The Effect of Endophytic *Fusarium verticillioides* on Infestation of Two Maize Varieties by Lepidopterous Stemborers and Coleopteran Grain Feeders

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ABSTRACT

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A series of experiments were conducted to test the effect of the presence of *Fusarium verticillioides* in the maize plant on subsequent infestation by coleopteran and lepidopteran pests. The effect of percent internodes 1 to 5 infected with *F. verticillioides*, time after planting, and maize variety on attacks of stem and ears by lepidopterous and coleopteran pests was assessed in field experiments in early and late season 1998 and early season 1999 in Benin Republic. Artificial inoculation of the first internode with fungal-treated toothpicks was compared with a hot-water-fungicide seed treatment and a control. In 1998, two varieties that differed in husk tightness, the improved DMRLSR-W and the local Gbogbe, were used. Percentage of node 1 to 5 and plants infected was highest with the inoculation treatment but tended to be similar in the seed treatment and the control. The infection rate tended to increase with time and, within sampling date, decreased with node level. Ear infection was strongly correlated with percent infected nodes, indicating that *F. verticillioides* in the stem predisposed kernel infection. *F. verticillioides* incidence was higher in Gbogbe than in DMRLSR-W. Stem and ear infestations by the pyralid *Eldana saccharina*, the major pest in the area, tended to be highest in inoculation and lowest in the protection treatment. The same trends were found for the pyralid *Chilo* spp., the tortricid *Cryptophlebia leucotreta*, and beetles pooled across species. Significant positive correlations were found between ear/stem *F. verticillioides* infection and *E. saccharina*, *Cryptophlebia leucotreta*, *Mussidia nigrivenella*, and the noctuid *Sesamia calamistis*, but the latter three pest species were only significantly correlated with fungal infection of the upper nodes of the plant. Similar to disease incidence, *E. saccharina* numbers in stem and ear were higher in Gbogbe than DMRLSR-W in late 1998, whereas for the pyralid ear feeder *M. nigrivenella*, it was reversed. It was suggested that some lepidopterous and coleopteran pests are attracted by and survive longer (or have lower mortality) on plants infected with *F. verticillioides*.

Additional keywords: fungus–insect interaction.

Fusarium verticillioides Sacc. (Nirenberg) (synonym *F. moniliforme* Sheld.) [teleomorph: *Gibrella fujikuroi* (Sawada)] is worldwide one of the most common pathogens of maize. It attacks all stages of plant growth and plant parts, and may cause root (23), shank, stalk (12,34,36), and ear rot (11,24,59). Seed transmission via nonsymptomatic kernel infection is common and may affect emergence of seedlings (30). In addition, *F. verticillioides* may also produce mycotoxins such as fumonisin (41), which promotes esophageal cancer in humans (48) and leucoencephalomalacia in horses (5). Symptomless endophytic infections are common and can exist throughout the plant (7,43). In a recent survey in southern Benin, *F. verticillioides* was the most common endophytic fungus inhabiting maize stalks (4). Incidence was higher in plants damaged by insect pests. The fungus was cultured from stems of 71 to 80% of plants attacked by *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Eldana saccharina* Walker (Lepidoptera: Pyralidae), both key pests of maize in West Africa (50). Fungal incidence was highest inside the tunnel bored by the insect (4), indicating that they are vectoring the fungus or corroborating results by Christensen and Wilcoxon (16) that frass and feces of stemborers are an ideal medium for development of microflora. Insects reported to vector *F. verticillioides* by damaging the stem or ear are beetles (63,64), thrips (24), and especially lepidopteran stem and ear borers such as the pyralid *Ostrinia nubilalis* (Hübner) (15, 21,44), and the noctuids *Sesamia* spp. and *Busseola fusca* (Fuller) (25). By contrast, a recent study carried out at the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria, showed that ears artificially inoculated with *F. verticillioides* had significantly more cucurlionid, silvanid, and nitidulid beetle species, which are common pests of stored maize (19), and lepidopteran borers, such as *E. saccharina* and *Mussidia nigrivenella* (Ragonot) (Pyralidae) (12). Hepperly and Rodriguez-Cancel (32) and Bartelt and Wicklow (8) showed that volatiles produced by *F. verticillioides* were attractive to nitidulid beetles. *M. nigrivenella* is a polyphagous species that feeds in the maize ear and is also a storage pest (54,57). *S. calamistis*, on the other hand, oviposits on pretasseling plants only, whereas *E. saccharina* lays the eggs preferably on older leaves or debris on the soil and older larval stages attack the plant and bore into the stem around and after tasseling (52,54). Both species may move from the stem into the ear. In view of this oviposition behavior, it was postulated that, in contrast to grain-feeding beetles, the higher lepidopterous borer densities found in *F. verticillioides*-infected ears were mainly due to higher survival of immatures rather than increased oviposition (51). The present work investigates the effect of systemic stem infection by *F. verticillioides* on colonization of maize stems and ears by lepidopterous and coleopteran pests.

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MATERIALS AND METHODS

Seasons. The study was conducted on-station at IITA in Calavi, Republic of Benin. The station is situated in the derived savanna

characterized by bimodal distribution of rainfall, with peaks in June and September and an annual precipitation of about 1,200 mm. The main growing season (first) is from April to July and the minor (second) from September to November and a short dry spell of about 4 weeks may occur in August. The major dry season normally starts in November and lasts through March. Monthly mean temperatures range from approximately 24 to 29°C, with minima in July and August and maxima during the dry season. Experiments were conducted during the first and second growing seasons in 1998, and the first season in 1999.

