Aggressiveness to Mature Maize Plants of *Fusarium* Strains Differing in Ability to Produce Fumonisin

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ABSTRACT

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Four strains each of *Fusarium moniliforme* (syn. *Fusarium verticillioides*) and *Fusarium thapsinum* were tested for aggressiveness toward two maize inbred lines grown under greenhouse conditions. All strains induced significantly longer stalk lesions than those observed in the controls. Mean lesion length resulting from inoculation with strains of *F. moniliforme* was longer than the mean lesion length resulting from inoculation with strains of *F. thapsinum*. Within each species, however, there was a broad range of lesion lengths observed, and all tested strains of both species probably should be regarded as potential pathogens of maize. No isolate $\times$ inbred interaction was detected. Fumonisin may play a role in aggressiveness, but under our conditions, stalk rot and the ability to produce fumonisins in vitro were not correlated.

Additional keywords: corn, *Gibberella fujikuroi*, *G. moniliformis*, *G. thapsina*, mycotoxin, *Zea mays*

One group of *Fusarium* species commonly associated with maize diseases belongs to *Fusarium* section *Liseola*, whose members have teleomorphs in the *Gibberella fujikuroi* species complex. This complex can be divided into at least eight biological species, also termed mating populations, and identified by the letters "A" through "H" (4,14,18,19,21). Two of these mating populations, A and F, until recently shared the *Fusarium moniliforme* anamorph. The F mating population has now been described as a separate species, *Fusarium thapsinum* (teleomorph *Gibberella thapsina*) (19), and the A mating population is termed by some *F. verticillioides*. In this presentation, we generally will use *F. thapsinum* to mean *Gibberella fujikuroi* mating population F and *F. moniliforme* to mean *Gibberella fujikuroi* mating population A.

Fusarium strains recovered from maize are commonly associated with root, ear, and stalk rots (31). These fungi may be seedborne endophytes or may infect the plant in other as yet poorly understood manners during various stages of plant development (13,27). Certainly the plant and the fungus can coexist without obvious disease symptoms for extended periods of time. In addition to maize, members of *F.*

moniliforme have been recovered from bananas, figs, rice, sorghum, and field soil, and members of *F. thapsinum* have been recovered from bananas, figs, sorghum, and field soil (11,21).

F. moniliforme sensu lato can produce noxious secondary metabolites such as fumonisins (22,24), fusaric acid (3), fusarins (32,36), and moniliformin (22,26,32), with additional compounds still remaining unidentified (22). Strains of *F. moniliforme* and *F. thapsinum* differ in their ability to produce these toxins and in their host preferences (21–23).

The fumonisins are the most prominent class of mycotoxins produced by *F. moniliforme*. The role this group of toxins plays in plant pathogenesis is not clear. Desjardins et al. (9) found that aggressiveness, as assessed by maize seedling blight, was correlated with the ability to produce high levels of fumonisin in vitro. Purified fumonisins can cause necrosis and other disease symptoms in maize seedlings (20) and to maize callus (33), and can induce apoptosis in tomato protoplasts (35) and cultured animal cells (34). In contrast, Abbas and Boyette (1) reported no phytotoxicity from fumonisin, at concentrations up to 1,000 $\mu\text{g/ml}$, to 7- to 10-day-old corn plants. In the field, location, hybrid, and environmental conditions all impact fumonisin contamination levels (5,10,30).

In an earlier study (12), we found no significant differences in aggressiveness toward mature sorghum between strains of *F. moniliforme* and *F. thapsinum*. Our objective in this study was to determine if strains of *F. moniliforme* and *F. thapsinum* differed in their aggressiveness toward

mature maize, and if these differences, if any, were correlated with the ability to produce fumonisins in vitro.

MATERIALS AND METHODS

Strains. Strains of *F. moniliforme* and *F. thapsinum* (18,19,21) used in this study are listed in Table 1. Six of the eight isolates (A-0102, A-0149, F-0728, F-1155, F-1163, and F-1183) were used in a similar study of aggressiveness toward grain sorghum (12). All of the isolates were heterokaryon self-compatible (7).

