Variation in *Fusarium graminearum* and Cultivar Resistance to Wheat Scab

Gui-Hua Bai, former Graduate Research Assistant, and **Gregory Shaner,** Professor, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907-1155

ABSTRACT

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Understanding variation in pathogen virulence and cultivar resistance is important for development of effective strategies for breeding wheat cultivars resistant to scab. Six isolates of *Fusarium graminearum* from China and the United States were compared for variation in cultural characteristics and virulence on nine wheat cultivars with different degrees of resistance to scab. The isolates varied in their cultural characteristics and ability to cause scab, but there was no consistent specificity of cultivar resistance or pathogen virulence. Therefore, a mixture of local isolates is an appropriate inoculum to screen for scab resistance. Subculturing the fungus on potato dextrose agar for eight generations did not reduce virulence. In the greenhouse, eight cultivars were tested five times over 3 years by inoculating one central floret in a spike with an Indiana isolate of the fungus. Cultivars Ning 7840, Sumai 49, Fu 5114, and Sumai 3 were consistently resistant. The fungus spread from the inoculated spikelet to noninoculated spikelets of resistant cultivars in less than 20% of the plants, and spread was not evident until 12 days after inoculation. All plants of susceptible cultivar Clark showed spread of infection, and symptoms appeared on noninoculated spikelets by 8 days after inoculation. Sudden blight on the top part of the spike may be an important characteristic of highly susceptible cultivars. Measurement of spread of scab within a spike is a stable and reliable estimate of cultivar resistance.

Scab of wheat, also called Fusarium head blight, is a destructive disease of wheat (*Triticum aestivum* L.) in many areas of the world (10). In the United States, scab is sporadic, and it can be severe when weather is favorable for infection. Scab was severe in the spring wheat areas of the northern United States in 1993 and in Indiana in 1986, 1990, 1991, and 1995, and it is becoming a greater threat to wheat production in many areas when warm, wet weather occurs during wheat flowering.

Wheat scab can cause considerable loss in grain yield and quality. Yield reduction results directly from shriveled grain, which is blown away with the chaff during harvest, and from lighter test weight of harvested grain (1). Indirect losses arise from infected grains that reduce germination and cause seedling blight and poor stand (14). Contamination of grain by mycotoxins can severely reduce the value of the harvested product (14).

Cultural variation is common in *F. graminearum* (Schwabe), the major causal agent of wheat scab. Subculturing the fungus for several generations may produce many variants, and some variants may be so different in cultural characteristics as to appear to be other species (8). Clear evidence of the existence of pathogenic races in *F. graminearum* is scanty. Tu (13) investigated 10 cultures of three *Fusarium* species and claimed that there are at least three physiologic forms of *F. graminearum* that are differentiated by their pathogenicity toward different species and cultivars of cereals. Purss (9) reported that isolates of *F. graminearum* that cause crown rot and head scab of wheat are different races.

Isolates of *F. graminearum* have been divided into groups I and II based on their life cycles and ecological requirements (5, 6). Group I isolates are normally associated with crown rot, do not form perithecia in culture, rarely produce the *Gibberella* stage in nature, and can cause scab only during abnormally wet weather in semiarid regions. Group II isolates are associated with head scab in cereals and stalk and ear rots of corn in humid climates and can produce the *Gibberella* stage in nature (6,9). However, further investigation indicated no difference in pathogenicity between the two groups of isolates on wheat heads under field conditions in 1983 (4).

Isolates of *F. graminearum* from different regions of China were reportedly differ in pathogenicity (16). Van Eeuwijk et al. (15) concluded that specific interactions between wheat cultivars and pathogen isolates from different geographic areas do not exist and that resistance to scab in wheat is horizontal (i.e., race-nonspecific). An identical conclusion was reached in a study of *F. graminearum* as a seedling blight pathogen (7).

Two types of resistance to scab of wheat have been reported: resistance to primary infection and resistance to spread of the disease within a spike (10). Measurement of spread of scab within a spike has been recognized as a relatively reliable index of cultivar resistance (2,10,17). Spread of the disease within a spike also may have two distinct stages: spread of scab symptoms into the rachis and subsequent spread of scab symptoms through the rachis into other spikelets (18). Different cultivars may have resistance genes that affect different stages of scab development (18).