Maize genotype. The improved IITA variety DMRLSR-W (hereafter referred to as DMR) and the local variety Gbogbe were used in experiments I and II. Both are white-seeded late genotypes that reach maturity at approximately 110 days. DMR is resistant to downy mildew [*Peronosclerospora sorghi* (Weston & Uppal)] and *Maize streak virus*. Gbogbe, a local floury-endosperm cultivar, known for good storability and husk cover, was back-crossed for two generations with the IITA population Tropical Zea Streak Resistant White (TZSR-W) to improve yield (35). Good husk cover is considered key to protecting the ear from fungi and insects (43,60,62). In experiment III, only DMR was used.

Planting, infestation procedure, and field design. Experiment I—first season 1998. To increase borer populations in experimental plots, two spreader rows of maize were planted around each block on 25 April 1998 and each plant was infested with 20 *E. saccharina* eggs in the black-head stage 45 days after planting (DAP). On 21 May 1998, experimental plots of 16 × 12 m were planted at a spacing of 0.25 m within row and 0.75 m between rows. Distance between blocks was 4 m and between plots 1 m. Three seeds were planted and thinned to one plant 14 DAP. N-P-K 15-15-15 was applied at a rate of 3 g per plant 18 DAP. The plots were weeded at 30 and 60 DAP. A randomized complete block design with three replicates (blocks) was used.

Experiment II—second season 1998. The same procedures and experimental design as in experiment I were used. The spreader rows were planted on 20 August 1998. The experimental plots were planted on 15 September 1998. Twenty *E. saccharina* couples per plot were released in addition in the main plots 45 DAP. A randomized complete block design with three replicates (blocks) was used.

Experiment III—first season 1999. The spreader rows were planted on 8 March 1999. The main plots were planted on 1 April 1999 and plot size was 8 × 6 m. Twenty *E. saccharina* couples per plot were released in the main plots once at 45 DAP. A randomized complete block design with three replicates (blocks) was used.

Treatments. A stem-inoculation treatment, a hot water/fungicide seed treatment, and a control were used.

Inoculation treatment. A modified version of a method described by Drepper and Renfro (22) was used. Toothpicks were water-boiled several times, soaked in an *F. verticillioides* (IITAMCG 157) conidial suspension of 1×10^6 conidia per ml, and kept for 2 weeks in an incubator (Percival Boone, Iowa) at 25°C and 75% relative humidity in 12 h light/dark cycles. A fungal-treated toothpick was inserted in the center of the first internode above soil level at 35 DAP with sterilized forceps.

Hot water treatment. Maize kernels were first surface sterilized by dipping the grains in 0.525% sodium hypochlorite for 5 min (49). Thereafter, they were washed thoroughly for several minutes with sterile water, soaked for 5 h in tap water at room temperature, and transferred to a water bath at 53 to 56°C for 10 min. The kernels were immediately placed in cold water and treated with the seed protectant Super Homai (35% Thriophate-methyl, 20% Thiram, and 15% Diazinon; Nippon Soda Co., Tokyo, Japan). Diazinon, a contact insecticide with activity duration of around 2 to 3 weeks, was not expected to have an effect on insect behavior in treated plots at the time of sampling, which started about 6 weeks after planting. In addition, a solution of Benomyl 80% was directly applied to soil at a rate of 480 g a.i./ha with a back-pack sprayer.

Control. Seeds were planted without seed protectant, the plots were not sprayed with fungicide, and the plants were not inoculated.

Sampling procedure. ***Experiment I.*** Ten plants per plot (three replicates per treatment plot) were randomly sampled at 45, 77, and 90 DAP for evaluation of *F. verticillioides* infection and at 60, 77, 90, and 110 DAP for insect counts. Both stems and ears, if available, were dissected for assessment of insect numbers according to species for Lepidoptera. For assessment of presence of *F. verticillioides*, stem pieces from the first to the fifth internode and samples of grain were surface sterilized in a 5% sodium hypochlorite solution for 5 min. Five stem cross-sectional pieces (one from each node/plant) or five kernels were placed in 9-cm petri dishes on sterile Whatman No. 1 filter paper moistened with sterile distilled water. Plated samples were incubated in the lab at ambient temperature of ≈26°C for 5 days before identification of the fungal species (45).

Experiment II. In general, the procedure was the same as in experiment one, but samples were taken at 42, 56, and 70 DAP for evaluation of *F. verticillioides* infection and insect counts and, in addition, at 65, 80, and 93 DAP for insect counts only.

At 110 DAP, the ears were shelled by hand and assessed for insects. Grains were surface sterilized by soaking in a solution of 5% of sodium hypochlorite for 5 min. Subsamples of 25 kernels per plot were taken at random and distributed in five petri dishes (five kernels per petri dish) for plating. Plating and incubation was done as described previously. Percent infection was calculated as the proportion of infected kernels × 100.

Experiment III. Samples were taken at 39, 54, 67, and 83 DAP, and the number of samples per plot was 20 (three replicates of each treatment plot). Due to technical problems, no plating of kernels was done in this experiment. In experiments II and III, both Lepidoptera and Coleoptera were counted according to species.

Data analysis. For each experiment, an analysis of variance (ANOVA) using a mixed model (SAS Institute, Cary, NC) in repeated measures over sampling dates was used to assess the effect of fixed effects, variety, and treatment on percent infected nodes and plants and on the number of insects according to species across and within random effects, sampling date, and replicate. Orthogonal contrasts of inoculation treatment across sampling time were used to calculate probability of linear and quadratic responses. To compare infection rates between internodes within sampling date and treatment, linear or polynomial trends were tested using means across varieties (contrasts, general linear means [GLM], repeated measures, $P \leq 0.05$). For each sampling date, the data were subjected to ANOVA to identify significant main effects and interactions of treatments, percentage of infected nodes at a given node level or across node levels (Fig. 1), and to assess the effect of treatment on numbers of *E. saccharina* in the stem and ear (Fig. 2). Treatment means were separated with Student-Newman-Keuls at $P \leq 0.05$.