Toothpick inocula for stalk inoculations were prepared as previously described (12). Specifically, strains of *F. moniliforme* and *F. thapsinum* were grown on minimal medium slants (6) for 7 days. Round wooden toothpicks about 6 cm long were boiled in distilled water for 1 h to remove any toxic substances that might inhibit fungal growth. The water was decanted and discarded, and the procedure was repeated three more times. Dry toothpicks were packed into glass jars (25 $\times$ 60 mm), and 5 ml of potato dextrose broth (Difco Laboratories, Detroit, MI) was added to thoroughly moisten the toothpicks. The jars were autoclaved, cooled, inoculated with pieces of agar cultures, and incubated at 20°C for 10 days under 12-h periods of alternating light and dark.

Fumonisin assays. Strains were cultured in 100 $\times$ 15 mm plastic petri dishes on sterilized commercial corn grits (Quaker Oats Co., Chicago, IL) for 4 weeks at 25°C under 12-h periods of alternating light and dark. Grits were prepared by moistening 1,400 g of "Quick" grits with 600 ml of distilled water, autoclaving for 1 h on each of 2 consecutive days, and then spreading a thin layer (approximately 25 g wet weight) in the petri dish. Each plate was inoculated with 1 ml of a spore suspension (approximately 10^7 spores/ml) and then transferred to the incubator. Duplicate plates were made on each occasion, and all incubations were repeated at least twice.

Fumonisin were extracted from the grits and assayed using HPLC and ELISA as described by Yu and Chu (37).

Pathogenicity tests with mature plants. Seeds of two corn inbreds (cvs. LH82 and LH132, Holden Foundation Seeds, Williamsburg, IA) were treated with hot water (8) to kill naturally occurring *Fusarium* that may have been in or on the seed. Corn plants were grown in a green-

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house in 25.4-cm plastic pots (one plant per pot) containing Sunshine Mix No. 1 (Fisons Horticulture Inc., Vancouver, BC). A 20-20-20 (N-P-K) soluble fertilizer was applied twice weekly at a rate of 166 mg per pot. Plants were inoculated approximately 2 weeks after tasseling. An ice pick was used to make a 1- to 2-cm-deep hole in the stalk midway between the second and third node above the soil line, and a toothpick colonized with the appropriate strain was inserted into the hole. Sterile toothpicks were inserted into the control plants. Inoculated plants were arranged on a greenhouse bench in a randomized complete block factorial design using five replicates per treatment. The experiment was conducted three times. Incubation conditions in the greenhouse varied depending upon the season. The first and third experiments were run in the winter, November through February and December through March, respectively. The second run of the experiment was conducted from April through June. Supplemental light was used as necessary to provide a 14-h light and 10-h dark cycle. Temperature control followed the same cycle and alternated between approximately 30°C (light) and 18°C (dark).

Eighteen days after inoculation, the stalk was split longitudinally, and stem discoloration was measured. Lesion length was the distance on either side of the inoculation point at which discoloration could be observed. Analysis of variance for a factorial design was performed on each data set and on the combined data set after a log transformation of the data. Corn inbred and fungal strain were used as variables. A separate analysis using a single degree of freedom contrast to test for differences in aggressiveness between species was also performed. All analyses were made with the Minitab statistical program (Minitab, Inc., State College, PA). Data were back-transformed from the log form for presentation.

