Spread of Maize Chlorotic Dwarf Virus from Infected Corn and Johnsongrass by *Graminella nigrifrons*

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ABSTRACT

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Early emerged adults (males and females) or last instar nymphs (males, females, or males and females together) of the leafhopper *Graminella nigrifrons* were allowed to acquire maize chlorotic dwarf virus (MCDV) from corn or johnsongrass source plants positioned in the center of maize plots in 1990. In 1991, two planting dates of maize were tested by using newly emerged adult males, females, or males and females. After leafhopper acquisition and potential flight to other plants, disease incidence was assessed throughout the plots. The log-logistic model provided an acceptable fit to the observed disease gradients. MCDV incidence was higher when infected corn was used as a virus source compared to johnsongrass in 1990 and both plantings of 1991. Leafhopper sex did not influence disease incidence. The intercept of the linearized log-logistic model (*a*) was higher for corn virus source only in 1990. The slope parameter (*b*), a gradient steepness, was not affected by leafhopper sex or virus source plant.

Maize chlorotic dwarf virus (MCDV) causes one of the two most important virus diseases of corn (*Zea mays* L.) in the United States (4). The virus is transmitted semipersistently by several leafhopper species (15), but the blackfaced leafhopper (*Graminella nigrifrons* (Forbes)) is considered the most important vector in the field (16).

Most MCDV host plants belong to the panicoid and andropogonoid grasses. MCDV has been isolated from field samples of corn (*Z. mays*), johnsongrass (*Sorghum halepense* (L.) Pers.), sweet sorghum (*Sorghum bicolor* (L.) Moench), giant foxtail (*Setaria faberii* Herrm.), and yellow foxtail (*Setaria lutescens* (Weigel) Hubb.). In addition to these naturally infected hosts, several other plants in the Gramineae are experimental hosts (14). Johnsongrass is considered the overwintering MCDV host from which *G. nigrifrons* acquires virus during early spring (4). At low temperatures, which typically occur in the spring, Larsen et al (11) showed that johnsongrass is a better host for *G. nigrifrons* than corn. Others (9,19) also found that johnsongrass is a better host for *G. nigrifrons* than corn. Maize chlorotic dwarf epidemics only have occurred when johnsongrass and *G. nigrifrons* were present in the same area (4). Few experiments on MCDV spread under field conditions have been conducted. Alverson et al (1,2) used RbCl-labeled leafhoppers to monitor leafhopper movement and simulate the spread of MCDV from a large area containing johnsongrass source plants. This experiment, which was done in only one plot and for one year, showed that leafhopper movement proceeded at about 3.8 m/day. Madden et al (13) quantified MCDV spread by releasing adult leafhoppers, previously exposed to MCDV in the laboratory, on the ground in the center of corn plots. The log-logistic model (8) gave the best fit of the disease gradients, and the spread velocity of the virus was about 3–37 cm/day. These latter experiments did not evaluate acquisition of MCDV from source plants in the field, nor did they test the effects of different source plant species or sex of the leafhoppers on spread of MCDV.

In contrast to the work by Madden et al (13), in experiments described here, *G. nigrifrons* leafhoppers were allowed to acquire MCDV from source plants in corn fields and to fly naturally from these plants. The objectives of these experiments were as follows: 1) to study whether corn or johnsongrass as virus source plants affects spread of MCDV; and 2) to determine whether the sex of *G. nigrifrons* impacts the spread of MCDV. The mating status of females (mated or virgin) also was evaluated in 1 yr.

MATERIALS AND METHODS

Experiments were conducted at the Ohio Agricultural Research and Development Center, Wooster, Ohio. *G. nigrifrons* occurs throughout Ohio; however, the overwintering host for MCDV, johnsongrass, is not found in the area where the experiments were conducted. Because MCDV is retained by vectors for only a few hours or days, leafhoppers in the natural population at the study site were not viruliferous (12). These conditions allowed for the investigation of MCDV spread without any interference from natural inoculum.

1990 Field experiment. In the 1990 field experiment, each plot was established by planting the 'Oh28' corn inbred. The distance between and within rows was 0.5 m, and there were 21 rows producing a plot 10 m on a side. The plots were planted by hand on 19 May 1990. There were 10 plots.

