Postemergence Control of Johnsongrass and its Effect on Maize Dwarf Mosaic Virus Incidence and Vectors in Corn

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ABSTRACT

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The number of alighting aphids and maize dwarf mosaic virus (MDMV, johnsongrass-strain) incidence were determined when johnsongrass was controlled with nicosulfuron or primisulfuron applied at different growth stages of corn. In 1990, more alighting aphids were found in alighting traps in weed-free plots than in weedy plots. Maize dwarf mosaic (MDM) incidence, calculated as area under the disease progress curve (AUDPC), was more prevalent when either nicosulfuron or primisulfuron was applied at the eighth compared to the fifth leaf collar stage. In 1991, more corn plants were infected with MDMV when johnsongrass remained throughout the season than when it was removed with a postemergence herbicide. Correlations between cumulative alate aphids and AUDPC were nonsignificant in both years. The proximity of infected johnsongrass to corn appeared to have a much greater impact on MDMV incidence than did the number of vectors in aphid traps. MDMV-infected johnsongrass can remain a source of inoculum for up to 7 days after the application of nicosulfuron or primisulfuron. In an aphid–host preference study (species × presence of MDMV × nicosulfuron application), apterous (wingless) *Rhopalosiphum maidis* continued to increase on johnsongrass not treated with nicosulfuron. However, when johnsongrass was treated with nicosulfuron, apterae numbers peaked 3–4 days after treatment, then declined. More winged (alate) *R. maidis* were found on corn than on johnsongrass in 1990. In 1991, fewer alate *R. maidis* were found on johnsongrass treated with nicosulfuron than in other treatments. The presence of systemic MDMV symptoms in corn or johnsongrass had no impact on the numbers of alate or apterous *R. maidis*.

Additional keywords: corn leaf aphid, senescence, *Sorghum halepense* (L.) Pers., and *Zea mays* L.

Maize dwarf mosaic (MDM), caused by maize dwarf mosaic virus (MDMV), is one of the most important viral diseases of corn (*Zea mays* L.) (8). MDMV (johnsongrass strains) overwinters in rhizomes of johnsongrass (*Sorghum halepense* (L.) Pers.) and is present in the tissue of sprigs at emergence in early spring. MDMV is a nonpersistently transmitted virus, vectored by at least 23 species of aphids.

In the absence of johnsongrass, MDMV is primarily spread in corn and sorghum (*Sorghum bicolor* (L.) Moench) by transient winged (alate) aphids (1,2,8). Alate behavior, consisting of many short meandering flights with frequent probing, has been related to dispersal rather than to host finding (27). Strong correlations have been found between aphid numbers in yellow water traps and MDMV (15,16,26). However, these studies were done in the absence of johnsongrass.

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is a vector of MDMV and has been observed colonizing both corn and johnsongrass in a johnsongrass-infested cornfield (14).

Reports from studies in a variety of crops show that alates of some aphid species prefer to land where crop rows and bare or tilled soil form a contrasting background (31). Other types of background could be vegetation, mulches, or nontilled soil.

All et al (3) observed a trend toward greater MDM incidence in no-till plots compared to conventionally tilled plots. No-till plots also had a greater infestation of johnsongrass. Studies examining the effect of removing or reducing background vegetation at various times in the growing season are lacking.

Nicosulfuron and primisulfuron are marketed for the control of johnsongrass and other weeds in corn. Both herbicides provide excellent johnsongrass control with good crop safety (7). Both are sulfonylurea herbicides that inhibit acetolactate synthase (20,22), which is required for synthesis of the essential amino acids valine, leucine, and isoleucine. Both herbicides are labeled for broadcast, postemergence application for field corn. Although growth of susceptible plants stops rapidly after treatment with either herbicide, plant death may not occur for several weeks.

This research was designed to observe the effect of johnsongrass and its postemergence control with nicosulfuron or primisulfuron on the alighting of MDMV vectors and the incidence of MDM. The objectives of this research were the following: 1) to examine how the presence of johnsongrass influenced the number of aphids alighting on corn; 2) to correlate the number of alighting aphids with MDM incidence in corn; 3) to measure changes in MDMV titer in johnsongrass treated with nicosulfuron or primisulfuron; and 4) to observe the influence of MDMV symptoms and the application of nicosulfuron on the abundance of transient and colonizing aphids on corn and johnsongrass.