Reduced tillage for soil conservation and extension of corn production into the northern plains of the United States increases the amount of inoculum for wheat scab epidemics, and epidemics of wheat scab are becoming more frequent and widespread (1). The objectives of this study were to investigate the stability of resistance, characterize resistance components, and determine interactions between pathogen isolates and wheat cultivars. This work was undertaken to improve our ability to select wheat cultivars for scab resistance in breeding programs.

MATERIALS AND METHODS

Preparation and characterization of fungal cultures. Each culture of *F. graminearum* was a mixture of field isolates obtained from infected seeds of a susceptible cultivar. WL1 and NWL were field isolates originating from cultivar Caldwell grown at the Purdue Agricultural Research Center, West Lafayette, IN, in 1986 and 1990, respectively. NJ1 and NNJ were two field isolates that originated from different seeds of cultivar Ningmai 6 grown in a breeding nursery of the Jiangsu Academy of Agricultural Sciences, Nanjing, China, in 1989. NJ1 was isolated in 1989, and NNJ was isolated in 1990 from stored seeds from the 1989 crop. EM and SI were field isolates from eastern Michigan and southern Indiana in 1990, respectively. WL9 and NJ9 were isolates from the ninth generation of subculturing of WL1 and NJ1, respectively.

To isolate the fungus, infected seeds were surface-sterilized for 1 min in sodium hypochlorite solution (0.25%) diluted 1:20 with distilled water and rinsed in sterile water three times. Seeds were placed on potato dextrose agar (PDA) medium in petri dishes. After 5 days, uncontaminated mycelium was transferred onto fresh PDA medium and

Current address of G-H. Bai: Plant Molecular Genetics Lab, Department of Plant and Soil Science, Mail Stop 2122, Texas Tech University, Lubbock 79409-2122.

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Corresponding author: G-H. Bai
E-mail: bwbgh@ttacs.ttu.edu.

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grown until it covered the surface. These first generation cultures were stored in a refrigerator at 4°C. Subcultures NJ9 and WL9 originated from cultures of NJ1 and WL1, respectively, and were obtained by sequentially transferring a 2-mm^2 disk of colonized medium of NJ1 and WL1 eight times. For each generation, the fungus was allowed to grow at room temperature for 1 week. To study cultural characteristics, a 2-mm^2 disk of colonized medium from different cultures was transferred to fresh PDA in petri dishes and cultured for 1 week in one of nine dark growth chambers at temperatures from 4 to 36°C, in increments of 4°C, or under constant light at room temperature. Each environment treatment had three replicate plates. Colony size and pigment produced by the fungus were noted.

Conidial suspensions were produced in a mung bean liquor medium. To prepare this medium, 40 g of mung beans was placed in a 1-liter Erlenmeyer flask containing 1 liter of boiling water. The beans in different flasks, five total, were boiled for 5, 10, 15, 20, or 30 min, respectively, and were filtered through cheesecloth. The mung bean filtrate in each flask was equally subdivided into 10 200-ml Erlenmeyer flasks, autoclaved, inoculated with a 2-mm^2 disk from a culture of *F. graminearum* grown on PDA, and placed on a shaker at 24°C for 4 days. After the incubation period, the liquid cultures were stored in a refrigerator. For inoculation, spore suspensions were prepared by filtering the aqueous culture through two layers of cheesecloth and adding sterile water to adjust the inoculum concentration. Conidia were counted under a microscope with the aid of a hemacytometer.

Plant materials. Based on percentage of scabbed spikelets observed in our preliminary study in the greenhouse and field evaluation in China (3), nine cultivars of wheat with different degrees of resistance to scab were selected for the study. Seeds of each cultivar were planted in 55 × 37 × 7-cm flats. After seeds germinated, winter wheat cultivar Clark was vernalized at 4°C for 8 weeks, and all spring wheat cultivars were vernalized for 6 weeks. After vernalization, seedlings were transplanted to clay loam soil with peat in 10-cm-diameter plastic pots. Plants were fertilized with ~1 g of urea (46-0-0 N-P-K) per pot three times at 1-week intervals after transplanting. Plants were grown under natural greenhouse lighting supplemented with fluorescent lights (cool white, 215-W bulb) with a 12-h photoperiod initially and a 16-h photoperiod after booting.