New colonies of *G. nigrifrons* were established by placing 400 adults into

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each Dacron organdy-covered rearing cages (0.4 × 0.2 × 0.4 m) (3) containing oats (*Avena sativa* L. 'Garland') for a 4-day oviposition period, after which time adults were removed. After the eggs hatched, oat plants were then gradually replaced with inbred corn plants. Colonies were kept in a rearing room at 25 ± 2 C until most of individuals were either last instar nymphs or early emerged adults, according to treatment requirements (17) (see below). To have enough leafhoppers at different stages, new leafhopper colonies were started each week for 3 wk.

Johnsongrass and corn virus-source plants were grown from seed in a greenhouse. The MCDV-WS isolate was used in these studies (7). To produce johnsongrass source plants, 100–200 viruliferous leafhoppers were placed into cages (0.4 × 0.3 × 0.5 m) containing 11 plants. Those cages containing both leafhoppers and johnsongrass plants were transferred to a growth chamber to allow a 2-day inoculation access period (IAP). Similarly, corn plants were placed in smaller cages (0.4 × 0.2 × 0.4 m) containing 18 plants and 100–200 viruliferous leafhoppers. Leafhoppers were removed after 2 days in both cases. Johnsongrass plants were 3 wk old and corn plants were 1 wk old when inoculated. Johnsongrass source plants were then kept in the greenhouse for 1–2 wk and corn source plants were then kept for 2 wk before pots containing the source plants were buried in the field. One johnsongrass or three corn plants were used as a MCDV source per plot because of differences in biomass of the plant species. Eight additional corn and johnsongrass source plants were tested for virus infection by enzyme-linked immunosorbent assay (ELISA) using the identical procedures of Knoke et al (10). All assayed inoculated plants had positive reactions with ELISA (C. M. Rodriguez, *unpublished*). Tests did not permit the quantification of virus titer in the plants.

Leafhoppers were released in a transfer chamber, aspirated, and separated by sex. Then 500 leafhoppers were placed into Dacron-organdy cages without bottoms, which were in the center of each plot containing the source plant(s). The leafhoppers had a 96-hr acquisition-access-period (AAP) on source plants infected with MCDV. After the AAP, cages were removed at 4 a.m. when leafhopper flight activity is minimal (17). Source plants were kept in the field for 10 days after the cages were removed.

The experimental design was a randomized complete block with one experimental factor (treatment). There were five treatments: 1) virgin males and females on johnsongrass source plants, 2) mated males and females on johnsongrass, 3) mated males and females on corn, 4) virgin females on johnsongrass, and 5) virgin males on johnsongrass. For treatments 1, 4, and 5, leafhoppers were separated by sex as last-instar nymphs and placed on the source plants in the field. Nymphs molted into adults in the field before the cages were removed. An equal number of adult males and females were used for treatments 1–3. There were two replications of each treatment. Disease assessments were made at 4, 11, 14, and 18 days after leafhoppers were released (37 days after planting), although only the 18-day data are presented here. Distance from the virus-source plants to the infected plants was calculated based on distances between plants within and across rows, and then the number of infected plants in each 80-cm wide annulus from the source was determined. The 80-cm width was chosen based on previous results (13). For presentation, the midpoint distance of each annulus from the source is shown in the figures (e.g., 40 for 0–80 cm, 120 for 80–160 cm). The log-logistic regression model of Jeger (8) was fitted to the disease gradient in each plot (13).

1991 Field experiment. In the 1992 field experiment, the experimental setup in the field was similar to that in 1990. Plots were machine-planted with inbred Oh28, leafhoppers were allowed a 48-hr AAP on the virus source plants in the field, and only early emerged adult leafhoppers were used. There were six treatments: 1) males and females together on johnsongrass source plants, 2) females on johnsongrass, 3) males on johnsongrass, 4) males and females on corn source plants, 5) females on corn, and 6) males on corn.

Two corn-planting dates were evaluated for MCDV incidence in two fields that were planted on 1 May and 29 May.