Pearson correlations were computed to investigate interactions between percentage of infected nodes and insect numbers using data from the last sampling date when both sets of variables were assessed (90, 70, and 83 DAP in experiments I, II, and III, respectively). In addition, for experiment II, data on percentage of infected internodes at 70 DAP were analyzed with kernel infection and insect data collected at 110 DAP to evaluate the long-term effect of stem infection.

Before analyses, pest numbers were log(×+1) and percentages were arcsine square root transformed, but back-transformed results are shown in the Tables and Figures.

RESULTS

Fungal stem infection. For all internodes, except node 1 in the second season 1998, sampling date had a significant effect on the

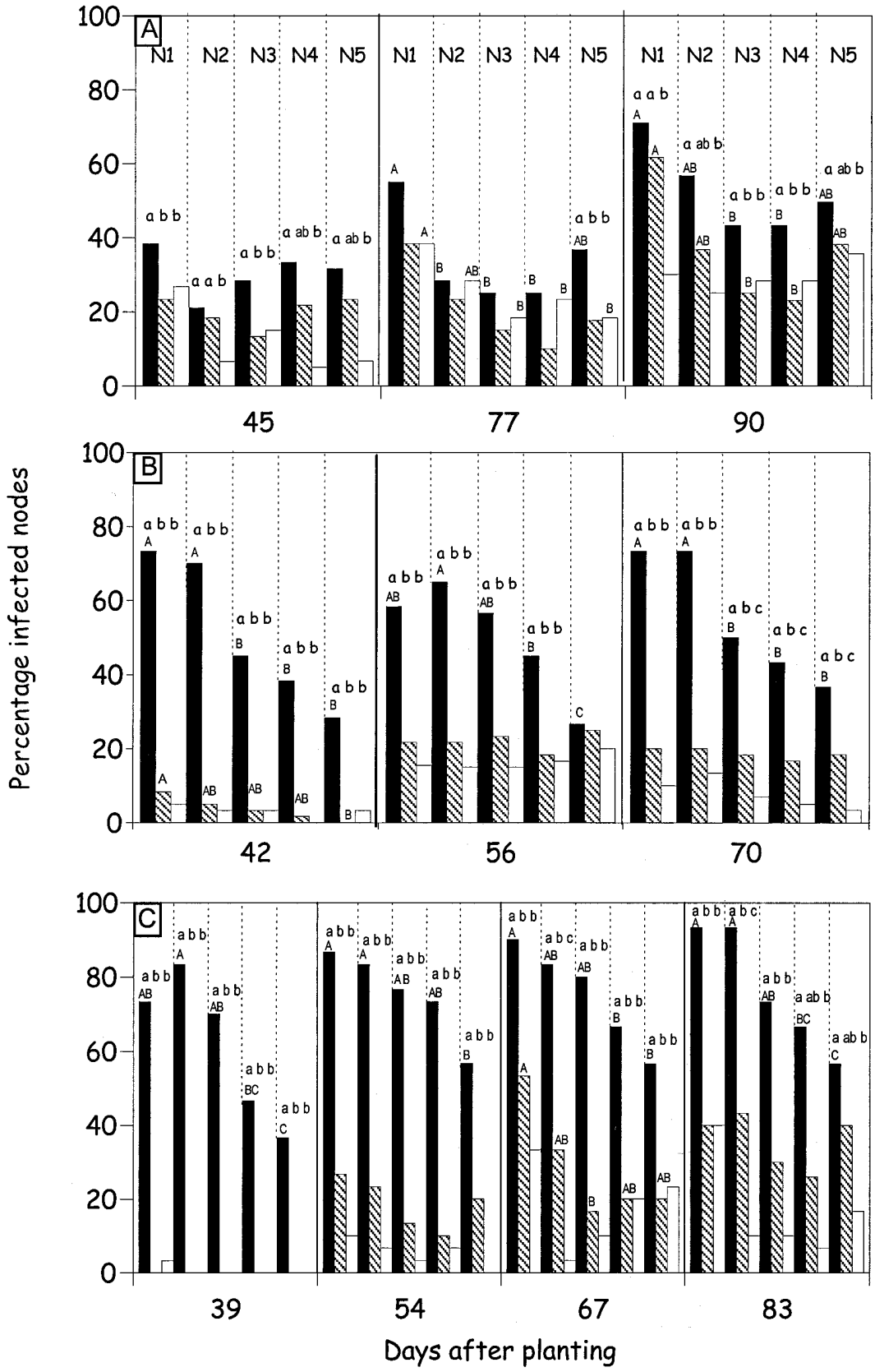

Fig. 1. Percentage of infected internodes 1 to 5 (N1 to N5) in inoculated plants (black bars), plants from hot-water-fungicide-treated seeds (white bars), and the control (striped bars) in **A,** first season 1998, **B,** second season 1998, and **C,** first season 1999. Within internode level and sampling date, treatment means followed by the same lowercase letter were not significantly different, and within treatment and sampling date, node means followed by the same capital letter were not significantly different according to Students-Newman-Keuls ($P \leq 0.05$). Absence of letters indicates no significant difference.

percentage of infection with *F. verticillioides* (Table 1). Means across treatments had either significant linear and/or quadratic responses across sampling date. In each experiment, the percentage of infected nodes 3 to 5 tended to increase with sampling date (Fig. 1). Within sampling date, the percentage of infection tended to decrease linearly from node 1 to 5 in the *F. verticillioides*-inoculated treatments second season 1998 and first season 1999 (GLM, $P < 0.05$) (Fig. 1), whereas for the control and seed treatments there was no clear trend. In the control and the fungicide treatments of second season 1998 and first season 1999, infection rates were zero to very low at the first sampling occasion and within sampling date, differences among nodes of the same treatment were mostly not significant (Fig. 1). Thus, there were no discernable trends within sampling date, with exception of the control and the fungicide treatment at 67 DAP in the first season of 1999 (linear and quadratic trends, respectively, $P \leq 0.01$).

