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ABSTRACT

Fusarium head blight (FHB), incited by *Fusarium graminearum* Schwabe [telomorph *Gibberella zea* (Schwein)], has caused devastating losses to yield and quality of barley (*Hordeum vulgare* L.) produced in the upper U.S. Midwest from 1993 to 2000. Design of an efficient breeding strategy for developing FHB resistant cultivars is dependent on knowing (i) the heritability of FHB resistance and accumulation of deoxynivalenol (DON), a mycotoxin contaminant produced by *F. graminearum* and (ii) the correlated response of other traits during selection for reduced FHB. We conducted field studies in FHB disease nurseries using $F_{4:5}$ and $F_{4:6}$ families from the cross between the FHB susceptible six-rowed cultivar Foster and the resistant two-rowed accession CIho 4196 to gain knowledge in the areas listed above. Heritability of FHB severity and DON accumulation was 0.65 and 0.46, respectively. A moderately strong positive association between FHB severity and DON accumulation was observed ($r = 0.62$). FHB severity and DON accumulation were negatively associated with plant height, days to heading, spike angle, and spike density. The selection differentials calculated between the top $F_{4:6}$ families selected for low FHB severity and the unselected $F_{4:5}$ families were moderately high for FHB severity, DON accumulation, and days to heading. Less than 14% of the selected lines had six-rowed spikes. No difference in plant height was observed between the selected and unselected families. Thus, development of FHB resistant lines with acceptable DON accumulation and days to heading is obtainable. However, because no lines were as short as Foster, development of FHB resistant plants with acceptable plant height from a cross using CIho 4196 as a parent will be difficult.

NORTH DAKOTA is the leading state in barley production with 30.6% of the overall U.S. production (USDA, 2000). The area sown and harvested has been significantly reduced in the last few years because in part of FHB. Since 1993, barley losses due to FHB in the upper U.S. Midwest have exceeded $200 million (U.S. GAO, 1999). Some of the losses due to FHB are attributed to accumulation of DON, a mycotoxin contaminant of cereals produced by *F. graminearum*. Barley containing DON accumulations greater than 0.6 μg g^{-1} may be rejected by the malting and brewing industries because of marketing and processing concerns.

Tillage, crop rotation, and chemical control have been suggested as methods for reducing FHB severity; yet, success with these methods has been limited. Genetic resistance offers the greatest potential for reducing FHB. Nearly 40 barley genotypes have been identified with partial resistance to FHB (Prom et al., 1996). One

of the most resistant two-rowed barley accessions identified is CIho 4196 (Prom et al., 1996; Takeda, 1992). This accession originates from China and is being used extensively as a parent by the six-rowed barley breeding program at North Dakota State University (NDSU). In general, CIho 4196 and most of the other resistant genotypes identified by Prom et al. (1996) tend to head and mature later, and are taller than cultivars currently grown in the upper U.S. Midwest.

To design an efficient breeding strategy for developing FHB resistant cultivars, we need to know several things about the accessions used as parents; particularly we need to know the heritability of FHB resistance and DON accumulation. Information on the heritability of FHB resistance and DON accumulation in barley is limited. Takeda (1990) studied the genetic behavior of FHB resistance in five crosses between two-rowed and six-rowed barley in the F_2, F_3, and F_4 generations. He suggested that resistance to FHB is under the control of quantitative genes. Heritability estimated from the genetic gain:selection differential ratio was 0.25 in the F_2–F_3 selection response and 0.33 in the F_3–F_4. Takeda (1992) reported that heritability for FHB resistance in barley was 0.6 in the broad sense and 0.4 in the narrow sense, and that resistance was under the control of predominantly additive genes.

Development of a suitable breeding strategy is also dependent on knowing the correlated responses of selecting for reduced FHB severity on DON accumulation, days to heading, and plant height. Limited information is available on this topic for these traits. The objectives of this study were (i) to estimate the heritability of FHB resistance and DON accumulation and (ii) to evaluate the selection for reduced FHB severity at an intensity of 40% and to determine the correlated responses on DON accumulation, days to heading, and plant height in a population derived from the cross Foster/CIho 4196.