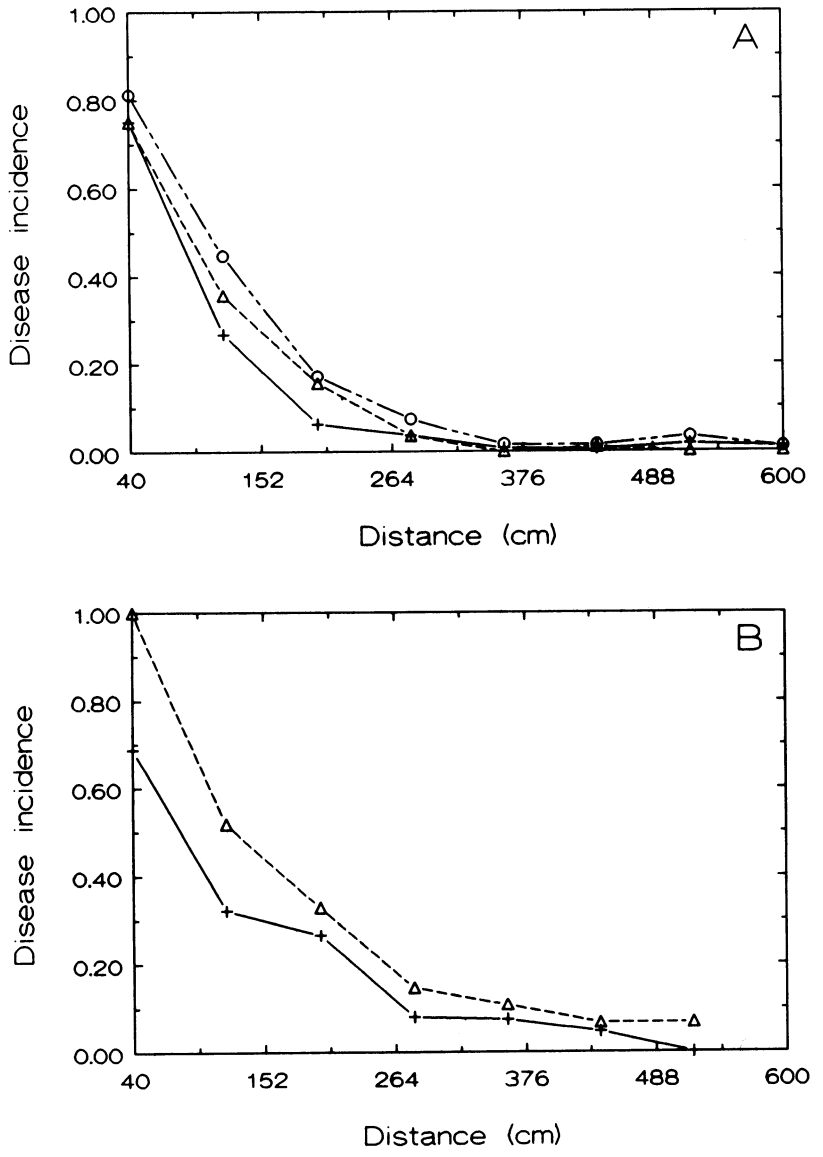

Fig. 1. Average maize chlorotic dwarf virus (MCDV) incidence in relation to distance from the source for 1990 experiment. (**A**) Disease gradients when late instar nymphs of males (+), females (△), or both (○) were placed on MCDV-infected johnsongrass. (**B**) Disease gradients when adults were placed on MCDV-infected johnsongrass (+) or corn (△). Points represent the average of two replications.

There were two replications of each treatment within each planting date. The experimental design was a randomized complete block factorial, with the experimental factors of leafhopper sex and source plant species grouped within the additional factor of planting date.

Insect-rearing procedures and virus source plant growth conditions were the same as in 1990. Leafhoppers were separated by sex in the adult stage within 2 days of molting, and 700 insects per cage were used.

Leafhoppers were released 39 days after planting in the first planting and 49 days after planting in the second. Disease assessments were made at 6, 10, and 20 days following leafhopper release for both plantings, although only the data from the last assessment are presented.

Data analysis. Analysis of variance (ANOVA) was used to evaluate the effect of the treatment (in 1990) or leafhopper sex, plant species, planting date, and their interactions (1991) on MCDV disease incidence for entire plots (y), and the estimated intercept (a) and the spread (slope) parameter (b) of the log-logistic model (13), which was fitted to the gradient data.

