Phytopathological Society, Charlotte, NC, August 2003).

TRANSFER AND EXPRESSION OF RESISTANCE TO FUSARIUM HEAD BLIGHT FROM WILD EMMER CHROMOSOME 3A TO BREAD WHEAT

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ABSTRACT

One of the main goals in breeding for resistance to Fusarium head blight (FHB) is to diversify the resistance gene pool available. To date most FHB resistant spring wheat lines trace back to the Chinese line "Sumai-3" or its derivatives, most of which share the same QTL's. Stack et al. found resistance located on three chromosomes (1A, 3A, 6B) of *T. dicoccoides* when these were substituted into a durum background (Crop Sci. 42:637-642. 2002). The major FHB resistance was present on the wild emmer chromosome 3A and was expressed in the durum disomic substitution line "LDN(DIC-3A)". This line was the resistant parent in a cross with the hexaploid spring wheat "Reeder." Reeder is a good quality, well adapted North Dakota hard red spring wheat cultivar which is quite susceptible to FHB. Lines were advanced by single seed descent. In 2002, F4 seed of this population was planted in an inoculated and mist-irrigated FHB screening nursery. FHB severity was scored at 3 weeks postanthesis; plots were harvested when mature and proportion of scabby kernels determined. In 2003, the F5's of this population were planted in this nursery. In addition the parent line Reeder and two check lines, Alsen, a moderately resistant cultivar of Sumai3 parentage, and 2398, a highly susceptible cultivar, were included. In several previous trials, the FHB severity of LDN(DIC-3A) was similar to that of Alsen. FHB severity was scored at 3 weeks after anthesis. Distribution of FHB scores of lines in this population showed a mean similar to the mean of the parents and some lines showed moderately resistant FHB scores, similar to Alsen the surrogate for the resistant parent. The results indicate that the 3A resistance was successfully transferred to bread wheat. Preliminary results indicate that a sample of the most resistant of the lines in this population carry the 3A QTL marker while a sample of the susceptible lines do not. (This poster was presented at the ASA/CSSA Annual meeting, Denver, Colo. November 2003.)

A POPULATION APPROACH FOR IDENTIFYING FUSARIUM HEAD BLIGHT RESISTANCE IN BARLEY

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ABSTRACT

Several composite cross populations of barley have been developed for breeding and basic genetic research. One of these populations (composite cross XXX or CC XXX) originated from natural crosses between the USDA world barley collection and a male sterile line (Ramage et al. 1976, Crop Sci. 16:314). Each accession in the world collection had an opportunity to contribute pollen for seed set on the male sterile line in the original population grown in the field. Thus, CC XXX represents an extremely diverse assemblage of gametes segregating in a single population. As an alternative means for identifying Fusarium head blight (FHB) resistance in barley, bulked seed (~1 kg or 25,000-32,000 seeds) of CC XXX-G (an F₁Sib₄F₂ derivative of CC XXX) was evaluated in the 1997 FHB nursery at Hangzhou, China. Uniform and heavy disease pressure allowed for easy differentiation of lines with low and high disease levels and reduced the chance of selecting escapes. From this population, over 350 early maturing, six-rowed lines with low (<5%) infection were selected for further evaluation in the Midwest. From this second round of screening, only 20 lines were found to possess an adequate level of resistance (i.e. less than 15% infection) under Midwest conditions. Two (COMP 351 and COMP 355) of these 20 selections exhibited consistently low levels of FHB and deoxynivalenol (DON) after several successive years of field testing (1998-2003). Overall average FHB and DON levels were 1.9% and 4.5 ppm for COMP 351, 1.8% and 3.5 ppm for COMP 355, 2.0% and 4.0 ppm for Chevron (six-rowed resistant check), 3.9% and 4.2 ppm for CIho 4196 (two-rowed resistant check), 8.4% and 22.9 ppm for Stander (widely grown six-rowed cultivar), and 42.1% and 36.9 ppm for PI 383933 (susceptible six-rowed control). If COMP 351 and COMP 355 carry resistance alleles that are different from those found in other sources, they will be useful in barley programs breeding for FHB resistance.