MATERIALS AND METHODS

Plant Materials

One spike was harvested from 250 individual F_2 plants from the cross Foster/CIho 4196 grown at Fargo, ND, during summer 1996. Two cycles of generation advancement were done in the greenhouse during the fall of 1996 and the spring of 1997. In each cycle, seed from one plant of each line was harvested and advanced to the next generation. Finally, three plants per line grown in the spring 1997 greenhouse were selfed and harvested in bulk to generate the $F_{4:5}$ generation.

Field Experiments

One hundred fifty of the 250 $F_{4:5}$ recombinant inbred lines were randomly selected and sown at Langdon, ND, on 17 May

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1997 in an FHB disease nursery. The soil at this location is a fine, montmorillonitic Utric Natriborroll. Experimental units were one, 1-m row. Entries were assigned to experimental units by an augmented block design (Federer, 1993), and each experiment was repeated twice. Block size in each experiment was 25 entries, and each block included the parents Foster and CIho 4196. The FHB epidemic nursery was inoculated four times with *F. graminearum*, beginning 1 wk before heading, and once a week for four consecutive weeks by the method of Prom et al. (1996).

This experiment was repeated in spring 1998 with $F_{4:6}$ seed harvested from the 150 families the previous year. Experiments were sown in FHB disease nurseries located at Fargo on 15 May, at Langdon on 27 April, and at Osnabrock, ND, on 15 May. The same experimental design, plot size, and FHB inoculation methods were used as in 1997. The soil at Langdon and Osnabrock was a fine, montmorillonitic Utric Natriborroll. At Fargo, the soil was a fine montmorillonitic, frigid Typic Haploboroll.

Inoculum Preparation

Fusarium graminearum inoculum was prepared according the methods of Xia (1956) as modified by Prom et al. (1996). First, equal parts, by volume, of barley and maize (*Zea mays* L.) grain are soaked separately in water for 48 h. After soaking, the barley and maize are put in stainless steel pans and covered with aluminum foil. Next, the barley and maize grain are autoclaved for 20 min at 121°C, in each of two consecutive days, to sterilize the grain substrate. Pieces of agar containing five isolates of *F. graminearum* (KB-172, KB-173, KB-176, KB-582, and KB-672) (Salas et al., 1999) then are added individually to each pan containing the sterilized grain, and the grain is incubated at 25°C for 14 d under complete darkness. Ten days later, the inoculum is mixed by hand in each pan.

Prior to inoculation, the colonized seeds of barley and maize are mixed in equal proportions. The mixed grain then is spread over the barley plots at a rate of 50 g colonized grain m^{-2} for four consecutive weeks, beginning 1 wk before heading of the earliest entries. At Osnabrock in 1998 and 1999, plots were irrigated at a rate of 1.20 L hr^{-1} with a model XS-360 F xerispray sprinklers (Rain Bird, Glendora, CA). Sprinkler heads were spaced 4 m apart and 120 cm above the ground. Irrigation was done early in the morning (0600–0800 h) and late in the afternoon (1600–1800 h) to provide favorable conditions for ascospore liberation and infection. The irrigation was done for 30 s every 30 min during this period. At Fargo and Langdon in 1997 and 1998, plots were irrigated at a rate of 0.19 L h^{-1} with 1800-SAM-PRS sprinklers (Rain Bird, Glendora, CA). Sprinkler heads were spaced 3 m apart and 120 cm above the ground. Irrigation was done once for 10 min at 0700 and 1700 h.