The parameter a of the log-logistic model represents $\ln(y_1/(100-y_1))$, where y_1 is estimated y at 1 cm from the source and is also a measure of the height of the disease gradient curve. The parameter b is a measure of the steepness of the disease gradient and reflects the movement of the vectors through the corn plot, as well as vector behavior. To stabilize variances, y was transformed to logits $[\ln(y/(100-y))]$ before ANOVA.

RESULTS

Late in the morning after the cages were removed from source plants, leafhoppers were observed on virus source plants, on the ground around source plants, and on corn plants near (≤1 m) the source plants. Leafhoppers on the ground were very passive, but during the afternoon of the release day, most were observed in the plots on plants displaying a feeding behavior. Male and female leafhoppers had a similar dispersal pattern. By late afternoon of the release day, most of the leafhoppers were observed <3 m away from the source and some leafhoppers could still be seen on the source plants. Differences in leafhopper behavior on corn or johnsongrass were not visually apparent.

1990 Experiment. In 1990, gradients of MCDV incidence were very smooth (Fig. 1). MCDV-infected plants were observed as far as 6 m from the source by the last assessment date, and the incidence adjacent to the source was as high as 100%. ANOVA indicated a significant effect of treatment on transformed MCDV incidence ($P < 0.05$). Disease incidence was highest (14.6%) when infected corn was used as a virus source and least when either males (5.0%) or females (5.8%) transmitted virus from johnsongrass (Table 1). Sex of the leafhoppers and their mating status had no effect on disease incidence.

The log-logistic model provided an excellent fit to the disease gradients (e.g., Fig. 2). Most coefficients of determination (R^2) were greater than 90%, and the residual plots had a random scatter. ANOVA indicated that treatment had a significant effect on a of the log-logistic model ($P < 0.05$) (i.e., height of the gradient curve) but not on b ($P > 0.10$) (steepness of the curve) (Table 1). The corn source plant treatment had an a value greater than some of the other treatments. The spread coefficient was very similar for the five treatments, with adults on johnsongrass tending to have a lower b (i.e., closer to 0). Leafhopper sex and mating status did not significantly affect a or b.

1991 Experiment. In general, incidence of MCDV was lower in 1991 than in 1990 (Table 2). The disease gradients also were more erratic, especially near the source plants. For some treatment combinations, the highest incidence was not found adjacent to the source (Figs. 3 and 4). The highest mean incidence of MCDV at any distance was less than 50%.

ANOVA indicated that virus source plant had a significant ($P < 0.05$) effect on (transformed) disease incidence. However, leafhopper sex, planting date, and all interactions were not significant ($P > 0.10$). This indicates that the comparison between johnsongrass and corn can be made with the overall (main effect) means. There was a significantly higher incidence of MCDV with corn source plants than with johnsongrass (Table 2).

Because of the more erratic gradients, the log-logistic model provided a poorer fit in 1991 than in 1990. Although some

Table 1. Effect of source plant and leafhopper treatments on incidence of maize chlorotic dwarf virus and the estimated intercept and spread (slope) parameters of the log-logistic model fitted to the disease gradient data for 1990

Treatment[a]	Incidence	Intercept (a)	Slopes (b)	R^2 range[b]
Male and female nymphs on johnsongrass	8.15 (0.25)[c] [−2.42][d]	8.99 (0.91)[c]	−2.04 (0.16)[c]	79–95
Male and female adults on johnsongrass	8.70 (3.10) [−2.22]	6.65 (1.80)	−1.56 (0.26)	91–96
Male and female adults on corn	14.60 (0.10) [−1.77]	10.65 (0.55)	−2.17 (0.11)	95–97
Female nymphs on johnsongrass	5.75 (0.55) [−2.80]	9.09 (1.12)	−2.12 (0.24)	84–99
Male nymphs on johnsongrass	5.05 (2.15) [−3.03]	8.19 (2.31)	−2.00 (0.34)	80–89
SED[e]	[0.30]	2.09		

[a] Johnsongrass source plant except for the third treatment. Nymphs molted into adults on the source plants in the field.
[b] R^2: coefficient of determination. Range of R^2 values for the different replications is shown.
[c] Standard error from two replications.
[d] Mean logit-transformed value.
[e] Standard error of a difference; shown if treatment is significant ($P < 0.05$).