MATERIALS AND METHODS

Field study. Field studies were conducted in 1990 and 1991 at the Umstead State Farm near Butner, North Carolina. Fields were 2 km apart and naturally infested with MDMV-infected rhizome johnsongrass. The presence of MDMV was confirmed serologically, and no maize chlorotic dwarf virus (MCDV) was detected with enzyme-linked immunosorbent assay (ELISA) for a limited number of tissue samples. In 1990, the test was conducted on a Congaree loam, pH 5.1 and 1.8% organic matter; and in 1991, the soil was a Wehadkee loam, pH 5.3 and 1.9% organic matter. Field plots were disked twice in the spring and fertilized according to soil-test recommendations. On 24 April 1990 and 9 May 1991, corn hybrid Pioneer Brand 3147, which is moderately resistant to MDMV (Pioneer Hi-Bred International, Johnston, IA, *personal communications*), was planted in 76-cm-wide rows, with no soil-applied insecticide, at a rate of 62,500 seeds per hectare. Plots were 15 × 15 m in 1990, and 14 × 14 m in 1991. The first and last five rows of each plot were used as a border, and a 2-m vegetation-free buffer separated plots between blocks. A broadcast, preemergence treatment of atrazine (Aatrex, 4 L, 1.1 kg a.i./ha) and alachlor (Lasso, 4 EC, 2.2 kg a.i./ha) was applied to all plots. Additional nitrogen (80 kg/ha) was applied by approximately the tenth leaf stage, and no further cultivation was used.

The treatments were full-season mechanical johnsongrass control by hand hoeing; no postemergence weed control; nicosulfuron (Accent, 75 DF) or primisulfuron (Beacon, 75 DF) applied at detection of the fifth leaf collar of corn (early application); and nicosulfuron or primisulfuron applied at detection of the

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eighth leaf collar (late application). Early and late are terms referring to the time the treatments were applied in relation to each other, not according to the manufacturer's recommended usage. Nicosulfuron and primisulfuron were applied at 35 and 40 g/ha, respectively. All herbicide treatments were applied broadcast with a nonionic surfactant (X-77, Valent, U.S.A. Corp., Walnut Creek, CA) at a rate of 0.25% v/v, delivered with a CO_2-pressurized backpack sprayer (250 kPa), in 187 L/ha, with 11002 flat-fan nozzles.

The experiments were arranged as a latin square design with six treatments. The number of johnsongrass sprigs and seedlings per square meter was visually estimated at four 1-m^2 quadrats in each plot 3 wk after planting. Johnsongrass control, rated as percent reduction in weed biomass compared to the uncontrolled check, was visually determined 2–3 wk after the late applications.

At five random locations within each plot, a wooden pole, 5 × 5 cm × 2.4 m, with holes drilled horizontally every 15 cm, was placed in the ground extending 2 m above the soil surface. Clear plastic alighting traps, 11 × 11 × 3 cm, attached to a metal pipe, were inserted into a hole in each pole (one trap per pole). This permitted traps to be repositioned weekly, to keep them in proximity to the corn whorl. The traps were filled with 1:1 ethylene glycol and water.

At approximately weekly intervals, aphids were collected from the traps and stored at 4 C until they could be counted and identified. R. Wilfert-Eckel confirmed aphid identification (North Carolina State University, Raleigh). Aphid sampling began at the sixth leaf stage of corn. Also at weekly intervals, corn plants were rated for MDM symptom incidence. At five locations in each plot, 10 consecutive corn plants were observed over the period for MDM symptoms. MDM-incidence ratings started 2 wk after late herbicide application, and evaluations continued until tasseling.

Cumulative alate aphids (CAA) and area under the disease progress curve (AUDPC) were determined (23,28). AUDPC was calculated with incidence of MDM. There were five observations for MDM incidence and aphids in 1990, and five for MDM incidence and six for aphids in 1991.

MDMV titer study. The initial source of maize dwarf mosaic virus strain A (MDMV-A) was infected tissue obtained from R. Toler (Texas A & M University, College Station). Johnsongrass seedlings grown in 18-L pots were repeatedly inoculated with MDMV-A infected corn sap and allowed to grow for 4 mo before harvesting the rhizomes. The collected rhizomes were surface-sterilized in 10% sodium hypochlorite solution for 2 min. Rhizomes were cut into 4-cm segments, each with a bud. Four rhizomes were planted per pot (22 cm tall and 22 cm in diameter) in a mixture of peat, vermiculite, and loamy sand (2:2:3 v/v/v). An average of two plants per pot emerged. Plants were maintained for the entire experiment in a greenhouse under metal halide lamps (300 $\mu E \cdot m^{-2} \cdot s^{-1}$ photosynthetic photo flux density) to extend day length to 14 hr. Day/night temperatures were approximately 30/20 C. Plants were watered once daily to excess and fertilized twice each week with 150 ppm N, 300 ppm P_2O_5, and 150 ppm K_2O.