Morphological, Agronomic, and FHB Data Collected

Data on morphological and agronomic characteristics that were variable in the parents (Foster and CIho 4196) were collected. Data collected in the field were days to heading (number of days after 31 May when 80% of spikes were fully emerged from the boot), plant height (distance from soil surface to the tip of spikes, excluding awns), spike type (*vrs1vrs1Int-cInt-c* = normal six-rowed, *Vrs1Vrs1int-cint-c* = normal two-rowed, and *Vrs1Vrs1Int-cInt-c* = hybrid two-rowed), presence of lemma awn spiculation (smooth, semi smooth, and rough), spike angle (1 = erect spike, 90° from horizontal; 5 = bent spike, 0° from horizontal), and spike density (number of rachis nodes per cm of rachis).

Disease readings were done at the soft dough stage (Zadoks

85) of development. Fifteen spikes within each row were harvested at random and the number of infected kernels per spike was counted. The percent FHB severity was calculated by dividing the total number of infected kernels by the total number of kernels and multiplying by 100.

At maturity, each plot was harvested with hand shears. Grain samples were dried at 35°C in a forced dryer to approximately 100 g kg^{-1} moisture, deawned, and cleaned. Deoxynivalenol accumulation (μg g^{-1}) of harvested grain was determined by the gas chromatograph method of Tacke and Casper (1996).

Statistical Analyses

Data for parents and progeny in each experiment in an environment were analyzed as an augmented block design. Adjusted means (i.e. least square means) were calculated for each line, and these means were used to perform the analysis of variance across experiments as a randomized complete block design. Within a year, each experiment at an environment was considered a replicate. Combined analyses across environments within a year were done for all traits in which the error mean squares were homogeneous. In the combined analyses, environments and entries were considered random effects. Mean separation between parents was done by *t*-tests. *F*-tests and *t*-tests were considered significant at $P \leq 0.05$.

The adjusted means for the progeny from each environment for FHB severity and DON accumulation were used to estimate heritability. Heritability of FHB severity and DON accumulation were estimated using the standard unit method of Frey and Horner (1957). The parent-offspring regression of data coded in terms of standard units is equivalent to the coefficient from simple parent-offspring correlation (r). An r value was calculated for each parent-offspring combination in 1997 and 1998 ($F_{4:5}$ and $F_{4:6}$ generations, respectively). In the analyses, the $F_{4:5}$ and $F_{4:6}$ generations corresponded to parent and offspring, respectively. The homogeneity of heritability values across different environments was tested by the chi-square test of Edwards (1976). Pooled heritability values across all environments for FHB severity and DON accumulation were calculated by the method described by Edwards (1976).

The correlation between FHB severity and DON accumulation, and the correlation of FHB severity with all morphological and agronomic data collected were determined. To facilitate the calculation of the correlation between FHB severity and spike type, six-rowed lines were assigned a value of 1 and two-rowed lines were assigned a value of 2. Correlation values were calculated for each environment, and homogeneity of correlation values across environments were tested. Pooled correlation values were calculated as specified in Edwards (1976) for correlation values deemed to be homogenous.

The correlated response of selecting for reduced FHB severity on DON accumulation, days to heading, and plant height was determined by calculating the selection differential between FHB severity and each of the traits. The selection differential was the difference between the mean of the 40% most resistant $F_{4:6}$ lines and the mean of the unselected population comprised of 150 $F_{4:5}$ lines (Helms and Orf, 1998). All statistical analyses were done by SAS (SAS, 1992).

RESULTS AND DISCUSSION

CIho 4196 had lower FHB severity and DON accumulation than Foster in 1997 and 1998 (Table 1). Averaged across both years, CIho 4196 had FHB severity 40.7 percentage-units lower and DON accumulation 28.7 μg g^{-1} less than Foster. Mean FHB severity and DON accumulation of the Foster/CIho 4196 population was inter-

Table 1. Least square mean Fusarium head blight (FHB) severity, deoxynivalenol (DON) accumulation, days to heading, and plant height of Foster, CIho 4196, and progeny averaged across one environment in 1997, and three environments in 1998.