Treatment had a significant effect on stem infection with *F. verticillioides* (Table 1) in all experiments, and in all cases but the fifth internode in the first season 1998. The infection rate was highest in the inoculation treatment (Table 2). Percent internode infection was not significantly different between the fungicide treatment and the control in the first and second seasons of 1998, but was in the first season 1999 (Table 2).

In the inoculation treatment, the percentage of plants infected was high and reached nearly 100% in the second season 1998 and the first season 1999 (Table 2). Across treatments, the relationship between infected plants and time was linear (experiment III; $P \leq 0.0001$) or quadratic (experiments I and II, $P \leq 0.0001$ and 0.001, respectively).

Variety effect could only be seen in the total percent infected plants [P(I)] in first season 1998, but in the second season, both P(I) and percentage of infected node 5 was significantly higher for the local variety Gbogbe than for DMR (Table 2). The sampling date–variety and treatment–variety interactions were mostly not significant, whereas the treatment–sampling date interactions were significant for nodes 1 to 3 in first season 1998, nodes 1 and 5 in second season 1998, and nodes 1 and 2 in first season 1999 (Table 1). As indicated by the frequency of significance among treatments, the efficiency of the inoculation treatment increased from experiments I to III (Fig. 1).

Insect infestations. The lepidopterous borers encountered were *E. saccharina*, *S. calamistis*, *Chilo* sp. (Crambidae), *M. nigrivenella*, and the ear-feeder *Cryptophlebia leucotreta* (Meyrick) (Tortricidae). Beetles attacking the ear were the *Cathartus quadricollis* Guerin-Meneville (Silvanidae), *Carphophilus* sp. (Nitidulidae), and *Sitophilus zeamais* Motschulsky (Cucurlionidae). Because treatment and variety had no significant effect on the numbers of beetles (data not shown), these were pooled across species and reanalyzed, and the results presented under beetles. For most species and in all experiments, sampling date (DAP) had a significant positive effect on pest densities (Table 3), and the relationship was either linear or quadratic (contrasts, GLM, repeated measures, $P \leq 0.05$; Fig. 2 for *E. saccharina*).

Variety only had an effect in second season 1998. *E. saccharina* densities in the stem and ear were higher on Gbogbe than DMR, but for *M. nigrivenella* in the ear, they were higher on DMR (Tables 3 and 4). Treatment had a significant positive effect on *E. saccharina* in the stem in experiments I to III, and in the ear in second season 1998, on beetles in the first season of each year, and *Chilo* sp. and *Cryptophlebia leucotreta* in first season 1999 (Table 3). In general, when there were differences, insect densities were highest in the inoculation and lowest in the fungicide treatment (Table 4; Fig. 2).