EVALUATION OF SWISS BARLEY LANDRACES FOR RESISTANCE TO FUSARIUM HEAD BLIGHT

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ABSTRACT

The deployment of resistant cultivars is one of the best means for combating Fusarium head blight (FHB) in barley (*Hordeum vulgare*). To increase the diversity of FHB resistance in breeding programs, we have evaluated thousands of accessions of *Hordeum* from the USDA National Small Grains Collection (NSGC) from 1995-2003. The germplasm screened included the entire six-rowed spring barley collection (>8,100 accessions), over a third of the winter six-rowed collection (900 accessions), and over half the wild barley (*Hordeum vulgare* subsp. *spontaneum*) collection (585 accessions). The six-rowed cultivar Chevron is one of the best sources of FHB resistance and was discovered over 70 years ago. Chevron originated from Switzerland. Several of the most resistant accessions from our recent screening effort of the NSGC also originated from Switzerland. To further characterize germplasm from this region, we obtained 74 Swiss barley landraces from Geert Kleijer (Nyon, Switzerland) and evaluated them for their reaction to FHB at St. Paul and Crookston, Minnesota. The foliar spray (using macro-conidia) and grain spawn (ascospores) methods of inoculation were used at the St. Paul and Crookston nurseries, respectively. In general, two-rowed accessions exhibited lower levels of FHB and deoxynivalenol (DON) than six-rowed accessions. Thirteen accessions (11 two-rowed and 2 six-rowed) exhibited FHB severities less than 3%, which was comparable to the range observed on the Chevron control (0-3.6%). Three of these 13 accessions had very low DON levels of <2 ppm (Chevron average=5.6). Additional screening tests will be made in both the greenhouse and field to confirm the resistance of these landraces. We will also genotype these accessions with molecular markers to determine whether they possess the same alleles as Chevron.

MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS ASSOCIATED WITH FUSARIUM HEAD BLIGHT RESISTANCE IN BARLEY

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ABSTRACT

We have investigated barley traits in relation with FHB infection to see if it was possible to establish a breeding strategy for the development of FHB-resistant cultivars. Recent mapping studies indicate that many of the quantitative trait loci (QTL) for FHB resistance coincide with the QTL for plant height, heading date, and spike characteristics. Therefore, this study was conducted to investigate the relationship of morphological and physiological traits to FHB infection and deoxynivalenol (DON) accumulation in a doubled-haploid (DH) population derived from a Léger/CI9831 cross of barley. During two years, 190 DH lines were grown at Ottawa (Ontario) and Hangzhou (China) and also in Charlottetown (Prince Edward Island) for one year. The field plots were inoculated with *Fusarium graminearum* at each location. FHB incidence was positively correlated with DON content. Resistance to FHB was associated with two-row spike, purple lemma, long glume awn, tall stature and/or resistance to lodging, but it was not associated with long rachilla hairs, rough lemma awn, or heading date. Two-row was associated with tall stature and resistance to lodging. These associations in two-row lines combined with spike characteristics helped reduce FHB infection and DON accumulation to a greater extent compared to six-row lines. Purple lemma contains a high level of phenolic compounds, which in turn could inhibit FHB development. The association between long glume awn and FHB resistance could be due to genetic linkages. Therefore, trait associations should be taken into consideration when breeding for FHB resistance in barley.