Herbicide treatments were applied when johnsongrass had four fully expanded leaves, a label-recommended stage for treatment. Treatments were arranged as a 2 × 3 factorial with nicosulfuron and primisulfuron as the first factor and herbicide rates of 0, 0.1X, and 1X as the second factor. Rates of nicosulfuron were 3.5 g a.i./ha and 35 g a.i./ha, and rates for primisulfuron were 4 g a.i./ha and 40 g a.i./ha. The higher rate for each herbicide (1X) is the manufacturer's recommended use rate. Treatments were arranged in a randomized block design. The experiment was conducted three times with a total of eight replications. All herbicide treatments contained the nonionic surfactant X-77 at 0.25% v/v. Treatments were applied with a single nozzle (8001 even) track sprayer delivering 187 L/ha at 117 kPa.

Two leaf disks (6 mm in diameter) were taken midway between tip and base on each side of the midrib from the fifth and sixth leaves. To ensure that plants were MDMV-infected, only symptomatic plants were tested (average of two plants per pot). Subsequent samples were taken from the same leaves progressively toward the leaf base. Samples were taken just before herbicide application and 1, 3, and 7 days after treatment (DAT). Samples were collected from the same leaf because MDMV-A titer is not consistent among leaves (11,29). Disk samples from both leaves were combined and stored at −18 C until virus titer was determined.

MDMV-A titer was assayed with a modified double antibody sandwich ELISA (6). Immunolon 1 plates were coated for the modified ELISA with polyclonal MDMV-A antiserum (0.3 μg/ml) at 37 C for 2 hr and then washed with PBS-Tween (0.15 M phosphate-buffered saline, pH 7.4, containing 0.05% Tween 20). Plant extracts were prepared by pulverizing leaf disks in liquid N and grinding them in PBS-Tween (1:25, w/v). Extracts were incubated overnight in plates at 4 C, washed in PBS-Tween, and incubated in 0.3 μg/ml of the second MDMV-A antibody (conjugated with bovine intestinal alkaline phosphatase) for 2 hr at 37 C. After a standard wash, *p*-nitrophenyl phosphate substrate was added, and plates remained at 25 C for 1 hr for color development. Absorbance at 405 nm (A_{405}) was measured to determine virus titer (21).

At 7 DAT, three leaf disks (6 mm in diameter) were removed from the sixth leaf. Disks were placed in *N,N*-dimethylformamide (DMF), at one disk per milliliter of DMF, for extraction of total chlorophyll. Disks and DMF were placed in a bag to exclude light and stored at 4 C overnight. Absorbance of the DMF solution was measured at 647 and 664 nm to determine total chlorophyll content (18).

Also at 7 DAT, percent moisture was determined. Plants were cut at the soil level, and fresh weights were recorded. Excised shoots were stored at 70 C for 4 days before dry weight was determined.

Aphid-host preference study. This experiment was a 2 × 2 × 2 factorial. Treatments were arranged as a randomized block design, with 5 replications each year. The factors were the following: corn or johnsongrass; inoculated with MDMV-A or noninoculated; and treated with nicosulfuron or nontreated. Seeds were planted in pots 27 cm deep by 27 cm in diameter, filled with commercial potting soil, and initially maintained in a greenhouse under metal halide lamps (300 $\mu E \cdot m^{-2} \cdot s^{-1}$ photosynthetic photo flux density) to extend day length to 14 hr. Day/night temperatures were approximately 30/20 C. Plants were watered daily to excess and fertilized twice each week with 150 ppm of N, 300 ppm of P_2O_5, and 150 ppm of K_2O. At the two- to three-leaf stage, plants were thinned to one plant per pot. Those plants which were to be systemically infected were rub inoculated with plant sap from MDMV-infected Seneca Chief sweet corn. The initial inoculum source was obtained from R. Toler. Plants were inoculated at least twice at 2-day intervals. Approximately 14 days after planting (DAP), pots were moved outdoors and arranged 1 m equidistantly in a rectangular pattern. On 17 August 1990 (22 DAP) and 28 July 1991 (20 DAP), plants treated with nicosulfuron (35 g a.i./ha + 0.25% v/v X-77) were sprayed with a CO_2-pressured backpack sprayer delivering 187 L/ha at 250 kPa.

Beginning with the nicosulfuron application and continuing every 2–3 days until the treated johnsongrass was dead (14 DAT), aphids from individual plants were counted. Aphids were recorded as alatae or apterae, and by location on the plant. All alatae were removed at each sampling period to ensure that only transient aphids were counted. The incidence of systemic MDM symptoms was recorded before nicosulfuron application and at the end of the experiment (boot stage, 14 DAT).

A subsample of aphids was collected, and species identification was made (confirmed by R. Wilfert-Eckel).