Inoculation and disease assessment. Plants at early anthesis were inoculated by injecting a suspension of ~1,000 conidia into a central floret of each spike with a hypodermic syringe. Inoculations were conducted from 1400 to 1600 h each day. After inoculation, the plants were placed in a moist chamber and sprayed with tap water from a hand-powered atomizer. The chamber was set up on a bench in the greenhouse. Within the chamber, temperatures ranged from 23 to 25°C, and relative humidity was 95%. Inoculated plants were placed in the chamber for three successive nights from 1600 until 0800 h the next morning. On day 4 after inoculation, the plants were returned to the greenhouse bench. The greenhouse temperature averaged 23°C during the day, with a range of 19 to 30°C, and 19°C at night, with a range of 17 to 21°C.

Symptoms of scab ranged from dark-brown, water-soaked spots on the glumes to bleached spikelets. Spikelets with any of these symptoms were recorded as diseased. Diseased spikelets were counted in situ from 3 to 21 days after inoculation at 3-day intervals. Final disease severity was calculated as the percentage of diseased spikelets per spike on day 21 after inoculation. Also, an area under the disease progress curve (AUDPC) for each plant was derived from the proportion of diseased spikelets in a spike at each observation date as previously described (11). The time required for appearance of scab symptoms on noninoculated spikelets was calculated as the number of days from inoculation to when symptoms appeared on any noninoculated spikelet.

For isolate pathogenicity tests, nine wheat cultivars and eight fungal cultures were tested. The plants were arranged in a completely randomized design. Ten plants of each cultivar were inoculated with each isolate by injecting 1,000 spores into a central spikelet of a spike, and the experiment was repeated once. Experiments to test cultivar resistance were conducted five times over different greenhouse crop cycles from 1990 to 1993. The experiments were arranged in a completely randomized design in each trial. For each cultivar, the population size varied among experiments from 20 to 50 plants. Single-factor analysis of variance (ANOVA) was performed on the data from each trial. A randomized complete block design was used to evaluate overall resistance of cultivars based on means of five trials. Statistical analysis was performed with the SuperANOVA program (Abacus Concepts, Berkeley, CA). Arcsine (square root) transformation was performed to normalize percent data in variance analysis, but transformation of data did not change the result, so the analysis of original data was retained.

To relate spread of symptoms in the spike to spread of the fungus within the spike, single florets of Ning 7840 and Clark were inoculated with isolate WL1. Fifteen days after inoculation, infected spikes were cut from the peduncle, placed on two layers of

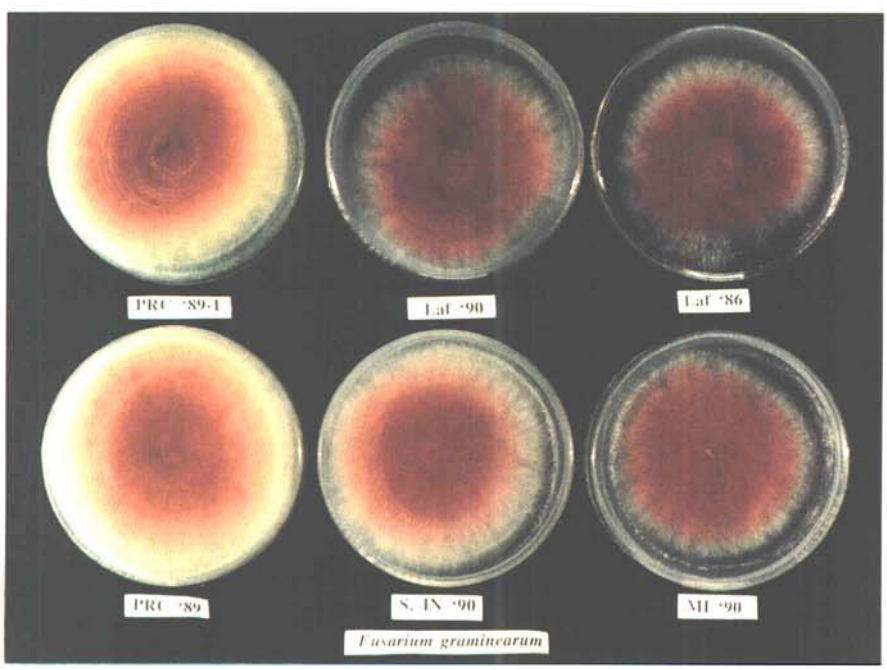

Fig. 1. Six isolates from four geographic areas were grown on potato dextrose agar medium. Isolates from China (left two dishes) grew faster and produced lighter pigments than isolates from the United States (right four dishes) in petri dishes.