Year	Entry	FHB severity		DON accumulation		Days to heading		Plant height	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
		$\overline{\hspace{2em}\%\hspace{2em}}$		$\overline{\hspace{1em}\mu g\ g^{-1}\hspace{1em}}$		days after 31 May		$\overline{\hspace{2em}cm\hspace{2em}}$	
1997	Foster	47.2a†		42.5a		53.2a		88.2b	
	CIho 4196	6.4b		7.7b		57.2a		113.0a	
	F$_{4:5}$ population	24.1	−13.4–86.5	25.9	−17.7–123.0	57.8	49.3–72.6	106	96.0–128.0
1998	Foster	48.4a		26.9a		30.8b		89.4b	
	CIho 4196	7.8b		4.4b		36.5a		108.1a	
	F$_{4:6}$ population	30.7	0.8–66.1	21.2	−1.0–61.5	34.9	29.5–40.8	102.3	77.7–124.3

† Means for a trait within a year followed by the same letter are not significantly different at $P = 0.05$ as determined by a t-test.

mediate to that of the parents in 1997 and closer to the susceptible parent Foster in 1998. Transgressive segregation in both directions for the two traits was observed in the Foster/CIho 4196 population in both years. This indicates that both parents contributed alleles that conferred low levels of FHB severity and DON accumulation.

Significant differences in days to heading between Foster and CIho 4196 were observed only in 1998 (Table 1). Plant height of CIho 4196 was significantly greater than Foster in both years. On average, CIho 4196 headed 4.9 d later and was 21.8 cm taller than Foster (Table 1). Mean days to heading and plant height of the F$_{4:5}$ and F$_{4:6}$ populations more closely resembled CIho 4196 than Foster. Transgressive segregation in both directions was observed only for plant height.

Spike angle and kernel density were measured only in 1998. We began collecting data on these traits on all our breeding lines with putative FHB resistance in 1998 because it appeared that these traits could be associated with FHB resistance. Significant differences were observed between the spike angle and kernel density of the two parents (Table 2). The spike of Foster was more erect and had a lower kernel density than the spike of CIho 4196. This observation differs from that of Zhu et al. (1999) in which dense spikes were observed to have greater FHB susceptibility. This suggests that development of lax spikes in itself will not result in lower levels of FHB. Mean spike angle and density of the F$_{4:6}$ was intermediate to that of the two parents. Transgressive segregation in both directions was observed in the F$_{4:6}$ population for both traits.

The F$_{4:5}$ and F$_{4:6}$ populations were segregating for spike type. The ratio of two-rowed to six-rowed lines fit a 1:1 ratio ($P = 0.05$).

Table 2. Least square mean spike angle and kernel density of Foster/CIho 4196, and their progeny across three environments in 1998.

Entry	Spike angle		Kernel density	
	Mean	Range	Mean	Range
	$\overline{\hspace{1em}Score†\hspace{1em}}$		nodes per cm of rachis	
Foster	1.3b‡		0.14b	
CIho 4196	3.9a		0.20a	
F$_{4:6}$ population	2.1	0.8–5.2	0.17	0.08–0.30

† 1 = erect spike, 90° from horizontal; 5 = bent spike, 0 from horizontal.
‡ Means within a column followed by the same letter are not significantly different at $P = 0.05$ as determined by a t-test.

Heritability of FHB Severity and DON Accumulation

The heritability values for FHB severity and DON accumulation from each of the environments were homogenous ($P < 0.05$); thus, pooled heritability values were calculated. The estimated narrow-sense heritabilities were 0.65 for FHB severity and 0.46 for DON accumulation. These results agree with Takeda (1992) who reported that heritability for barley FHB resistance was 0.6 in the broad sense and 0.4 in the narrow sense, and that resistance was under the control of predominantly additive minor genes. Our results also agreed with those of Zhu et al. (1999) and differed with those of Ma et al. (2000). Zhu et al. (1999) observed narrow-sense heritabilities calculated on an entry-mean basis ranging from 0.50 to 0.81. Ma et al. (2000) found a narrow-sense heritability of 0.31. The moderate heritability values found in this study suggest that FHB resistance and DON accumulation are multigenic traits that may be strongly influenced by the environment. Thus, selection for FHB resistance and DON accumulation needs to be based on observations from many environments. In our breeding program, we require favorable FHB data from a minimum of four FHB screening nurseries before we can confidently state a line is resistant. This stringent requirement results in delaying selection for FHB resistance and DON accumulation until later generations.