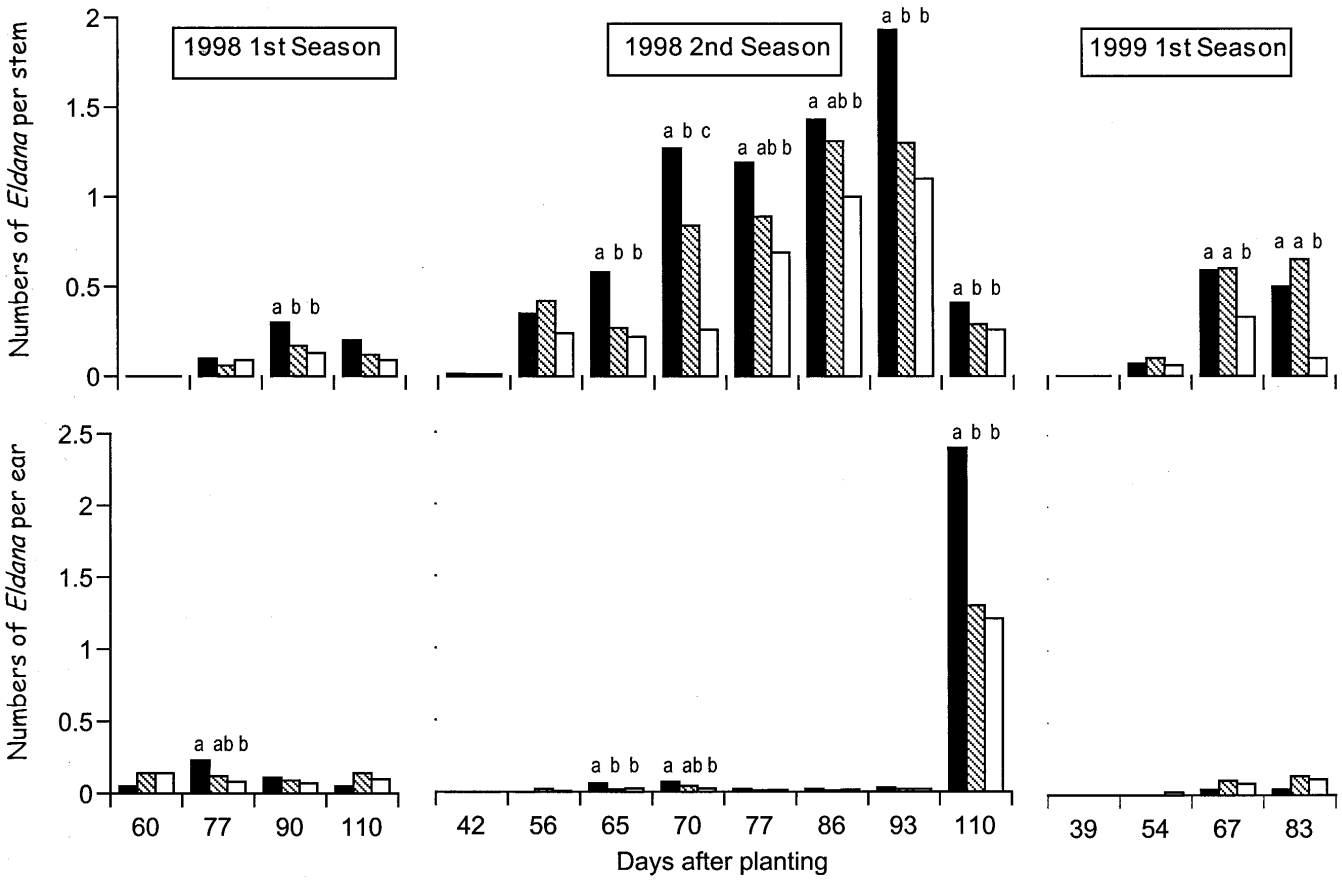

Fig. 2. Numbers of *Eldana saccharina* in stems and ears in inoculated plants (black bars), plants from hot-water-fungicide-treated seeds (white bars), and the control (striped bars) in first and second seasons 1998 and first season 1999. Within sampling date and experiment, treatment means followed by the same letter are not significant at $P \leq 0.05$ according to Students-Newman-Keuls. Absence of letters indicates no significant difference.

Kernel infection. Percentage of kernels infected with *F. verticillioides* was significantly highest in the inoculation treatment and similar in the control and fungicide treatment (Table 5). No differences were found for *Penicillium* spp., whereas *Aspergillus flavus* was significantly lowest in the fungicide treatment. Gbogbe had significantly higher *F. verticillioides* infection, whereas for *A. flavus* the situation was reverse with more than three times higher incidence on DMR.

Correlations between fungal stem and kernel infections and insect infestations. In general, the infection rates among internodes, and internodes and percentage of *F. verticillioides*-infected plants [P(I)] were highly correlated in all experiments (Table 6). Likewise, strong relationships were found between percentage of Lepidoptera-infested nodes and kernel infection (Table 6).

In all experiments, significant positive relationships were found between stem infestation by *E. saccharina* and infected nodes, but in the first season 1998, only infection in node 2 to 4, and in the first season 1999, only node 5 had significant positive relationships with infestation. In first season 1998 and at 110 DAP, *E. saccharina* in the ear was significantly correlated with percentage of stem infection (Table 6). The relationships with *S. calamistis* were generally weak and only significant for node 5 in first season 1998, node 4 in second season 1998, and at 110 DAP in first season 1999. Similarly, *M. nigrivenella* was significantly positively related with percentage of node 4 infected in first season 1998, and *Cryptophlebia leucotreta* with nodes 4 and 5 in second season 1998, and node 3 in first season 1999. No relationships were found between beetles and stem or ear infection or between kernel infections by *F. verticillioides* and other fungi (data not shown). In the first season 1998, significant correlations were found between *E. saccharina* in stem and ear ($r = 0.59$**), *E. saccharina* in stem, and *M. nigrivenella* in ear ($r = 0.47$**), and in experiment II between *S. calamistis* and number of beetles in the ear ($r = 0.84$**).

DISCUSSION

The inoculation treatment always yielded higher percentage of infected nodes than the fungicide treatment or the control, except during the first sampling occasion in the first season of 1998 when natural infections were relatively high and artificial inoculation yielded relatively low percentages of infected nodes 1 to 3 compared with subsequent experiments (Fig. 1). The differences in natural infection between experiments, especially during the first sampling date, may have been due to differences in wind conditions and rainfall intensity (47), infected corn residue left over from the previous season (46,61), and frequency of tillage (20). However, insects recorded here likely did not play a significant role because infestations were lowest during the first season in 1998 when natural *Fusarium* infection of the plants was highest (Figs. 1 and 2). Similar to Munkvold and Carlton (42), who used direct seed inoculation or silk inoculation with various *F. verticillioides* strains, the infection rate decreased with node level or distance from inoculation point. However, they often found zero infection after node 2, indicating that the stem inoculation treatment used in this study was more efficient than seed treatment at introducing the fungus into the stem. Also, in their experiments, systemic movement within the plant depended on the fungal strain used. The hot-water-fungicide treatment was for the most part not different from the control corroborating results by Baba-Moussa, which showed equivalent levels of upper node infection between seed-treated and control treatments (4). The fungus appears to be able to infect the plant at all stages of growth, independent of initial seed infection. Total percentage of plants infected with *F. verticillioides* [P(I)] in the inoculation treatment was similar to that found by Drepper and Renfro (22) using various stem inoculation methods.

Incidence of *F. verticillioides* in the stem was significantly higher in Gbogbe than in DMR. Varietal differences in incidence of asymptomatic and symptomatic infection of kernels were also found by Headrick and Pataky (30). Munkvold et al. (44) found that in hybrids expressing CrylA(b), the incidence of kernel infection and severity of infection of Fusarium ear rot was reduced compared with the nontransgenic hybrid. Considering individual internodes, the only difference between varieties was found in the second season 1998 experiment when the percentage of infected node 5 was higher on Gbogbe than DMR. This could have been

TABLE 1. Effect of sampling date or days after planting (DAP), variety (VAR), and treatment (TRT) on percentage of plants infected [P(I)] and of infection of internodes 1 to 5 by *Fusarium verticillioides* during the first and second season of 1998 (experiments I and II) and first season of 1999 (experiment III)[z]

	1998 first season						1998 second season						1999 first season					
ANOVA	P(I)	1	2	3	4	5	P(I)	1	2	3	4	5	P(I)	1	2	3	4	5
DAP	***	***	***	*	**	***	***	ns	*	**	**	**	***	***	**	*	**	***
TRT	***	***	***	**	**	ns	***	***	***	***	***	***	***	***	***	***	***	***
TRT × DAP	ns	**	**	*	ns	ns	*	*	ns	ns	ns	*	***	**	*	ns	ns	ns
VAR	*	ns	ns	ns	ns	ns	***	ns	ns	ns	ns	*	na	na	na	na	na	na
VAR × DAP	***	**	ns	ns	*	ns	**	ns	ns	ns	ns	ns	na	na	na	na	na	na
TRT × VAR	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	na	na	na	na	na	na
TRT × VAR × DAP	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	*	ns	na	na	na	na	na	na

[z] *, **, and *** indicate significant at $P \leq 0.05$, 0.001, and 0.0001, respectively, according to analysis of variance (ANOVA). ns = nonsignificant; na = not available.