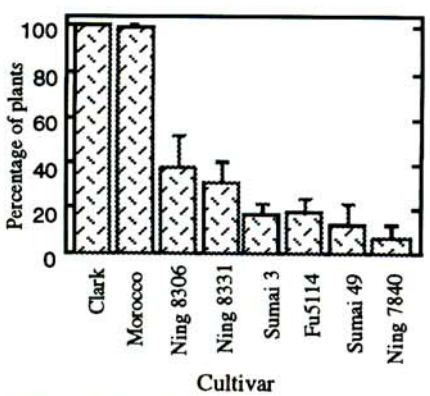

Fig. 2. Percentage of plants of eight wheat cultivars on which scab symptoms spread from the inoculated spikelet to other spikelets. Values are averages from five greenhouse trials.

wet filter paper in petri dishes, and incubated under constant light at room temperature. The infected spike was incubated in the dish either as the whole spike or as five pieces of the spike. Ten plants of each cultivar were tested. After 4 days of incubation, the spikes were photographed, and the mycelia were examined.

RESULTS

Cultural characteristics of isolates. When isolates were placed on fresh PDA medium and incubated at room temperature under constant light, the isolates from China fully covered the agar surface with dense mycelium after 1 week (Fig. 1). Light reddish pigment also was observed from the bottom of the petri dishes. The isolates from the United States produced less mycelium but more and darker pigment than the isolates from China. In the dark, isolates NJ1 and WL1 did not grow on PDA at 4 or 36°C, grew slowly at 8°C (1.9 cm^2 of medium colonized) and 32°C (3 cm^2 of medium colonized), and grew rapidly between 12 and 28°C (8.7 cm^2 of medium colonized), with the most growth at 28°C (9 cm^2 of medium colonized). Reddish pigment was produced from 12 to 32°C with peak production at 28°C. NJ1 and WL1 did not differ in the area of growth, but the isolate from China had much denser mycelium and produced less pigment than WL1.

In mung bean medium, cultures differed significantly in conidial yield. Overall, isolates from the United States (WL1, NWL, EM, SI, and WL9) produced significantly more spores (4.6 to 5.5 × 10^5 spores per ml) than isolates from China (2.9 to 3.9 × 10^5 spores per ml). Mung bean boiling period (5, 10, 15, 20, or 30 min) also significantly affected conidial yield. For most isolates, the most spores were produced when mung beans were boiled for 15 to 20 min.

Cultivar response to infection by different isolates. The six isolates from four geographic areas were pathogenic on the wheat cultivars studied (Table 1). Disease severity did not differ significantly among isolates from the United States. Isolates from China caused somewhat greater scab severity as measured by AUDPC. Subculturing the fungus for eight generations (isolates WL9 and NJ9 compared to WL1 and NJ1, respectively) did not decrease the ability of the fungus to cause scab.

Cultivar differences in resistance were significant across all isolates (Table 1). The most resistant and susceptible cultivars responded consistently to each isolate. Each isolate differentiated resistant from susceptible cultivars based on AUDPC. However, for moderately resistant (Ning 8331 and Ning 8306) and susceptible cultivars (Ning 84r10 and Morocco), there were interactions between isolates and cultivars that led to a significant interaction term in ANOVA.

Cultivar response to scab infection. In further experiments to evaluate resistance to isolate WL1, all cultivars developed scab, but there was a wide range in susceptibility (Table 2). Overall, Ning 7840 had the fewest diseased spikelets, and Clark had the most. Analysis of AUDPC revealed that all

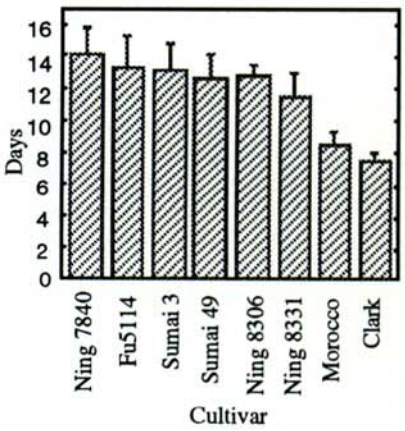

Fig. 3. Time (days) until appearance of scab symptoms on noninoculated spikelets on eight wheat cultivars after inoculation with isolate WL1 of *Fusarium graminearum*. Values are averages of five greenhouse trials. Plants that did not show spread of scab within a spike were not included in the calculation.