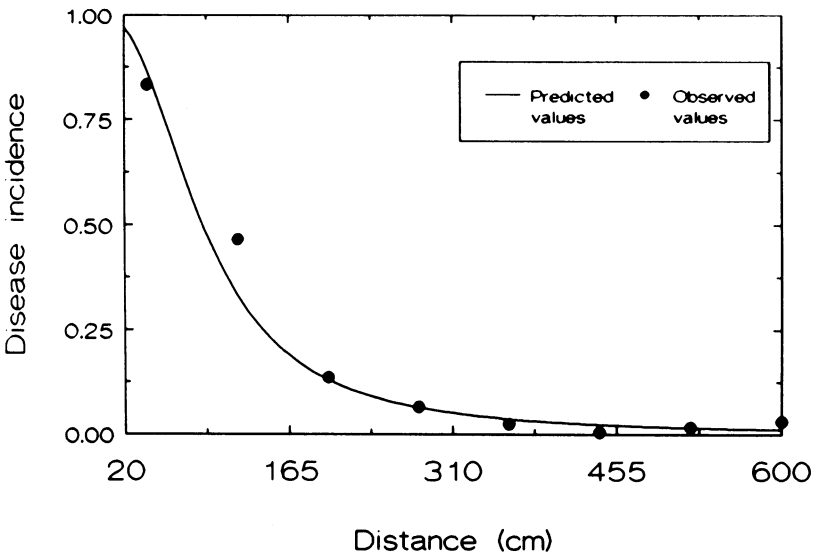

Fig. 2. Maize chlorotic dwarf virus (MCDV) incidence in a single plot (●) in 1990 (male nymphs) and predicted values (—) obtained by fitting the log-logistic model to the data. Estimates of the parameters: $a = 10.5$; $b = 2.34$; coefficient of determination (R^2) = 89.0%.

Table 2. Effects of source plant and leafhopper treatments on incidence of maize chlorotic dwarf virus and the estimated intercept and spread (slope) parameters of the log-logistic model fitted to the disease gradient data for 1991

	Incidence			Intercept (*a*)			Slopes (*b*)			R^2 range[a]	
	Johnsongrass	Corn	Mean	Johnsongrass	Corn	Mean	Johnsongrass	Corn	Mean	Johnsongrass	Corn
First planting											
Males and females	2.01 (0.31)[b] [−3.90][c]	5.51 (1.03)[b] [−2.86]	3.76	4.00 (4.58)[b]	12.40 (0.20)[b]	8.20	−1.25 (1.0)[b]	−2.72 (0.08)[b]	−1.99	33.4–76.7	79.6–94.8
Females	3.19 (1.92) [−3.64]	7.41 (3.00) [−2.62]	5.30	8.72 (4.18)	6.42 (3.68)	7.57	−2.18 (0.62)	−1.39 (0.95)	−1.79	60.9–92.0	86.2–88.8
Males	2.66 (2.40) [−4.46]	5.08 (0.04) [−2.93]	3.87	2.64 (4.64)	4.85 (0.50)	3.75	−1.04 (0.75)	−1.39 (0.06)	−1.22	13.2–61.0	30.5–77.3
Mean	2.62 [−4.00]	6.0 [−2.80]		5.12	7.89		−1.49	−1.83			
Second planting											
Males and females	5.37 (1.02) [−2.89]	8.38 (3.19) [−2.47]	6.88	12.22 (2.99)	7.61 (3.29)	9.92	−2.64 (0.55)	−1.78 (0.69)	−2.21	87.3–89.5	41.4–72.3
Females	6.35 (1.03) [−2.70]	6.02 (1.31) [−2.77]	6.19	6.86 (5.21)	10.58 (0.62)	8.72	−1.40 (1.14)	−2.37 (0.02)	−1.88	54.5–81.9	86.4–95.5
Males	3.79 (2.51) [−3.52]	5.71 (1.06) [−2.82]	4.75	4.69 (1.27)	5.18 (0.17)	4.94	−1.39 (0.12)	−1.39 (0.06)	−1.39	65.3–94.8	61.5–77.3
Mean	5.17 [−3.04]	6.70 [−2.69]		7.92	7.79		−1.81	−1.85			
Combined plantings											
Mean	3.89 [−3.52]*[d]	6.35 [−2.75]		6.52	7.84		−1.65	−1.84			