RESULTS OF SSR FINGERPRINTING OF 94 NEWLY IDENTIFIED FUSARIUM HEAD BLIGHT RESISTANCE SOURCES

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ABSTRACT

Molecular analysis of the parents is the first step for a marker-assisted breeding. This poster reports a molecular fingerprinting of 96 bread wheat accessions with 32 simple sequence repeat (SSR) markers. 93 of the 96 accessions came from Europe, Asia and South America and were selected from the entries of the Spring Wheat Germplasm Survey of the US Wheat Barley Scab Initiative for their excellent performance for fusarium head blight (FHB) resistance in the multi-year examination. The objectives of this study were: 1) study the novelty of these newly identified FHB resistance sources by comparing them with 'Sumai 3', 2) analyzing the genetic background of these lines and 3) provide breeders a molecular fingerprint for each of the accessions assayed. A total of 254 alleles at 105 loci were uncovered. Most of these SSR alleles were not evenly distributed worldwide. A total of 49 alleles were not observed in any Asian accessions assayed, while 34 and 32 alleles were respectively absent from the European and the South American accessions. Forty-four alleles were found to be continent-specific. Genome-wide cluster analysis clearly divided the 96 accessions into two groups with 48 accessions per group. Accessions in the group where 'Sumai 3' is not in should be a good source for novel FHB resistance QTLs if they are also different from 'Sumai 3' for the 3BS chromosomal region defined by SSR markers *Xgwm389*, *Xgwm493* and *Xgwm533*. Examples of such FHB resistance sources include 'Tokai 66' and 'Nobeoka Bozu' from Japan 'Laureano Alvarez Laah' and 'Tezanos Pintos Precoz' from Argentina, 'Chudoskaja' and 'Ostka Wierzbienska' from Poland, and 'Abura' from Brazil.

EFFECTS OF ROW TYPE, FLOWERING BEHAVIOR AND SEVERAL OTHER SPIKE CHARACTERS ON RESISTANCE TO FUSARIUM HEAD BLIGHT IN BARLEY

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ABSTRACT

Barley varieties show a wide range of resistance to Fusarium head blight (FHB), however, the expression of resistance to FHB is complex and various spike characters such as row type, kernel density, etc. are thought to possibly influence the FHB resistance in barley. The possible effect of row type have been particularly noted, because two-rowed types generally are more resistant than six-rowed types, and the most resistant barleys recognized so far are all two-rowed types. Our test also showed obvious difference in resistance level between two-rowed and six-rowed Japanese varieties. Two-rowed and cleistogamous (closed-flowering) varieties in Japan belonged to the highest resistant group, while six-rowed and chasmogamous (opened-flowering) varieties were mostly susceptible. In order to assess effects of several spike characters including row type and flowering behavior to FHB resistance, we investigated the resistance level of near-isogenic lines (NILs) with genetic background of Japanese two-rowed varieties differing for the traits. The evaluation of FHB resistance was performed using “pot-plant” and “cut-spike” method reported previously. In both cases, spikes exactly at anthesis were spray-inoculated with macroconidia suspension of *F. graminearum*. The chasmogamous and six-rowed NILs were tend to be more diseased than cleistogamous and two-rowed NILs, respectively, and the difference in FHB severity was greater and more consistent in chasmogamous/cleistogamous NIL pairs than in two-/six-rowed pairs. No or little differences were observed in lax/dense spike, normal/uzu type (semi-dwarf and have dense spike), and wax-coated/wax-less spike NIL pairs. Our results indicate that cleistogamy and genetic background of the resistant two-rowed varieties contribute to FHB resistance more greatly than row type and spike density, and therefore, that trait and the germplasms are useful for the resistance breeding of barley.

EVALUATION OF SPRING WHEAT GERMPLASM FOR FUSARIUM HEAD BLIGHT RESISTANCE

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OBJECTIVE

To identify sources of resistance to Fusarium head blight in spring wheat germplasm.

INTRODUCTION

The use of host resistance will be one of major components in managing Fusarium head blight (FHB) in wheat. Success of breeding for resistance relies on the availability of a diversified and well-characterized resistant germplasm pool. Evaluation of the spring wheat germplasm collections deposited in the USDA National Small Grain Collection has enabled us to identify diverse sources of putative resistance (Zhang and Jin 2003). This report summarizes the progress made in 2003 in the spring wheat germplasm screening.

MATERIALS AND METHODS

In the 2003 field season, a multi-nursery system (Zhang et al. 2000) was used. This system composed of several inter-related nurseries and environments (field and greenhouse), each of which handles germplasm at different stages of evaluation/characterization. Below is a brief description of the experiments.