Table 1. Area under the disease progress curve for nine wheat cultivars inoculated with eight isolates of *Fusarium graminearum*

	Isolate[y]								
Cultivar	ME	WL9	NWL	IS	WL1	NJ9	NJ1	NNJ	Mean[z]
Ning 7840	0.6	0.5	0.6	0.5	0.6	0.8	0.5	0.7	0.6 a
Fu 5114	0.6	0.7	0.8	0.6	0.6	0.5	0.6	0.8	0.7 a
Sumai 49	0.6	0.7	0.6	0.6	0.7	0.6	0.7	0.8	0.7 a
Sumai 3	1.1	0.8	1.4	0.8	0.2	0.6	0.7	0.3	0.7 a
Ning 8331	0.8	0.9	1.5	0.7	1.0	2.7	2.9	1.7	1.5 b
Ning 8306	0.9	1.3	0.7	1.5	1.2	1.3	4.5	0.7	1.5 b
Ning 84r10	0.8	3.4	2.1	0.9	3.7	3.5	2.1	6.2	2.8 c
Morocco	2.9	2.7	2.4	3.5	4.2	1.7	2.2	6.8	3.3 c
Clark	8.5	6.6	6.8	9.6	8.2	8.7	10.1	11.2	8.7 d
Mean[z]	1.9 a	1.9 a	1.9 a	2.1 ab	2.3 ab	2.3 ab	2.7 bc	3.2 c	

[y] NJ1 and NNJ were originally from China, EM was from eastern Michigan, SI was from southern Indiana, WL1 and NWL were from West Lafayette, IN, and WL9 and NJ9 were subcultures of WL1 and NJ1, respectively.

[z] Values within a column or row followed by the same letter are not significantly different at $P = 0.05$ according to Fisher's protected least significant difference test.

Table 2. Area under the disease progress curve (AUDPC) and percentage of diseased spikelets[y] in eight wheat cultivars inoculated with isolate WL1 of *Fusarium graminearum* over five greenhouse experiments from 1990 to 1993

	AUDPC[z]			% Diseased spikelets[z]		
Cultivar	Min	Max	Mean	Min	Max	Mean
Ning 7840	0.7	0.9	0.8 a	4	7	5 a
Sumai 49	0.7	2.2	1.1 a	4	22	9 ab
Fu 5114	0.7	1.6	1.0 a	5	19	9 ab
Sumai 3	0.8	1.6	1.1 a	4	16	10 ab
Ning 8331	1.5	4.2	2.2 ab	5	51	23 b
Ning 8306	1.2	3.8	2.5 ab	10	48	29 c
Morocco	4.5	9.7	7.8 c	57	90	75 d
Clark	9.3	15.0	11.6 d	90	100	95 e

[y] Final scab severity was assessed 21 days after inoculation.

[z] Min and max are the highest and lowest means among experiments for each cultivar. Mean is a mean value over five experiments for each cultivar. Within each experiment, there were 20 to 50 replicate plants of each cultivar. Mean values followed by the same letter are not significantly different at $P = 0.05$ according to Fisher's protected least significant difference test.

Fig. 4. Wheat spikes were inoculated in the greenhouse by injecting 1,000 spores of *Fusarium graminearum* into a central floret of a spike. Fifteen days after inoculation, infected spikes were incubated for 4 days in covered petri dishes with two layers of wet filter paper. Cultivar Ning 7840 (left) had little mycelium on the inoculated spikelet. Abundant mycelium covered the bottom half of the spike of cultivar Clark (right), but no mycelium grew from the top half of the blighted spike.

cultivars previously regarded as having some resistance had significantly lower values than moderately susceptible cultivar Morocco and susceptible cultivar Clark. AUDPC for Morocco also was significantly different from Clark, and Ning 8331 showed significantly more diseased spikelets than Ning 7840. AUDPC for Ning 8306 and Ning 8331 did not differ in AUDPC from other resistant cultivars.

Analysis of final disease severity led to conclusions similar to analysis of AUDPC, except the difference in final disease severity between Ning 8331 and Ning 8306 and other resistant cultivars was significant. The correlation between AUDPC and percentage of diseased spikelets was very high (r = 0.99). Based on AUDPC and final disease severity of these cultivars over five trials, we consider Ning 7840, Sumai 49, Fu 5114, and Sumai 3 to be resistant; Ning 8331 and Ning 8306 to be moderately resistant; Morocco to be moderately susceptible; and Clark to be susceptible.