[a] R^2: coefficient of determination. Range of R^2 values for the different replications is shown.
[b] Standard error for the two replications.
[c] Mean logit-transformed values.
[d] Main effect mean for johnsongrass different from corn at $P < 0.05$ based on analysis of variance of logits.

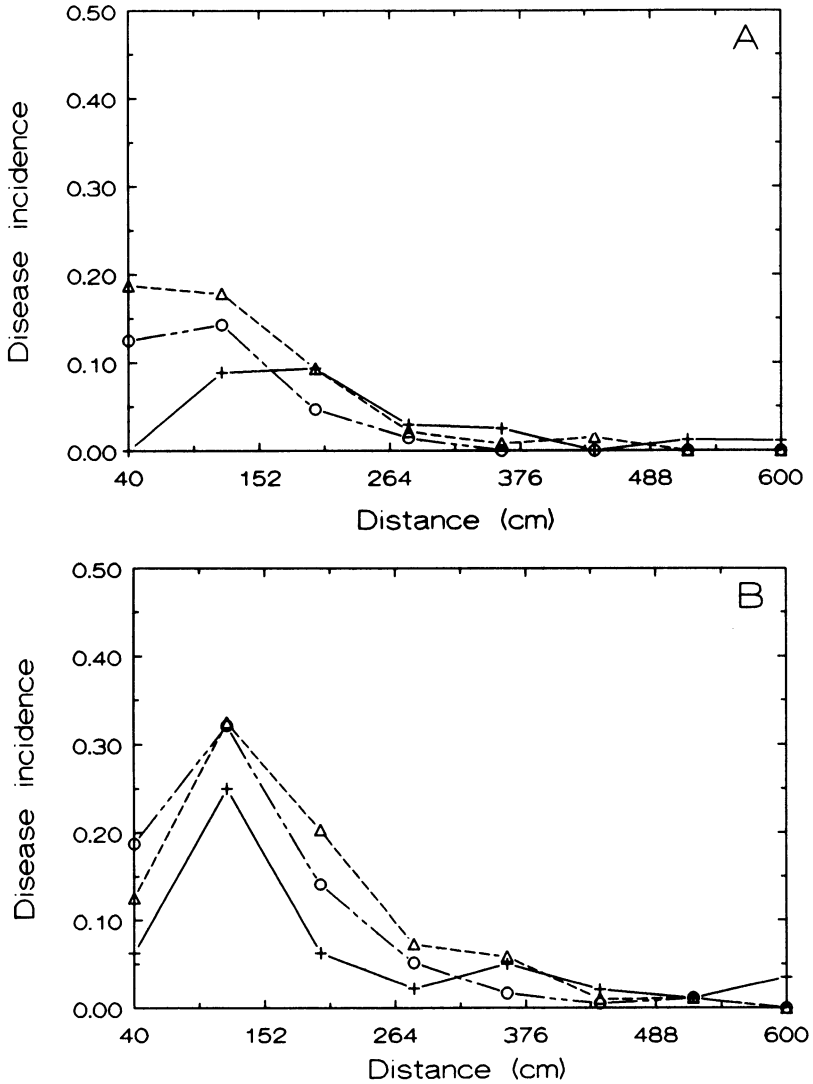

Fig. 3. Average maize chlorotic dwarf virus (MCDV) incidence in relation to distance from the source for the first planting in 1991. (**A**) Disease gradients when early emerged males (+), females (Δ), or both (O) were placed on MCDV-infected johnsongrass. (**B**) Disease gradients when early emerged males (+), females (Δ), or both (O) were placed on MCDV-infected corn. Points represent the average of two replications.

replications were well described by the model (R^2 = 80–95%), others were not as well described (R^2 = 30–60%). All regression equations, however, were significant ($P < 0.05$), and residual plots were random. ANOVA indicated that none of the experimental factors or their interactions had a significant effect on *a* or *b* of the log-logistic model ($P > 0.10$). The spread coefficient (*b*) was similar for all the treatments.