Data analysis. Analysis of variance

(ANOVA) was performed on all data after homogeneity of variances was determined. Number of johnsongrass plants per square meter was used as a covariant for ANOVA of all field data except johnsongrass control. Because of the factorial nature of treatments in the field study, treatment degrees of freedom were partitioned into contrasts of single degrees of freedom for determination of treatment differences (25). ANOVA for johnsongrass control included only those treatments receiving a postemergence herbicide. For the MDMV titer study, ANOVA was performed with replications nested within runs. Total chlorophyll was sampled only in runs 2 and 3. Treatment means for the MDMV-A titer study were separated by Fisher's protected least significant difference test (LSD). In the aphid–host preference study, apterous aphids were analyzed with repeated measures (25). Alate aphids were analyzed as cumulative alate aphids (CAA). Because of year-by-treatment interactions, each year was analyzed separately for field and aphid–host preference studies.

Table 1. Postemergence johnsongrass control in corn with nicosulfuron and primisulfuron at Umstead State Farm, 1990 and 1991[x]

Treatment[y]	Johnsongrass control[z] (%) 1990	1991
Nicosulfuron early	91	98
Primisulfuron early	93	95
Nicosulfuron late	86	86
Primisulfuron late	79	84
Standard errors	3	2

[x]Comparisons between years are not valid.
[y]Early treatments were applied at detection of fifth leaf collar of corn, and late treatments were applied at detection of eighth leaf collar.
[z]Reduction in biomass.

RESULTS

Field study. Weed control with a postemergence herbicide treatment ranged from 79 to 91% reduction in johnsongrass biomass in 1990, and from 84 to 98% in 1991 (Table 1). In both years, there was no difference between treatments with nicosulfuron or primisulfuron. In both years, better johnsongrass control was obtained when either herbicide was applied early.

Macrosiphum and *Rhopalosiphum* were the predominant genera of alate aphids identified in 1990, at 24 and 23%, respectively (total of 109 aphids collected). *Rhopalosiphum* species comprised 47% of the identified aphids in 1991 (total of 16 aphids collected).

In 1990, more alate aphids, as determined by CAA, were found in aphid traps in weed-free plots (Table 2). Nicosulfuron- or primisulfuron-treated plots had similar numbers of alatae in aphid traps, and weedy plots had the fewest aphids. The correlation between johnsongrass control and CAA was highly significant ($\alpha = 0.002$ and $R = 0.54$).

In 1991, only 16 alate aphids were found in aphid traps throughout the study. This is reflected in the lower incidence of MDM in 1991 compared to 1990 (Table 2). No significant differences among treatments were detected, with a CAA range from 1 to 3. Other researchers observed low aphid populations early in the 1991 growing season in the same county (R. Wilfert-Eckel, *personal communications*).

In both years MDM incidence, as measured by AUDPC, was lower for plots receiving an early application of either nicosulfuron or primisulfuron, than for plots receiving late applications (Table 2). Also in 1991, MDM was more prevalent when johnsongrass was not controlled than when it received postemergence herbicide applications. Earlier onset of MDMV infection can increase the severity of MDM. AUDPC accounts for the time of infection by incorporating time of disease onset, rate of increase, and final MDM incidence. In both years, the correlation between CAA and AUDPC was not significant.

MDMV titer study. No significant difference in MDMV was detected when plants were treated with either nicosulfuron or primisulfuron. Herbicide rate was the only significant factor in all measurements and thus will be the only effect discussed. The 0.1X and 1X rates caused plant growth to cease at the time of treatment, while plants without a herbicide application continued to grow and developed two new leaves by 7 DAT. At 7 DAT the 1X rate caused treated plants to become flaccid and necrotic with a considerable amount of purple discoloration in the leaves. Plants treated with 0.1X rate showed some reddening of leaf margins, but the plants never became flaccid. Total chlorophyll, a method used to measure tissue senescence (19), was similar for the 0 and 0.1X rates, and lowest for the 1X rate (Table 3). As the rate of herbicide increased, moisture content decreased.

At 1 and 3 DAT, there were no significant differences among treatments in johnsongrass analyzed for MDMV titer, although there appeared to be a rate response (Table 4). At 7 DAT, MDMV titer in samples treated at a 1X rate was significantly higher than in plants not treated. There was a poor correlation between virus titer at 7 DAT and total chlorophyll, $R = -0.4$. Correlation between percent moisture and virus titer at 7 DAT was not significant ($\alpha = 0.9$).

Aphid-host preference study. In 1990 and 1991, *R. maidis* was the only aphid species in the samples. In 1990, more alate *R. maidis* were found on corn plants than on johnsongrass (Fig. 1). In 1991, similar numbers of *R. maidis* were found on corn plants and johnsongrass not treated with nicosulfuron.