Percentage of diseased spikelets for the four cultivars regarded as resistant ranged from 4 to 22% over five experiments (Table 2). Ning 7840 had the smallest standard error (SE, 0.6%). The SE was largest on cultivars with moderate reactions to scab (6 to 9%). For a given cultivar in a given test, variation among individuals was even larger. For Ning 8331 and Ning 8306, the largest SE was 12%. In some trials, a few plants of Ning 7840 (1%) had 77% diseased spikelets, but most spikes (90%) had only 4 to 5% diseased spikelets.

The proportion of plants that showed spread of disease symptoms from the inoculated spikelet to other spikelets was very low in resistant cultivars (Fig. 2) but extremely high in moderately susceptible or susceptible cultivars. In spite of the variation among trials, ranks of degree of resistance, as reflected by final percentage of diseased spikelets and AUDPC, were consistent in all trials, except for Ning 8306 and Ning 8331 in experiments 3 and 4 (data not shown). The results indicate that testing for scab resistance in the greenhouse by the single-floret inoculation method is reliable.

The time required for scab symptoms to appear on noninoculated spikelets was longer in resistant cultivars than in susceptible cultivars (Fig. 3). Symptoms on noninoculated spikelets of resistant or moderately resistant cultivars usually were not evident until 12 days after inoculation, if spread occurred at all. In contrast, it took only 7 to 8 days for symptoms to spread to noninoculated spikelets of susceptible or moderately susceptible cultivars.

Disease symptoms on resistant cultivars differed from those on the susceptible cultivar. The inoculated spike of cultivar Clark was often completely blighted with bleached spikelets and a dark-brown rachis and culm about 12 days after inoculation. The seeds were shriveled, or no seeds developed. When a blighted spike was incubated on wet filter paper in a petri dish for 4 days, mycelium grew abundantly over the bottom half of the spike (Fig. 4) but did not grow from the top part of the spike, although this part of the spike was also blighted. In resistant cultivars, for most plants, the symptoms were confined to the inoculated spikelet and did not spread to noninoculated spikelets. Noninoculated spikelets were apparently healthy and produced seeds.

On resistant plants, a dark-brown discoloration could be seen on the inoculated spikelet, or in some cases, there was only a small spot on the lemma. On a few resistant plants, symptoms spread within the spike, but symptoms usually did not appear on noninoculated spikelets until 12 days after inoculation. Seeds still developed, although they were contaminated. The noninoculated spikelets remained green or turned dark brown in spikes of resistant cultivars over a long period of time, and sudden desiccation never occurred in the spike. When spikes were incubated on wet paper in a petri dish, the fungus grew from the spikelets, the rachis, and even the culm when these tissues showed disease symptoms, but less mycelium grew from the resistant cultivars than from the susceptible cultivar (Fig. 4).

DISCUSSION

Variation in cultural characteristics is a common phenomenon in the genus *Fusarium* (8). In this study, isolates from different geographic areas exhibited variation in yield of conidia, growth rate of mycelium, and production of pigment in growth media. Because most isolates produced the highest conidial yields when mung beans were boiled for 20 min, we regard this as the best boiling duration for preparation of mung bean medium to produce conidial suspensions.

Large variations in scab severity among isolates were observed on cultivars with a moderate degree of resistance to scab but not on highly resistant and susceptible cultivars. The same pattern of reaction was seen when several trials were conducted with a single isolate. Highly resistant and susceptible cultivars had a more constant reaction to infection across isolates and environments. Evidence of the existence of stable pathogenic races was not found in this study, as was found by other authors (5,12,16). Subculturing an isolate for eight generations did not reduce its ability to cause scab.

Cultivars Ning 7840, Sumai 49, Fu 5114, and Sumai 3 showed consistently lower scab severity than other cultivars in all trials, indicating that resistance to spread of scab within a spike on those cultivars was relatively stable. Their resistance to different isolates also was stable. Van Eeuwijk et al. (15) obtained similar results and concluded that resistance is horizontal (i.e., race-nonspecific).

When highly resistant cultivars were inoculated with different isolates of the fungus in the same trial or with the same isolate in different trials, the results were the same: in most plants, scab symptoms were confined to the inoculated spikelet, and in only a few plants did symptoms spread to noninoculated spikelets through the rachis. The cultivars we identified as resistant may be valuable sources of stable resistance for genetic studies and breeding. Clark was consistently highly susceptible to all isolates in all trials and would be a good susceptible control for genetic studies.