Recovery of *Fusarium* isolates from infested stalks. Tissue samples, 2 mm³, were taken from the pith of each split stalk after the first run of the experiment. Samples were taken from the end of each lesion, as denoted by discoloration of the tissue, and from each additional internode within the lesion if the discolored region spanned more than two nodes. If only two samples were taken, then they were taken within the lesion but as far as possible from one another and from the site of the toothpick inoculation. Tissue blocks were placed on a peptone-pentachloronitrobenzene (PCNB) medium (28) and incubated for 7 to 10 days at 25°C. Only one fungal isolate was taken per tissue sample, unless colonies or colony sectors with different morphologies were observed, in which case a sample representing each morphology was taken. (Maize plants have been reported to be infected simultaneously with multiple *Fusarium* species and by as many

as five different *Fusarium* strains from the same species (13). Small mass transfers, 1 mm³ agar blocks, were made from the peptone-PCNB medium to a complete medium (6) and maintained on these slants at 4°C until the analyses of vegetative compatibility were complete.

Vegetative compatibility group (VCG) tests. VCG tests were made with *nit* mutants derived from the eight strains used for inoculating maize plants and the *Fusarium* isolates recovered from the first run of the experiment. For each of the eight strains, two complementary NitM mutants were generated on minimal medium + 2% KClO₃ to serve as tester strains (6,15). These NitM testers were purified by isolating an uninucleate microconidium via micromanipulation. The *nit* mutants in *Fusarium* isolates recovered from stalk tissue were derived by culturing these isolates on potato dextrose agar (Difco) + 3.0% KClO₃, a procedure known to yield an excess of *nit* mutants (6,15). Chlorate-resistant nitrate-utilizing (crn) sectors (17) resulting from this process were discarded, but no *nit* mutants obtained on this medium were phenotyped any further.

For vegetative compatibility tests, the NitM testers derived from the strain in-

oculated into the plant were paired with *nit* mutants derived from the *Fusarium* isolates recovered from that plant using a multiwell plate technique (16). When both pairings with the NitM testers were negative, the pairing test was repeated once.

RESULTS

Isolate aggressiveness. No isolate × inbred line interactions were observed, so data across the main effects of inbred lines and strains could be combined. There was some variability among each of the three experiments. In particular, strain differences were not detected in the second run. For the combined analysis, however, all strains used produced significantly ($P = 0.003$) longer lesions than did the uninoculated control (Table 2). Only the lesion lengths from strains A-0149 and F-1183 were significantly different from each other, 21 and 13.9 cm, respectively. However, when the mean lesion length of all of the *F. moniliforme* strains was compared with the mean of all of the *F. thapsinum* strains, the *F. moniliforme* strains had a significantly higher ($P = 0.04$) mean lesion length, 20.2 and 16 cm, respectively.

Inbred resistance. Inbred corn line LH 82 was previously observed to be suscepti-

Table 1. Strains of *Fusarium moniliforme* (*Gibberella fujikuroi* mating population A) and *F. thapsinum* (*G. thapsina*) tested for aggressiveness to maize plants grown under greenhouse conditions

Strain ^w	MT ^x	VCG ^y	Geographic origin	Host material	Fumonisin (µg/g) ^z
A-0102	A ⁺	A-1	San Joaquin Co., CA	Sorghum stalk	1,000 +
A-0149	A ⁻	A-7	Visalia, CA	Maize stalk	1,000 +
A-0489	A ⁻	A-?	Transkei, South Africa	Maize	850-920
A-4515	A ⁻	A-?	Kathmandu, Nepal	Maize seed	ND
F-0728	F ⁺	F-11	Powhattan, KS	Sorghum stalk	ND
F-1155	F ⁺	F-9	Atlanta, KS	Sorghum stalk	ND
F-1163	F ⁻	F-7	Latimer, KS	Sorghum stalk	ND
F-1183	F ⁺	F-2	Moundridge, KS	Sorghum stalk	ND

^w A = *F. moniliforme*, F = *F. thapsinum*.

^x Mating type.

^y VCG = vegetative compatibility group. A-? indicates that isolate has not been assigned to a numbered VCG.

^z Fumonisin levels reported as µg/g. ND ≤ 10 µg/g.