Correlation between Traits

Days to heading, plant height, spike angle, spike density, and spike type were negatively associated with increased FHB severity (Table 3). Other researchers made similar observations using different sources of FHB resistance (Ma et al., 2000; de la Pena et al., 1999; Zhu et al., 1999). On the basis of a cross between six-rowed genotypes (M69/'Chevron'), de la Pena et al. (1999) stated that the undesirable linkage between FHB resistance, and late heading and taller plants need to be

Table 3. Genetic correlation between Fusarium head blight (FHB) severity and deoxynivalenol (DON) accumulation, days to heading, plant height, awn type, spike angle, spike density, and spike type in 1998.

DON	Days to heading	Plant height	Awn type	Spike angle	Spike density	Spike type
0.62**	−0.43**	−0.43**	0.05	−0.20*	−0.20*	−0.68*

* indicates significance at $P = 0.05$.
** indicates significance at $P = 0.01$.

broken. In another study using Chevron as the FHB resistant parent, Ma et al. (2000) found that many of the quantitative trait loci (QTL) for FHB severity and DON accumulation coincided with QTL for heading date, plant height, and spike morphology traits. On the basis of their observations, they stated that QTL with major effects for FHB severity and DON accumulation probably do not exist in Chevron. In a study involving a cross between two two-rowed genotypes, Zhu et al. (1999) found FHB resistance to be associated with taller plants, more seeds per spike, low-density spikes, and small lateral florets.

Ma et al. (2000), de la Pena et al. (1999), and Zhu et al. (1999) mapped QTL for FHB resistance to a region near the *vrs1* locus in chromosome 2H. Franckowiak (2000, 2001) hypothesized that within a 20- to 30-centimorgan region including the *vrs1* locus are 1 to 2 putative loci for FHB resistance, and loci controlling plant height (*hcm1*) and maturity (*eam6*). If this hypothesis is correct, development of FHB resistant six-rowed cultivars with plant height and maturity similar to currently grown cultivars is going to be difficult.

Other researchers found no associations between FHB severity, and days to heading and plant height. Zhu et al. (1999) found no associations between days to heading and FHB severity in barley. Hilton et al. (1999) suggested that there are independent genes affecting FHB and plant height in wheat that may allow plant breeders to select resistant cultivars of any height. Deoxynivalenol accumulation was positively associated with FHB severity (Table 3). This association indicates that if we select for lower FHB severity, we also select for lower DON accumulation. Using the mapping population derived from the cross M69/'Chevron', de la Pena et al. (1999) found DON to be positively correlated to FHB severity at Crookston, MN, in 1995, but no association was found between these two traits at Hangzhou, China in 1997.

Presence of lemma awn spiculation was not associated with FHB severity (Table 3). This indicates that awn roughness will not affect FHB severity, allowing development of the smooth awn FHB-resistant cultivars preferred by producers. Spike angle and density were both negatively associated with FHB severity (Table 4). The negative correlation between FHB severity and spike density in this study may be surprising to some since the resistant parent CIho 4196 had a denser spike than Foster; however, the correlation was weak (−0.20). Thus, as stated earlier, development of cultivars with lax spikes will not ensure greater FHB resistance.

The negative correlations observed between FHB se-

verity and some of the desirable agronomic traits suggest that breeding for FHB resistance with CIho 4196 as the resistant parent will be difficult. Barley growers prefer cultivars that are moderate in height (i.e., 70–85 cm) so lodging is reduced, and mature before their other crops mature so the workload at harvest can be spread out.