DISCUSSION

In agreement with Madden et al (13), it was shown that viruliferous leafhoppers transmitted MCDV to neighboring rather than distant corn plants. Infected plants were found up to 6 m from the source, and incidence was as high as 100% near the source in some cases. The magnitude of disease spread also was similar to that found previously (13). However, unlike the previous study, leafhoppers were allowed to acquire MCDV from plants in the field and were not forced to fly to corn plants to feed.

The major determinant of the magnitude of spread, as measured by disease incidence (*y*), was the species of the source plant. The steepness of the gradient, as measured by *b*, was not affected by any of the experimental factors. The estimates of *a* were affected by the experimental factors only in 1990, even though *a* is usually correlated with *y*. The lower R^2 values for 1991 probably contributed to the high variability in *a*. Over 2 yr and the two plantings in the second year there was more spread of MCDV from corn than johnsongrass. There are some reports that indicate the poor quality of corn as a host plant for *G. nigrifrons* compared to other plant species, although the leafhopper has a wide host range within the Gramineae (20).

Sedlacek et al (18) developed life tables for *G. nigrifrons* using corn and johnsongrass as host plants and demonstrated a net reproductive rate of 0.5 on corn, which means a reduction in the leafhopper population over time. Other variables, such as the probability of leafhopper survival and cohort fecundity, also were lower on corn compared to johnsongrass. However, in a laboratory study, Hunt and Nault (5) found that corn is a good host plant during the early growth stages, but its quality declines as it matures, and, as a consequence, *G. nigrifrons* may then seek other host species. Knoke et al (9) suggested that *G. nigrifrons* prefers johnsongrass and ryegrass as feeding plants, compared to corn, and believed this could explain the movement of *G. nigrifrons* within corn fields, as well as MCDV spread in the field. Triplehorn et al (21) found that *G. nigrifrons* fed for a longer time, had fewer probes, and fed more frequently from the sieve elements on johnsongrass than on corn or oats. Moreover, Sedlacek and Freytag (18) found a high dependence of *G. nigrifrons* population density on corn-planting date, which coincides with the hypothesis proposed by Hunt and Nault (5) about the reduction of corn suitability as the nutritional quality of corn declines with age. Because corn is less suitable for *G. nigrifrons*, compared to johnsongrass, our results also suggest that leafhoppers move sooner or at a greater frequency from corn plants infected with MCDV than from johnsongrass.

Because corn is not as good a host plant as some other grasses for *G. nigrifrons*, at least under some conditions, leafhoppers may only feed on corn for a short time. However, this period is sufficient to acquire and spread MCDV to healthy plants while leafhoppers are still viruliferous. Interestingly, in laboratory studies, *G. nigrifrons* had a greater acquisition rate of the MCDV-WS isolate from corn than johnsongrass. Insects given a 2-day AAP on johnsongrass had a 18% transmission rate to corn compared to 47% for those insects given an AAP on corn (A. Wayadande and L. R. Nault, *unpublished*). Therefore, the greater transmission rate from corn and the lower suitability of corn as a host likely resulted in greater spread of MCDV from this host compared to johnsongrass.

The experimental condition with corn as the virus source in our field studies simulated the natural situation in which *G. nigrifrons* adults move the virus from one field (perhaps from one planted earlier) to another, as well as the secondary spread of the virus disease within a corn field. In contrast, plots with johnsongrass more closely resembled the manner in which *G. nigrifrons* moves the virus from the overwintering host to newly planted corn. Although less spread occurs from johnsongrass than from corn, the movement of the virus as indicated by *b* is sufficient to initiate epidemics wherever johnsongrass and *G. nigrifrons* coexist. Once leafhoppers leave the original source plants, spread within corn plots is the same, as indicated by the *b* parameter. Differences in *b* would be apparent if insect movement and feeding behavior varied on corn between field plots but not on the source plants.