Table 2. Greenhouse test of strain aggressiveness of four strains of *Fusarium moniliforme* (*Gibberella fujikuroi* mating population A) and *F. thapsinum* (*G. thapsina*) to two inbred lines of *Zea mays*

Strain ^x	Mean lesion length (cm) ^y			
	Experiment 1	Experiment 2	Experiment 3	Mean
A-0102	13.1 bc ^z	21.6 a	16.2 ab	16.6 ab
A-0149	40.6 a	17.8 a	12.9 ab	21.0 a
A-0489	26.3 ab	17.3 a	14.7 ab	18.8 ab
A-4515	22.6 abc	16.8 a	20.5 a	19.8 ab
F-0728	16.1 abc	19.6 a	17.6 a	17.7 ab
F-1155	12.8 bc	20.3 a	14.0 ab	15.1 ab
F-1163	15.6 abc	11.3 a	16.4 ab	14.2 ab
F-1183	9.4 c	22.4 a	12.7 ab	13.9 b
No fungus	10.7 bc	9.7 a	7.0 c	9.0 c

^x A = *F. moniliforme*, F = *F. thapsinum*.

^y Lesions were evaluated 18 days after inoculation, and each value for experiments 1 to 3 represents the mean of five plants. Lesion length = distance on either side of the inoculation point at which discoloration could be observed.

^z Means followed by the same letter within a column are not significantly different according to Fisher's LSD ($P \leq 0.05$).

ble to *F. moniliforme* and LH 132 to be less susceptible (L. E. Claflin, *personal communication*). The mean lesion lengths (Table 3) averaged over all strains for LH 82 and LH 132 were 22.1 and 11.5 cm, respectively, and the difference was significant at $P \leq 0.05$.

Recovery of inoculated strains. After the first experimental trial, we reisolated *Fusarium* spp. from infected tissue to determine if the isolates from the discolored area were the same as the strains that had been used to inoculate the tissue. Our previous work with sorghum suggested that cross-contamination was a possibility (12), and individual maize plants are known to be infected with multiple strains of *F. moniliforme* (13). *Fusarium* isolates were recovered from all plants, whether inoculated or not. Recovery rates ranged from 16 to 100% (Table 4). In only two cases (F-1155/LH82 and F-1163/LH82) were more than 50% of the recovered isolates in a different VCG than the inoculated strain. By comparison, in 9 of 16 cases, more than 80% of the recovered isolates were the same as the inoculated strain.

DISCUSSION

In a previous study, Jardine and Leslie (12) did not detect differences in aggressiveness among members of the common

VCGs of *F. thapsinum* from Kansas toward four inbred lines of sorghum. Similarly, in this study, we detected no differences in aggressiveness among the four *F. moniliforme* strains tested against two corn inbreds. While there were some differences from experiment to experiment, particularly in the second one where significant differences were not detected due to increased variability, the trends for each were consistent. The increased variability in the second experiment may have been caused by different growing conditions in the greenhouse in spring compared with winter, such as increased solar radiation and water usage. For the combined analysis, however, all strains produced significantly larger lesions than did the uninoculated control. The only significant difference between the strains tested was between A-0149 and F-1183 (Table 2), although as a group, the *F. moniliforme* strains were more aggressive than were the *F. thapsinum* strains. This finding supports previous work, suggesting that there may be differences in host preference between these two species (24,25). There were no strain $\times$ inbred interactions, which is consistent with our previous sorghum study (12) and with the results of Bacon et al.

(2), who screened cultivars of corn against *F. moniliforme* strains for resistance to seedling blight.

For this study, we chose strain A-4515 because it was not known to produce any fumonisins and strain A-0489 because it produced a relatively low amount of fumonisin compared with isolates A-0102 and A-0149 (24,29). In addition, *F. thapsinum* strains are known to make relatively little, if any, fumonisins (22,24), even though they can synthesize other mycotoxins (3,22). We observed no relationship between aggressiveness and fumonisin production for the strains and inbred lines used in this study. Thus, the ability to synthesize fumonisin in vitro is not essential for either *F. moniliforme* or *F. thapsinum* to pathogenize maize, because A-4515 and all of the *F. thapsinum* strains are unable to produce significant quantities of this metabolite in vitro, and yet still caused significant disease.