TABLE 2. Mean percentage of plants [P(I)] and internodes 1 to 5 infected with *Fusarium verticillioides* (N1 to N5) according to treatment and variety in the first and second seasons of 1998 and the first season of 1999[z]

	1998 first season						1998 second season						1999 first season					
Treatment	P(I)	N1	N2	N3	N4	N5	P(I)	N1	N2	N3	N4	N5	P(I)	N1	N2	N3	N4	N5
Inoculation	67.5 a	53.3 a	35.5 a	32.6 a	32.0 a	18.7	99.3 a	68.3 a	69.4 a	50.6 a	43.2 a	30.6 a	99.3 a	85.8 a	85.8 a	75.0 a	63.3 a	51.6 a
Control	41.7 b	33.6 b	19.2 b	15.3 b	18.3 b	11.2	29.1 b	15.0 b	13.3 b	12.2 b	11.6 b	12.8 b	48.3 b	30.0 b	25.0 b	15.0 b	14.2 b	20.0 b
Fungicide	47.4 b	25.7 b	15.5 b	15.0 b	11.7 b	9.9	23.4 b	12.2 b	12.7 b	11.1 b	7.7 b	10.6 b	28.3 c	21.7 b	5.0 c	5.8 b	8.3 b	10.0 c
Variety																		
DMR	48.1 a	33.7	22.5	20.7	22.7	10.5	53.5 a	28.9	31.9	22.9	18.9	14.1 a	…	…	…	…	…	…
Gbogbe	56.5 b	41.3	24.3	21.2	18.6	15.7	59.5 b	34.8	31.9	26.3	22.2	21.9 b	…	…	…	…	…	…

[z] Means within column, between treatments or varieties, followed by the same or no letter are not significantly different according to Students-Newman-Keuls ($P \leq 0.05$).

due to differences in growth and movement of the fungus inside the plant or higher feeding and development rates of insects acting as vectors of the fungus. Feeding rates may be affected by variety (37,38,58) and plant nutrient contents (18,56).

Kernel infection by fungus was generally low. In the second season 1998, most of the grain filling period coincided with the onset of the dry season when rainfall ceased and air humidity was low. Similar to percentage of stem infection, the percentage of kernels infected was significantly highest in the inoculation treatment and higher for Gbogbe than DMR. Thus, significant correlations were found between kernel infection, percentage of infected nodes 1 to 5, and number of plants infected [P(I)] (Table 6). Baba-Moussa (4), using the same treatments, showed that covering the ear with a pollination bag during silking reduced fungal incidence by 35 to 55% only, thus, corroborating the present results that fungal incidence in the stem is source for ear infection either through movement of the fungus or via increased activity of insects, which move from the stem to the ear thereby vectoring the fungus. This is in contrast to Ooka and Kommedahl (47) who stated that the majority of ear infection was coming via external inoculum on silk and insect feeding through the silk channel.

Stem inoculation had a less drastic effect on insect infestations than ear inoculation (12). In contrast to the whorl feeder *Chilo* sp., *S. calamistis*, which also attacks the plant at a early growth stages, was hardly affected by the presence of the fungus in the stem (Table 4). A weak correlation was found in experiment I between percentage of node 5 infected and *S. calamistis* numbers in the ear (Table 6), indicating that on those plants infected at node 5 a higher number of insects survived and moved into the ear. This is in contrast to the findings by Cardwell et al. (12) who showed significantly higher *S. calamistis* infestations on inoculated ears but the differences were variety-specific. *S. calamistis* only oviposits on pretasseling plants (53) and generally higher numbers in the ear found were due to higher survival of older instar larvae if the fungus was present (51). The large differences in the effect on *S. calamistis* infestation between stem and ear inoculation may have been due to differential reaction of the varieties to both the fungus and the insects. Higher stem infection with *F. verticillioides* had a striking effect on *E. saccharina* infestations in both stems and ears, and especially in second season 1998, when pest densities were high (Fig. 2). In areas of West Africa with bimodal rainfall distribution, *E. saccharina* infestations always peak during the second cropping season (2,26,27). As also shown by Cardwell et al. (12), who showed that higher ear infection consistently lead to significantly greater *E. saccharina* damage, the effect of stem infection on *E. saccharina* was strong and consistent in all three experiments reported in this paper (Fig. 2). Ako (3) and Baba-Moussa (4) showed that *E. saccharina* laid three to four times more eggs on infected plants and that survival of larvae was significantly longer than on control plants or plants from hot water or fungicide-treated seeds. Similarly, the results of the present field experiments indicate that the higher infestation of Lepidoptera on

TABLE 3. Effect of sampling date or days after planting (DAP), variety (VAR), and treatment (TRT) on insect infestations in stems and ears during the first and second season of 1998 and first season of 1999[y]