Table 2. Treatment means and analysis of variance (ANOVA) for cumulative alate aphid numbers (CAA) on corn and area under disease progress curve (AUDPC)[w], when johnsongrass is controlled with nicosulfuron or primisulfuron, for 1990 and 1991[x]

Treatment	df	CAA 1990	CAA 1991	AUDPC 1990	AUDPC 1991
Means[y]					
Weed-free (hand hoed)		39	2	106	54
Nicosulfuron early		22	3	87	40
Primisulfuron early		26	2	89	26
Nicosulfuron late		17	1	139	100
Primisulfuron late		17	2	134	114
Weedy		10	2	137	139
ANOVA ($P > F$)[z]	5	0.005	0.723	0.036	0.001
Weedy vs. herbicides	1	0.037	0.901	0.160	0.001
Weed-free vs. herbicides	1	0.006	0.841	0.770	0.361
Herbicide	1	0.580	0.999	0.918	0.938
Application time	1	0.113	0.205	0.006	0.001
Applic. time vs. herbicide	1	0.678	0.387	0.805	0.216

[w]Based on incidence of maize dwarf mosaic.
[x]Comparisons between years are not valid.
[y]Early treatments were applied at detection of fifth leaf collar of corn and late treatments were applied at detection of eighth leaf collar.
[z]Treatment degrees of freedom are partitioned into contrasts of single degrees for determination of treatment differences. Values are alpha levels for each source of variation. Alpha levels less than or equal to 0.05 are considered significant.

Table 3. Measurements of senescence of johnsongrass treated with nicosulfuron or primisulfuron at three rates. Because of lack of significance, data are averaged over herbicide. Parameters measured seven days after treatment[z]

Herbicide rate	Total chlorophyll ($\mu g/cm^2$)	Moisture (%)
0	15.0 a	87.2 a
0.1X	13.3 a	83.1 b
1.0X	8.9 b	80.3 c
LSD ($\alpha = 0.05$)	3.0	1.5

[z]0.1X rates of nicosulfuron and primisulfuron are 3.5 g a.i./ha and 4.0 g a.i./ha, respectively. 1X rates of nicosulfuron and primisulfuron are 35 g a.i./ha and 40 g a.i./ha, respectively.

Table 4. Enzyme-linked immunosorbent assay (ELISA) of maize dwarf mosaic virus (MDMV) titer in johnsongrass treated with nicosulfuron or primisulfuron at three rates, as measured at A_{405}[w]. Because of lack of significance, data are averaged for the two herbicides

Herbicide rate[x]	MDMV titer (A_{405})			
	0 DAT[y,z]	1 DAT	3 DAT	7 DAT
0	0.228	0.267	0.216	0.260 a
0.1X	0.241	0.277	0.268	0.326 ab
1.0X	0.228	0.292	0.302	0.421 b
LSD ($\alpha = 0.05$)	NS	NS	NS	0.100

[w] Comparisons between days are not valid.
[x] 0.1X rates of nicosulfuron and primisulfuron are 3.5 g a.i./ha and 4.0 g a.i./ha, respectively. 1.0X rates of nicosulfuron and primisulfuron are 35 g a.i./ha and 40 g a.i./ha, respectively.
[y] Days after treatment.
[z] 0 DAT samples were taken just before treatment.

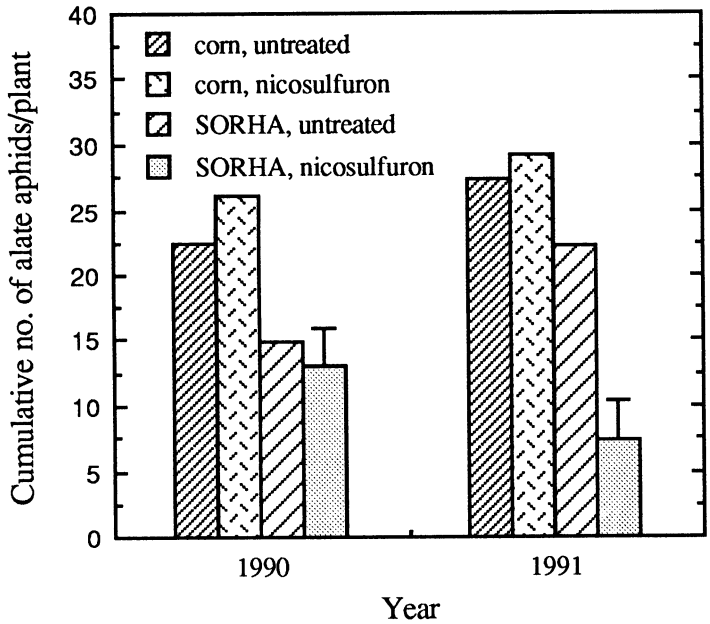

Fig. 1. Cumulative alate *Rhopalosiphum maidis* on corn or johnsongrass (SORHA), treated or not treated with nicosulfuron. Data are averaged over presence or absence of MDMV-A symptoms. Vertical bars represent standard error of the means, 2.8 for 1990 and 3.4 for 1991.