Because heading date and FHB severity are associated, we need to determine if field resistance is due to genes conferring FHB resistance or a pleiotropic effect of heading date. We attempted to reduce the confounding effect of heading date in the field by ensuring there was inoculum present from 1 wk before the earliest genotypes headed until maturity was reached by all genotypes. Mist-irrigation also was provided for the same time frame. However, there are conditions other than heading date that can confound FHB severity in field nurseries. These conditions include the time needed for the colonized grain to form perithecia and release ascospores, and the fluctuations in temperature, humidity, and precipitation.

To remove completely the effects of heading date and other environmental factors on FHB severity, it probably is necessary to evaluate plants in the greenhouse. In our greenhouse screening of breeding lines, we routinely sow checks weekly to ensure there are always ones at the proper growth stage when we inoculate the progeny. While screening plants for FHB resistance in the greenhouse is ideal from the standpoint of removing the possible confounding effects of heading date and environment, a limiting factor in greenhouse assessments is space because evaluations are done on adult plants.

Correlated Responses When Selecting for FHB Severity

To determine the effect that selection for reduced FHB severity had on other traits, the selection differential method of Helms and Orf (1998) was used. Values for differential selection in FHB resistance have not been previously reported. A selection intensity of 40% was chosen to select the 60 most FHB resistant $F_{4:6}$ lines. The selected lines had an adjusted mean FHB severity ranging from −13.4 to 14.0%. Less than 14% of the selected lines had six-rowed spikes. The difference in FHB severity, DON accumulation, days to heading, and plant height between the mean of the 60 selected $F_{4:6}$ families and the mean of unselected $F_{4:5}$ population were then calculated and are presented in Table 4.

Mean FHB severity, DON accumulation, and days to heading of the selected lines were all much lower than those observed in the mean of the unselected population. Fusarium head blight severity and DON accumulation were reduced by 28.6 and 58.7%, respectively, in the selected lines compared with the unselected lines. Days to heading were decreased by 37% in the selected lines even though there was a negative relationship between FHB severity and days to heading. This is not surprising since the correlation between these two traits was moderately weak (−0.43). Plant height was the only trait where the mean between the selected and unse-

Table 4. Selection differential for Fusarium head blight (FHB) resistance, deoxynivalenol (DON) accumulation, days to heading, and plant height of 60 $F_{4:6}$ barley lines selected solely for FHB resistance from 150 $F_{4:5}$ lines.

Population	FHB	DON	Days to heading	Plant height
	%	µg g^{-1}	days after 31 May	cm
Mean of selected $F_{4:6}$ lines	17.2	10.7	36.1	107.0
Mean of unselected $F_{4:5}$ lines	24.1	25.9	57.8	106.0
Selection differential	−6.9	−15.2	−21.4	1.0

lected families did not differ. In fact, none of the selected plants had plant height approaching that of Foster.

A challenge U.S. Midwest barley breeders have had is transferring FHB resistance from unadapted two-rowed barley accessions to six-rowed malting barley. This challenge was made more difficult becaue of the negative linkages in chromosome 2H between FHB resistance, row type, days to heading, and plant height described earlier. However, the linkage between row-type and resistance appears to have been broken and an FHB resistant six-rowed germplasm line (6NDRFG-1) from the cross Foster/CIho 4196 was recently released (Urrea et al., 2002). However, the linkage between FHB resistance, plant height, and, days to heading has not been broken. Plant height and days to heading of 6NDRFG-1 are similar to CIho 4196.

The differential selection values calculated for FHB severity, DON accumulation, and days to heading in this study indicate that development of FHB-resistant lines with acceptable DON accumulation and days to heading should be possible. However, when the failure to reduce plant height is considered, the difficulty in developing resistant plants with height similar to currently grown cultivars is quite evident. Thus, results from this study suggest that development of FHB-resistant lines with acceptable height from a cross with CIho 4196 as a parent will be difficult.

ACKNOWLEDGMENTS

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