	Eldana saccharina		*Sesamia calamistis*		*Chilo* sp.	*Mussidia nigrivenella*	*Cryptophlebia leucotreta*	Beetles[z]
	Stem	Ear	Stem	Ear	Stem	Ear	Ear	Ear
1998 first season								
DAP	***	**	**	*	–	*	***	ns
VAR	ns	ns	ns	ns	–	ns	ns	ns
VAR × DAP	**	ns	ns	ns	–	ns	ns	ns
TRT	***	ns	ns	ns	–	ns	ns	*
TRT × DAP	ns	ns	ns	ns	–	ns	ns	ns
TRT × VAR	ns	ns	ns	ns	–	ns	ns	ns
TRT × VAR × DAP	ns	ns	ns	ns	–	ns	ns	ns
1998 second season								
DAP	***	***	***	*	ns	***	***	***
VAR	***	**	ns	ns	ns	**	ns	ns
VAR × DAP	**	*	ns	ns	ns	ns	ns	**
TRT	***	***	ns	ns	ns	ns	ns	ns
TRT × DAP	*	***	ns	ns	ns	ns	*	ns
TRT × VAR	ns	ns	ns	ns	ns	ns	ns	ns
TRT × VAR × DAP	ns	ns	ns	ns	ns	ns	ns	ns
1999 first season								
DAP	***	***	ns	ns	***	*	***	***
TRT	***	ns	ns	ns	*	ns	*	*
TRT × DAP	**	ns	ns	ns	***	ns	*	ns

[y] *, **, and *** indicate significant at $P \leq 0.05$, 0.01, and 0.0001, respectively, according to analysis of variance. ns = not significant; – = not found.
[z] Beetles = pooled counts of all coleoptera.

TABLE 4. Least square means of insects per stem or ear according to inoculation treatment, variety, year, and first or second season[y]

	Eldana saccharina in stem			*Eldana saccharina* in ear			*Chilo* sp. in stem			*Mussidia nigrivenella* in ear			*Cryptophlebia leucotreta* in ear			Beetles in ear[z]		
Treatment	1998 1st	1998 2nd	1999 1st	1998 1st	1998 2nd	1999 1st	1998 1st	1998 2nd	1999 1st	1998 1st	1998 2nd	1999 1st	1998 1st	1998 2nd	1999 1st	1998 1st	1998 2nd	1999 1st
Inoculation	0.50 b	0.76 a	0.26 a	0.13	0.20 a	0.03	0.00	<0.0001	0.029 a	0.032	0.13	0.019	0.18	0.035	0.15 a	0.022 a	0.25	0.53 a
Control	0.31 a	0.58 b	0.31 a	0.10	0.16 b	0.05	0.00	<0.0001	0.042 a	0.022	0.17	0.014	0.21	0.039	0.09 b	0.012 ab	0.32	0.40 ab
Fungicide	0.27 a	0.41 c	0.12 b	0.09	0.13 c	0.05	0.00	<0.0001	0.008 b	0.012	0.13	0.020	0.23	0.022	0.11 b	0.002 b	0.26	0.38 b
Variety																		
DMR	0.34	0.44 a	–	0.12	0.18 a	–	0.00	<0.0001	–	0.026	0.17 a	–	0.20	0.036	–	0.012	0.29	–
Gbogbe	0.37	0.72 b	–	0.09	0.20 b	–	0.00	<0.0001	–	0.018	0.11 b	–	0.21	0.028	–	0.007	0.26	–

[y] Means within columns, between treatments or varieties, followed by the same or no letter are not significantly different according to Students-Newman-Keuls ($P \leq 0.05$).
[z] Beetles = pooled counts of all coleoptera.

infected plants might be due to higher attractiveness or higher survival of insects compared with control plants. The interactions of the fungus with the kernel feeders *Cryptophlebia leucotreta* and *M. nigrivenella* were not strong, and as for *S. calamistis*, significant correlations were only found with nodes 4 to 5 (Table 6), indicating that only in plants where the fungus moved from the upper nodes to the ear did it have an effect on insect numbers. This could have been due to both higher attractiveness, as shown by Ako (3) in oviposition experiments for *M. nigrivenella*, and higher survival of larvae in infected tissues.

The varietal differences in *E. saccharina* infestations in late 1998 (Table 4) corresponded with the differences in fungal incidence [P(I)] (Table 2), indicating again that the fungus promotes the borer, but the reasons for the higher infection on Gbogbe are not known. By contrast, the lower number of *M. nigrivenella* on Gbogbe was probably a result of better husk cover than DMR (12,35). Longer husk cover can lead to either increased cannibalism among young larvae entering through the silk channel (40) or prolonged feeding on an unsuitable substrate, i.e., husks or silk (55). Similarly, the lower *A. flavus* incidence on Gbogbe was probably due to superior husk cover and possible exclusion because of kernel pericarp properties (12). Cardwell et al. (12) also reported susceptibility of DMR to *A. flavus*. The significant differences in *A. flavus* between the *F. verticillioides* inoculation and control and the fungicide treatment was probably an artifact in both studies.

It is possible that the systemic fungal infection is interfering in some way with host plant insect resistance mechanisms. IITA breeders noticed that DMR had some borer resistance relative to other lines (9). It was also found to have a relatively stronger stalk measured by penetrometer readings (9). On this basis, and the fact that it was resistant to downy mildew caused by *Peronosclerospora sorghi*, it was used as a parental material for a stem borer resistance breeding program (9). Nevertheless, in attempting to breed for improved stalk strength, breeders were frustrated by erratic progress between cycles of selection (9), which might have been the result of differential systemic fungal infection levels from year to year. It is unclear whether resistance to *F. verticillioides* may be a factor in the resistance of DMR to stem borers. Gbogbe had significantly higher *F. verticillioides* infection than DMR and higher infestation of *E. saccharina* in the stem. Thus, systemic *F. verticillioides* infection is possibly a background environmental factor that may confound efforts to select for stem borer resistance.