Hunt and Nault (6) found that intra- and interplant-movement behavior of male and female *G. nigrifrons* differed greatly, especially for mated females. In general, mated females were less mobile than virgin females and males. However, sex of the leafhoppers had no significant effect on MCDV spread in this study. This discrepancy may be attributed to the different conditions used in the experiments. Hunt and Nault (6) used oats as the sole host plant and reared insects in a controlled indoor environment. In the field tests, johnsongrass and corn were the host plants, and both the leafhoppers and plants were exposed to quite variable weather conditions. The differences observed in mate-location behavior between males and females of *G. nigrifrons* in the laboratory may not be directly related to MCDV spread in the field. The lack of flight barriers, the short mate-finding range (< 0.5 m), and the more severe climatic and biotic conditions in the field for our study probably attenuated the differences in the mate-location behavior observed between male and female leafhoppers under laboratory conditions and the spread of MCDV.

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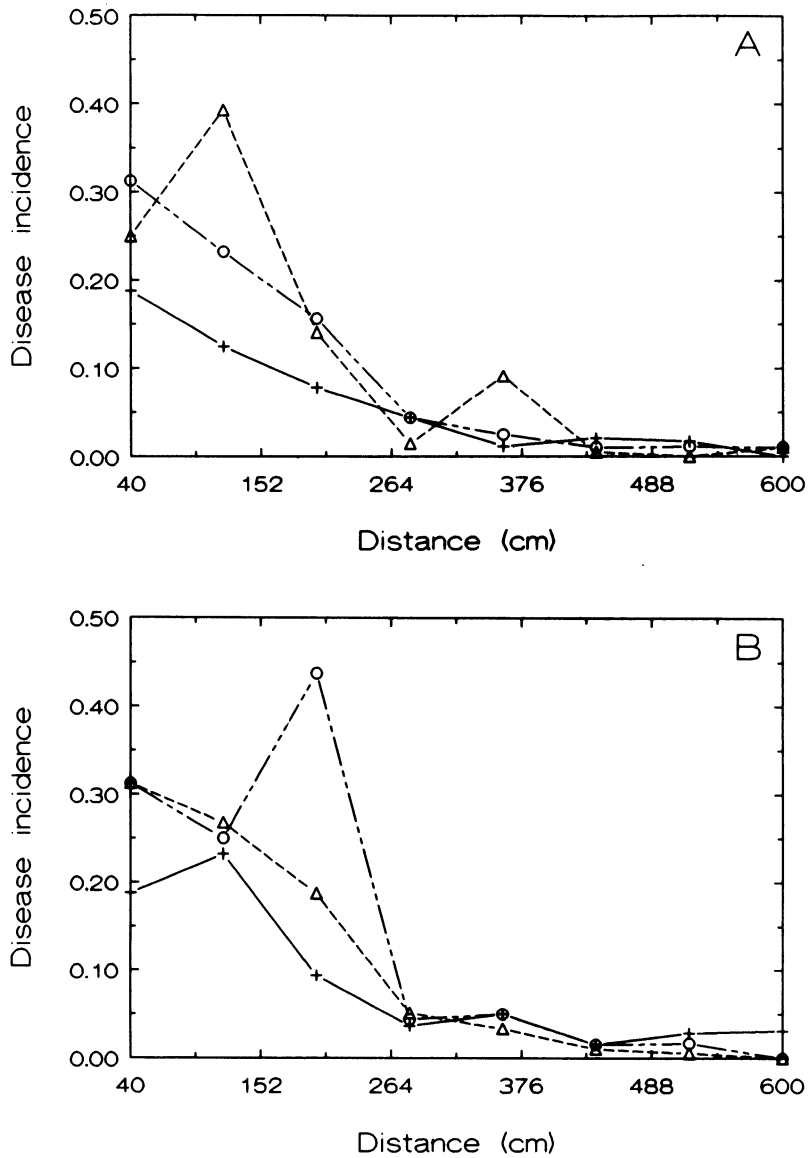

Fig. 4. Average maize chlorotic dwarf virus (MCDV) incidence in relation to distance from the source for the second planting in 1991. (**A**) Disease gradients when early emerged males (+), females (△), or both (○) were placed on MCDV-infected johnsongrass. (**B**) Disease gradients when early emerged males (+), females (△), or both (○) were placed on MCDV-infected corn. Points represent the average of two replications.

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