Field nurseries: Newly introduced materials were planted in non-replicated single-row plots and evaluated for FHB reaction in the Preliminary Screening Nursery (PSN). ND 2710 and BacUp were used as resistant checks and Sonalika and Wheaton as susceptible checks. The nursery was inoculated with corn grain (colonized by *Fusarium graminearum*) and conidial suspension (a mixture of ten isolates). Details in nursery management, inoculation, and data collection were as described previously (Zhang et al. 2000; Zhang and Jin 2002). Accessions or plants within an accession with a relatively low FHB index (incidence*severity) and/or low percentage of Fusarium damaged kernels (FDK) were selected. Selections were further evaluated in subsequent years in Elite Germplasm Nurseries (EGN). Entries of EGN were planted in row-plots with three replicates. The materials were blocked based on three maturity groups. For data analysis purpose, each maturity group was considered as an individual experiment. The EGN plots were hand-harvested. Yield, volume-weight, FDK, and DON of each plot were recorded.

Greenhouse characterization: Field selections were evaluated in the greenhouse by both point and spray inoculations in the fall and spring greenhouse seasons. When the plant was at full heading to the beginning of anthesis stages, the 11th floret (counting upward from the base of the spike) was inoculated with a conidial suspension (ca. 70,000 – 80,000 conidia/ml) using a single *F. graminearum* isolate. The inoculated spike was covered using a zip-loc specimen bag for 48 hours. The number of infected spikelets (counting downward from the inoculation site, i.e. the 11th spikelet) was recorded 21 days after inoculation. Spray inoculation was applied at the beginning to half anthesis stage. Inoculated plants were incubated for 72 hours in a mist chamber. Disease severity was collected seven days after inoculation. For each greenhouse season,

eight replicates per test-entry were planted for point inoculation or spray inoculation. Approximately 20-40 heads/entry/season were tested by either of the methods.

RESULTS AND DISCUSSION

The 2003 field experiment was conducted in Brookings, South Dakota. The PSN consisted of 466 accessions originated from India, China, Nepal and several other countries in Southeast Asia. Based on visual disease reading and FDK, eighty-five lines were selected for further evaluations. The EGN nursery included 326 accessions that were selected from the preceding three years. Lines in the second and third year of re-evaluation (i.e. selections from the 2001 and 2000 PSN) were subjected to DON analysis (by Dr. Y. Dong at the University of Minnesota). Table 1 presents the 2001-2003 field evaluation data of selections made in 2000. Disease severity and FDK of most lines in Table 1 varied considerably over the years. However, several accessions exhibited consistently low FHB index and low FDK (within the range of resistant checks of ND 2710 and BacUp). Evaluation from greenhouse experiments (data not presented) indicated that some of the selections were highly susceptible to point inoculation. For example, the average disease severity of PI 372137 by point inoculation (based on 40 inoculated spikes) was 99.0%. Greenhouse experiments are in progress to further characterize these selections.

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Table 1. Three-year (2001-2003) field data of spring wheat germplasm selections with low Fusarium head blight index and percentage Fusarium damaged kernel.