TABLE 5. Mean percentage of kernels infected with fungi by stem inoculation treatments and variety in first and second season 1998[z]

Treatment	*Fusarium*	*Penicillium*	*Aspergillus*
Inoculation	23.3 a	2.0 a	8.7 a
Control	8.0 b	1.3 a	6.0 a
Fungicide	3.3 b	1.3 a	0.001 b
Variety			
DMR	8.4 a	0.9 a	7.6 a
Gbogbe	14.6 b	2.2 a	2.2 b

[z] Means within column, between treatments or varieties, followed by the same letter are not significantly different according to Students-Newman-Keuls ($P \leq 0.005$). Numbers presented are back-transformed data.

TABLE 6. Correlations among percentage of *Fusarium verticillioides*-infected nodes (N1 to N5), percentage of plants infected [P(I)], and numbers of insects per stem or ear in first and second cropping season 1998 and first cropping season 1999 and among percentage of infected nodes at 70 days after planting (DAP) and grain at 110 DAP, and number of insects per stem or ear at 110 DAP during the second cropping season 1998[y]

Season	N1	N2	N3	N4	N5	P(I)
1998 first season						
N1	1.00	…	…	…	…	…
N2	0.66**	1.00	…	…	…	…
N3	0.17	0.58**	1.00	…	…	…
N4	0.24	0.64**	0.87***	1.00	…	…
N5	0.30	0.56*	0.48*	0.54*	1.00	…
P(I)	0.81***	0.62*	0.16	0.26	0.37	1.00
Sesamia calamistis ear	0.08	0.29	0.35	0.29	0.52*	0.08
Eldana saccharina stem	0.42	0.51*	0.74**	0.65**	0.34	0.29
Eldana saccharina ear	0.16	0.42	0.61**	0.70**	0.26	0.20
Mussidia nigrivenella ear	0.13	0.19	0.42	0.47*	0.36	0.21
1998 second season						
N1	1.00	…	…	…	…	…
N2	0.90***	1.00	…	…	…	…
N3	0.68**	0.70**	1.00	…	…	…
N4	0.73**	0.74**	0.77***	1.00	…	…
N5	0.64**	0.58*	0.62**	0.85***	1.00	…
P(I)	0.88***	0.86***	0.85***	0.81***	0.71**	1.00
Eldana saccharina stem	0.68**	0.69**	0.50*	0.56**	0.66**	0.51*
Cryptophlebia leucotreta ear	0.38	0.40	0.22	0.49*	0.48*	0.35
1999 first season						
N1	1.00	…	…	…	…	…
N2	0.76**	1.00	…	…	…	…
N3	0.67*	0.93**	1.00	…	…	…
N4	0.74*	0.90**	0.92**	1.00	…	…
N5	0.75*	0.88**	0.88**	0.84**	1.00	…
P(I)	0.91**	0.88**	0.84**	0.82**	0.94***	1.00
Eldana saccharina stem	0.28	0.59	0.52	0.53	0.64*	0.55
Cryptophlebia leucotreta ear	0.13	0.43	0.68*	0.37	0.47	0.32
1998 second season						
Sesamia calamistis ear	0.37	0.44	0.26	0.51*	0.25	0.36
Eldana saccharina stem	0.54*	0.42	0.27	0.44	0.57**	0.33
Eldana saccharina ear	0.70**	0.62**	0.53*	0.59**	0.68**	0.56**
Fusarium[z]	0.75**	0.59**	0.76*	0.56*	0.54*	0.73**

[y] Partial correlation coefficients marked with *, **, and *** indicate significant at $P \leq 0.05$, 0.01, and 0.0001, respectively.
[z] *Fusarium* = percentage of kernels infected with *F. verticillioides*.

For beetles, significant differences among treatments only became apparent if they were pooled across species. Ako (3), in olfactometer studies, showed that *Cathartus quadricollis* was attracted by and laid more eggs on postharvest kernels infected with *F. verticillioides* than uninfected kernels. Other authors showed similar increased attractiveness (8,14,19,32,33). However, Ako (3) found relatively small differences in attractiveness and numbers of eggs laid, which does not explain the large differences in beetle numbers in general found by Cardwell et al. (12), and to a lesser extent, in the present experiment. Thus, the question arises whether those differences were also due to higher attractiveness of ears damaged by stem borers (54), an indirect result of higher fungal incidence, or higher survival of beetles in infected ears.

The present results confirm those by Cardwell et al. (12) that the presence of the *F. verticillioides* in the plant can promote infestation of the plant by lepidopterous and coleopteran pests. As shown by Sétamou et al. (54) and Hell et al. (31), insect feeding renders the grain susceptible to *A. flavus* infection, resulting in higher potential aflatoxin levels of grain in both the field and during storage. Thus, keeping the *F. verticillioides* out of the plant could considerably reduce insect damage to both stem and grain and potentially lower both aflatoxin and fumonisin levels in grain.

Grass endophytes often have beneficial mutualistic effects because they enhance growth via increased tillering, increased insect resistance and drought tolerance, or cause toxic syndromes in cattle that consume infected grasses (6). *F. subglutinans* Wollenweber & Reinking produces beauvericin (29,39), which has insecticidal properties (1,17,28) and can protect the plant from herbivory. In contrast to beneficial endophytes, early infection by *F. verticillioides* in maize can cause malformation of the plant, which produces twisted foliage and tillers (Pokkah boeng disease), stem etiolation, and a multiple-ear phyllody, although for the most part, infection is asymptomatic (K. F. Cardwell, *personal observation*). Especially for a plant like maize that does not tiller, any stem damage is likely to affect yield (10,13,27). Thus, in coevolutionary terms, the increased borer attack due to *F. verticillioides* infection should be counter-productive for the plant if the host–fungus relationship is obligate or facultatively beneficial to the fungus. Thus, the question arises, by breeding for increased yields in the absence of heavy stem borer pressure, if we inadvertently increase the plants' susceptibility to the fungus and thereby to insect pests. The present results underline again the need for a more holistic approach in increasing agricultural production.

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