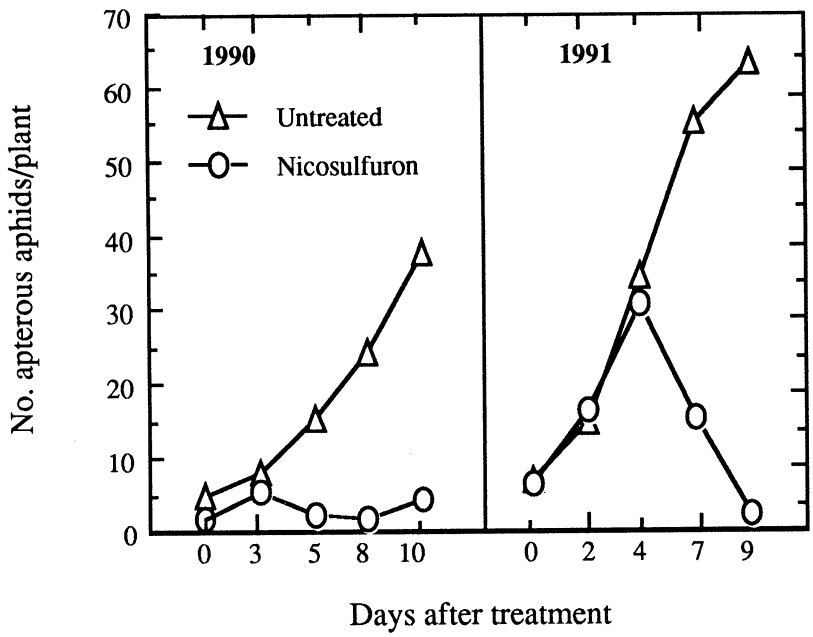

Fig. 2. Number of apterous *Rhopalosiphum maidis* on johnsongrass treated or not treated with nicosulfuron in 1990 and 1991. Data are averaged over presence or absence of MDMV-A.

In both years, 94% of the alate aphids were found on leaf tissue above the newest leaf collar of both corn and johnsongrass. Alate aphids were observed on nicosulfuron-treated johnsongrass up to 11 DAT both years, at which time the majority of leaf tissue was necrotic.

In both years of this study, aphids did not colonize corn plants, and as a result the ANOVA for apterae included only johnsongrass. Apterae were found only on young tissue of the main stem or tillers, often within rolled, emerging leaves. In both years, the interaction of sampling time and the application of nicosulfuron was significant (Fig. 2). With time, the number of apterous *R. maidis* increased on johnsongrass not treated with nicosulfuron. The number of apterae on nicosulfuron-treated johnsongrass peaked at 3–4 DAT and then declined. However, at 9 DAT in 1990 and 10 DAT in 1991, apterous aphids were observed on nicosulfuron-treated johnsongrass.

At the time of nicosulfuron application, only those plants inoculated with MDMV-A exhibited systemic MDMV symptoms. However, by 10 DAT all corn plants exhibited systemic MDMV symptoms. Only two johnsongrass plants not inoculated in 1990, and no plants in 1991, exhibited MDMV symptoms. The presence of MDMV symptoms was not significant in the ANOVA for the number of alate or apterous aphids in either year.

DISCUSSION

The number of winged aphids collected was highest in weed-free plots, less in all plots treated with a postemergence herbicide, and least in nontreated plots. Vectors of MDMV may be attracted to areas with a crop row and a contrasting background (9,24,31).

In contrast to previous reports, there was not a positive correlation between MDM incidence and number of vectors (15,16,26). Those studies were conducted in relatively weed-free plots and utilized painted yellow water traps that can bias the number and species of aphids collected (10). The traps used in this study were selected as a neutral surface that neither repelled nor attracted alighting aphids. Weed-free conditions may have increased the probability of an aphid alighting in a trap, because of the contrast between corn rows and the bare soil between rows. The amount of background vegetation may explain why more aphids were found in plots where a postemergence herbicide was applied than in weedy, nontreated plots. Alternatively, aphids may prefer johnsongrass over corn for colonization, as documented in the aphid–host preference study. As a result, once alatae probed johnsongrass, they continued to feed and were less likely to continue to search for a more suitable colonizing host.

Tu and Ford (29,30) have shown that transmission of MDMV is closely associated with MDMV titer. As MDMV titer increased, transmission efficiency also increased. Chlorsulfuron, another sulfonylurea herbicide, rapidly inhibited cell division but did not inhibit protein or RNA synthesis (4). Thus, if RNA and protein synthesis are still active after treatment with a sulfonylurea herbicide, viral replication may continue unimpeded while MDMV-infected johnsongrass declines; and johnsongrass can still serve as a source of inoculum for the aphid vector. This may pose a significant disease-management problem, because johnsongrass treated with either herbicide may not die for 2–3 wk after treatment. Alate aphids were documented on necrotic johnsongrass tissue 14 DAT.