Fusarium is ubiquitous in field and greenhouse grown maize, and field plants have been reported to be infected with up to five different strains of *F. moniliforme* (13). We recovered *Fusarium* from all of the noninoculated control plants, but none of these isolates was vegetatively compatible with any of the eight strains used for inoculations. In 14 of 16 of the sets of inoculated plants, we recovered *Fusarium* isolates that were not vegetatively compatible with NitM testers derived from the strain used to infect the plant. Average recovery of the *F. thapsinum* strains (65% of total isolates) was lower than for the *F. moniliforme* strains (88% of total isolates), but the difference was not statistically significant due to the wide range in recovery frequencies observed. The variability in strain recovery from maize is similar to what we previously reported for sorghum (12) using six of these eight strains.

In conclusion, our results are consistent with the hypothesis that the host preferences described for *F. moniliforme* and *F. thapsinum* are related to their ability to pathogenize their preferred hosts. Within each species, we observed a broad range of lesion lengths, however, and all strains of both species probably should be regarded as potential pathogens of both maize and sorghum. Fumonisins may play a role in pathogenicity, but under our conditions, it is clear that the ability to synthesize these toxins in vitro is not related to pathogenicity. Other secondary metabolites, e.g., fusaric acid and moniliformin, that are synthesized by some or all of these strains also may play a role in pathogenicity either alone or in combination with fumonisins, but additional work to verify or disprove such interactions remains to be done. The previously reported correlation between maize seedling blight and fumonisin synthesis in vitro does not extend to stalk rot as assessed in this study.

Table 3. Greenhouse test of cultivar resistance of two inbred lines of *Zea mays* to four strains each of *Fusarium moniliforme* (*Gibberella fujikuroi* mating population A) and *F. thapsinum* (*G. thapsina*)

Inbred line	Mean lesion length (cm) ^y			
	Experiment 1	Experiment 2	Experiment 3	Mean ^z
LH 82	23.3 a ^z	20.8 a	22.3 a	22.1 a
LH 132	12.0 b	13.6 b	8.9 b	11.5 b

^y Lesions were evaluated 18 days after inoculation, and each value for experiments 1 to 3 represents the mean of 45 plants. Lesion length = distance on either side of inoculation point at which discoloration could be observed.

^z Means followed by the same letter within a column are not significantly different according to Fisher's LSD ($P \leq 0.05$).

Table 4. Recovery of *Fusarium moniliforme* (*Gibberella fujikuroi* mating population A) and *F. thapsinum* (*G. thapsina*) strains from mature maize plants inoculated in the greenhouse

Inoculated strain ^w	Inbred line ^x	Number of plants	Number of <i>Fusarium</i> isolates	% isolates in same VCG ^y as inoculated strain
No fungus	LH 82	6	0	
	LH 132	5	0	
A-0102	LH 82	6	12	92 (6) ^z
	LH 132	5	10	90 (5)
A-0149	LH 82	6	12	92 (5)
	LH 132	5	10	80 (5)
A-0489	LH 82	6	12	66 (5)
	LH 132	5	10	100 (5)
A-4515	LH 82	6	12	100 (6)
	LH 132	5	10	80 (4)
F-0728	LH 82	6	12	75 (5)
	LH 132	5	10	60 (4)
F-1155	LH 82	6	12	16 (2)
	LH 132	5	10	70 (4)
F-1163	LH 82	6	12	42 (3)
	LH 132	5	10	90 (5)
F-1183	LH 82	6	12	75 (6)
	LH 132	5	10	90 (5)

^w A = *F. moniliforme*, F = *F. thapsinum*.

^x LH 82 (susceptible to *Fusarium* spp.) and LH 132 (tolerant to *Fusarium* spp.).

^y VCG = vegetative compatibility group.

^z Number in parentheses is number of plants from which originally inoculated isolate was recovered.

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