Because of the consistent performance of highly resistant and susceptible cultivars in the greenhouse, the resistance reaction to scab can be distinguished clearly in a single test. However moderately resistant or susceptible cultivars were variable among the trials and isolates, and multiple tests may be required for more informative results with such cultivars. A set of control cultivars, each with a known degree of resistance, would be helpful for assessing experimental errors when evaluating resistance in large-scale experiments. For disease assessment, AUDPC estimates overall resistance of a cultivar, but it is labor-intensive and costly. AUDPC may be useful for genetic studies and small-scale screening. Final percentage of diseased spikelets, however, was easy to estimate, was highly correlated with AUDPC in this study, and would be appropriate for large-scale screening.

In the greenhouse, scab symptoms usually appeared on the inoculated spikelet 3 days after spores were injected into it. In susceptible cultivar Clark, symptoms appeared on the rachis or noninoculated spikelets 6 to 8 days after inoculation, and by 12 days after inoculation, the entire spike was often blighted. Infected spikes blighted most rapidly under dry, hot conditions. Rapid blighting of the top part of the spike also was common in other susceptible cultivars in greenhouse and field tests (G-H. Bai and G. Shaner, *unpublished data*). Because no mycelium was found in the top half of the blighted spike under wet conditions (Fig. 4), the sudden blighting of the top part of the spike was probably caused by shortage of water and nutrients resulting from vascular dysfunction, rather than by direct invasion by the fungus. Desiccation in the top half of the spike may occur 1 day after symptoms appear on noninoculated spikelets and can be regarded as an important characteristic of highly susceptible cultivars.

Scab development on resistant cultivars was different from that on susceptible cultivars. For most resistant plants, only the inoculated floret showed symptoms. On a few resistant plants, symptoms spread from the inoculated spikelet to noninoculated spikelets, but the symptoms appeared on noninoculated spikelets 4 to 7 days later than on susceptible cultivars. Sudden desiccation in the top part of the spike never occurred in resistant plants. Only a limited amount of

mycelium grew from the symptomatic spike when it was inoculated under wet conditions, suggesting that resistant cultivars may have some substances that suppress growth of mycelium within a spike. Compared with resistant cultivars, in most trials, moderately resistant cultivars had more plants in which disease symptoms spread to noninoculated spikelets. Severity on these cultivars was comparable to severity on resistant cultivars in some trials but higher in others. Resistance to spread of disease symptoms to the rachis also was weaker, and there was greater variation among plants than was seen for resistant cultivars. On moderately susceptible cultivars, symptoms spread to noninoculated spikelets on almost all plants, but the spread was much slower compared to susceptible cultivars. Sudden blight on the top part of spike was not common on cultivars with a moderate reaction to scab infection.

Yu (18) investigated the inheritance of resistance, using the spikelet inoculation method, and concluded that resistance to spread of scab was determined mainly by two components: the rate at which symptoms spread from the inoculated spikelet into the rachis and the rate of spread of disease symptoms from the rachis to other spikelets. The two components were controlled by different genes, which were independent of each other. In this study, we demonstrated that cultivars differed not only in rate of symptom spread, but also in the frequency of spikes in which any spread occurred and in the time for appearance of symptoms on the rachis and noninoculated spikelets.

Characterizing major resistance components in cultivars with different levels of resistance may provide useful information for effective use of resistance sources in breeding resistant cultivars. Resistance to scab spread within a spike is a quantitative trait. Spread of the fungus from inoculated spikelets to noninoculated spikelets occurred in all cultivars but not with equal frequency. Resistant cultivars had consistently fewer plants in which scab spread into the rachis or through the rachis to noninoculated spikelets, and the spread was later and slower. These are important components of a cultivar's resistance. The difference in resistance between resistant and moderately resistant cultivars was mainly in the frequency of plants that showed spread of symptoms from the inoculated spikelet to noninoculated spikelets.

The spread of symptoms was seen in almost all plants of susceptible and moderately susceptible cultivars, but the rate of spread of symptoms on moderately susceptible cultivar Morocco was significantly slower than on susceptible cultivar Clark. Therefore, in breeding programs, moderately resistant cultivars can be obtained by selecting lines with less and slower spread of scab within a spike. The final goal of a breeding program, however, should be to develop cultivars with the greatest degree of resistance possible.

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