The increase in MDMV titer observed in nicosulfuron- or primisulfuron-treated tissue may be the result of continued viral replication with no virus transport to new tissues because no cell division is occurring; or flaccid tissue may have meant more cells in treated than in nontreated samples, resulting in a higher MDMV-A titer. However, in relation to epidemiology, either situation increases the likelihood of an aphid acquiring MDMV while probing nicosulfuron- or primisulfuron-treated tissue.

The incidence of MDM was greater in plots with more johnsongrass biomass. This is probably because of the close proximity of a source of MDMV inoculum to the corn. Knoke et al (13) found that MDM incidence decreased in sampled plants farther from the MDMV source. A viruliferous aphid loses the ability to cause infection with successive probes into healthy tissue (17). Although fewer aphids alighted in the weedy plots, we hypothesize that the aphids were viruliferous from feeding on nearby infected johnsongrass. We further hypothesize that if an aphid probed an MDMV-infected johnsongrass plant treated with nicosulfuron or primisulfuron, it may have acquired the virus more readily than from nontreated johnsongrass. The titer of MDMV-infected johnsongrass may increase after an application of nicosulfuron or primisulfuron, and a higher titer may increase acquisition of the virus (29,30).

It is difficult to account for the slight increase in AUDPC for weed-free treatments compared to early herbicide applications. This was consistent in both years and should be examined further.

Alate aphids are believed to be the cause of primary MDMV infection in areas without johnsongrass (1,2). However, the possibility of apterous aphids forced to leave johnsongrass treated with a herbicide cannot be ruled out as a possible form of virus spread within a johnsongrass-infested field. Most studies examining the relative contributions of alatae versus apterae for viral spread have utilized insecticides to control colonizing aphids on the crop plant. As observed in the aphid–host preference study, apterous aphids can be found in rolled, emerging leaf tissue, which makes chemical control of the aphids difficult. Wollcott (32) hypothesized that hoeing grass weeds in sugarcane (*Saccharum officinarum* L.) fields increased "mosaic diseases" because aphids were forced to move from the weed host to sugarcane plants. In a field situation, if the postemergence application of either nicosulfuron or primisulfuron is delayed, leaves of corn and johnsongrass could overlap and facilitate apterae movement. This scenario merits further research.

Different genotypes of *R. maidis* have been shown to be host selective for colonization (5). The *R. maidis* sampled in the aphid–host preference study were not identified to genotype. Our observations corroborate those of Kieckhefer and Gellner (12), who reported that corn leaf aphid (nonspecified genotype) failed to reproduce on seedling corn but readily colonized a sorghum species (grain sorghum, *S. bicolor*).

Understanding the behavior of aphids in a johnsongrass-infested corn field would further our knowledge of plant-to-plant movement of aphids. It may also explain inconsistencies between aphid numbers and MDM incidence. Yet from a production standpoint, early application of nicosulfuron or primisulfuron for johnsongrass control eliminates a source of MDMV-A and a host for MDMV vectors, and reduces weed competition for space. Early postemergence control of MDMV-infected johnsongrass with nicosulfuron or primisulfuron may reduce MDM incidence in corn.