Accession /ID	FHB index (%)				FDK (%)			Country of origin
	2001	2002	2003	Mean	2001	2002	Mean	
ND2710-ck	12.3	11.5	8.2	10.7	7.7	40.0	23.8	USA
BacUp-ck	24.0	28.8	20.5	24.4	20.0	33.3	26.7	USA
Wheaton-ck	88.7	87.0	76.0	83.9	90.0	83.3	86.7	USA
Sonalika-ck	83.0	87.8	85.5	85.4	95.0	85.3	90.2	India
PI 67392	15.1	11.0	7.2	11.1	21.7	40.0	30.8	Russia
PI 69251	22.5	22.0	3.9	16.1	8.3	53.3	30.8	China
PI 225448	18.7	22.1	14.8	18.5	8.3	53.3	30.8	Uruguay
PI 225382	10.9	31.9	17.3	20.1	12.5	53.3	32.9	Uruguay
PI 225449	16.8	26.3	17.5	20.2	11.7	46.7	29.2	Uruguay
PI 155266	19.0	29.7	17.1	21.9	13.3	66.7	40.0	Japan
PI 225396	19.0	34.3	15.8	23.0	11.7	53.3	32.5	Uruguay
PI 197664	21.3	39.7	11.3	23.9	6.7	40.0	23.3	Argentina
PI 225516	18.7	43.3	10.5	24.2	6.0	53.3	29.7	Uruguay
PI 372137	34.0	25.5	15.5	25.0	20.0	43.3	31.7	Ukraine
PI 351500	23.1	37.7	16.1	25.6	6.0	60.0	33.0	Russia
PI 225504	22.7	39.0	15.9	25.9	13.3	53.3	33.3	Uruguay
PI 225384	14.1	46.3	18.1	26.2	21.7	63.3	42.5	Uruguay
PI 225467	15.4	47.1	17.3	26.6	8.3	66.7	37.5	Uruguay
PI 233203	14.4	45.3	20.9	26.9	3.7	60.0	31.8	Russia
PI 285973	23.5	32.5	25.3	27.1	11.7	56.7	34.2	Russia
PI 225378	21.7	45.2	16.1	27.6	17.5	56.7	37.1	Uruguay
PI 285945	44.5	27.6	15.3	29.1	3.0	56.7	29.8	Poland
PI 572636	24.0	50.0	13.8	29.3	6.7	70.0	38.3	Ukraine
PI 584914	23.3	47.8	17.8	29.7	8.3	66.7	37.5	Brazil
PI 69260	29.8	21.8	38.2	29.9	3.0	26.7	14.8	China
PI 337149	37.8	35.2	20.9	31.3	36.7	56.7	46.7	Argentina
PI 285972	40.3	35.9	19.0	31.7	21.7	73.3	47.5	Poland
PI 74494	44.8	33.9	16.5	31.8	13.3	56.7	35.0	Russia
PI 69321	63.8	18.9	13.3	32.0	6.7	23.3	15.0	China
PI 225519	21.4	57.2	19.3	32.6	10.0	46.7	28.3	Uruguay
PI 225376	25.1	52.8	20.2	32.7	15.0	60.0	37.5	Uruguay
PI 372136	29.3	48.9	21.2	33.2	5.0	50.0	27.5	Russia
PI 520540	20.6	64.0	15.3	33.3	6.7	46.7	26.7	Brazil
PI 189816	29.8	56.8	15.7	34.1	23.3	63.3	43.3	Argentina
PI 225446	47.0	25.6	30.6	34.4	56.7	53.3	55.0	Uruguay
PI 225398	23.9	51.8	28.3	34.7	16.7	56.7	36.7	Uruguay
PI 69335	25.7	57.3	22.5	35.2	10.0	33.3	21.7	China
PI 352009	59.1	17.5	28.9	35.2	21.7	40.0	30.8	Russia
PI 70656	61.8	26.6	19.1	35.8	16.7	26.7	21.7	China
PI 74493	54.2	35.5	20.9	36.9	8.3	50.0	29.2	Russia
PI 225375	40.2	37.7	32.9	36.9	33.3	66.7	50.0	Uruguay
PI 281842	66.3	25.9	25.9	39.4	25.0	43.3	34.2	Ukraine

PI 225424	36.7	51.7	30.3	39.6	18.6	53.3	36.0	Uruguay
PI 225372	40.7	48.5	32.5	40.6	10.0	53.3	31.7	Uruguay
PI 225525	64.3	43.3	25.0	44.2	26.7	46.7	36.7	Uruguay
PI 168722	74.0	41.3	20.8	45.4	15.0	36.7	25.8	Argentina
PI 283806	42.8	70.4	29.8	47.7	5.0	53.3	29.2	Argentina
PI 74085	56.0	55.2	32.2	47.8	5.0	56.7	30.8	Russia
PI 69240	51.0	58.7	39.0	49.5	6.7	43.3	25.0	China
PI 62083	68.5	64.8	19.0	50.8	30.0	40.0	35.0	Argentina
PI 559686	53.2	42.8	57.8	51.3	11.7	56.7	34.2	Russia
PI 69261	69.8	54.4	30.2	51.5	23.3	23.3	23.3	China
PI 69747	62.0	32.7	62.0	52.2	26.7	30.0	28.3	China
PI 233204	51.8	49.1	55.8	52.3	10.0	50.0	30.0	Russia
PI 69243	49.2	68.7	47.2	55.0	8.3	23.3	15.8	China
PI 69270	67.8	57.3	46.7	57.3	41.7	33.3	37.5	China
PI 69265	56.8	45.7	75.5	59.3	13.3	33.3	23.3	China