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LITERATURE CITED

1. Alexander, J. D., and Toler, R. W. 1987. Primary infection and spread of maize dwarf mosaic virus in sorghum in central Texas. (Abstr.) Phytopathology 77:1730.
2. Alexander, J. D., and Toler, R. W. 1989. Relative importance of transient versus resident aphids in the spread of maize dwarf mosaic virus in sorghum. (Abstr.) Phytopathology 79:1189.
3. All, J. N., Kuhn, C. W., Gallaher, R. N., Jellum, M. D., and Hussey, R. S. 1977. Influence of no-tillage-cropping, carbofuran, and hybrid resistance on dynamics of maize chlorotic dwarf and maize dwarf mosaic diseases in corn. J. Econ. Entomol. 70:221-225.
4. Beyer, E. M., Duffy, M. J., Hay, J. V., and Schlueter, D. D. 1988. Sulfonylureas. Pages 117-189 in: Herbicides: Chemistry, Degradation, and Mode of Action. Vol. 3. P. C. Kearney and D. D. Kaufman, eds. Marcel Dekker, New York.
5. Blackman, R. L., Halbert, S. E., and Carroll, T. W. 1990. Association between karyotype and host plant in corn leaf aphid (Homoptera: Aphididae) in the northwestern United States. Environ. Entomol. 19:609-611.
6. Clark, M. F., and Adams, A. N. 1977. Characteristics of the microplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. J. Gen. Virol. 34:475-483.
7. Foy, C. L., and Witt, H. L. 1990. Johnsongrass control with DPX-V9360 and CGA-136872 in corn (*Zea mays*) in Virginia. Weed Technol. 4:615-619.
8. Gordon, D. T., Bradfute, O. E., Gingery, R. E., Knoke, J. K., Louie, R., Nault, L. R., and Scott, G. E. 1981. Introduction: History, geographical distribution, pathogen characteristics, and economic importance. Pages 1-12 in: Virus and Viruslike Diseases of Maize in the United States. D. T. Gordon, J. K. Knoke, and G. E. Scott, eds. South. Coop. Serv. Bull. 247.
9. Horn, D. J. 1981. Effect of weedy backgrounds on colonization of collards by green peach aphid, *Myzus persicae,* and its major predators. Environ. Entomol. 10:285-289.
10. Irwin, M. E., and Schultz, G. A. 1981. Soybean mosaic virus. FAO Plant Prot. Bull. 29:41-55.
11. Jensen, S. G., Palomar, M. K., Ball, E. M., and Samson, R. 1985. Factors influencing virus titer in maize dwarf mosaic virus-infected sorghum. Phytopathology 75:1132-1136.
12. Kieckhefer, R. W., and Gellner, J. L. 1988. Influence of plant growth stage on cereal aphid reproduction. Crop Sci. 28:688-690.
13. Knoke, J. K., Louie, R., Madden, L. V., and Gordon, D. T. 1983. Spread of maize dwarf mosaic virus from johnsongrass to corn. Plant Dis. 67:367-370.
14. Kuhn, C. W., Jellum, M. D., and All, J. N. 1975. Effect of carbofuran treatment on corn yield, maize chlorotic dwarf and maize dwarf mosaic virus diseases, and leafhopper populations. Phytopathology 65:1017-1020.
15. Madden, L. V., Knoke, J. K., and Louie, R. 1983. The statistical relationship between aphid trap catches and maize dwarf mosaic virus inoculation pressure. Pages 159-168 in: Plant Virus Epidemiology. R. T. Plumb and J. M. Thresh, eds. Blackwell Scientific Publications, Oxford.
16. Madden, L. V., Louie, R., and Knoke, J. K. 1987. Temporal and spatial analysis of maize dwarf mosaic epidemics. Phytopathology 77:148-156.
17. Messieha, M. 1967. Aphid transmission of maize dwarf mosaic virus. Phytopathology 57:956-959.
18. Moran, R. 1982. Formulae for determination of chlorophyllous pigments extracted with *N,N*-dimethylformamide. Plant Physiol. 69:1376-1381.
19. Nooden, L. D. 1988. The phenomena of senescence and aging. Pages 1-50 in: Senescence and Aging in Plants. L. D. Nooden and A. C. Leopold, eds. Academic Press, San Diego, CA.
20. Obrigawitch, T. T., Kenyon, W. H., and Kuratle, H. 1989. Effect of application timing on rhizome johnsongrass, *Sorghum halepense* control with DPX-V9360. Weed Sci. 38:45-49.
21. Olson, A. J., Pataky, J. K., D'Arcy, C. J., and Ford, R. E. 1990. Effects of drought stress and infection by maize dwarf mosaic virus on sweet corn. Plant Dis. 74:147-151.
22. Porpiglia, P. J., Collins, H. A., Peek, J. W., Iwanzik, W., Seiler, A., and Maurer, W. 1988. CGA-136872 - a new corn herbicide. (Abstr.) Weed Sci. Soc. Am. 28:14.
23. Ruppel, R. F. 1983. Cumulative insect-days as an index of crop protection. J. Econ. Entomol. 76:375-377.
24. Smith, J. G. 1976. Influence of crop background on aphids and other phytophagous insects on Brussels sprouts. Ann. Appl. Biol. 83:1-13.
25. Steel, R. G. D., and Torrie, J. H. 1980. Principles and Procedures of Statistics. 2nd ed. McGraw-Hill, New York.
26. Straub, R. W., and Boothroyd, C. W. 1980. Relationship of corn leaf aphid and maize dwarf mosaic disease to sweet corn yields in southeastern New York. J. Econ. Entomol. 73:92-95.
27. Swenson, K. G. 1968. Role of aphids in the ecology of plant viruses. Annu. Rev. Phytopathol. 6:351-374.
28. Tooley, P. W., and Grau, C. R. 1984. Field characterization of rate-reducing resistance to *Phytophthora megasperma* f. sp. *glycinea* in

soybean. Phytopathology 74:1201-1208.
29. Tu, J. C., and Ford, R. E. 1969. Infectivity changes of maize dwarf mosaic virus in vivo and in vitro. Phytopathology 59:1947-1949.
30. Tu, J. C., and Ford, R. E. 1971. Factors affecting aphid transmission of maize dwarf mosaic virus to corn. Phytopathology 61:1516-1521.
31. Williams, R. D. 1981. Complementary interactions between weeds, weed control practices, and pests in horticultural cropping systems. HortScience 16:508-513.
32. Wollcott, G. N. 1928. Increase of insect transmitted plant disease and insect damage through weed destruction in tropical agriculture. Ecology 9:461-466.