Effects of Drought Stress and Infection by Maize Dwarf Mosaic Virus on Sweet Corn

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ABSTRACT

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Infection of sweet corn (*Zea mays* L.) by maize dwarf mosaic virus (MDMV) and drought stress imposed during vegetative (early-stress) or reproductive (late-stress) growth stages were additive in their effects on ear and plant characteristics. Weight of ears was reduced 16% by MDMV in 1984 and 22% in 1985. Butt blanking of ears was increased by early stress in 1984 and by MDMV in both years. Leaf area was reduced 15 and 37% by early stress in 1984 and 1985, respectively; 13% by late stress in 1984; and 8 and 11% by MDMV in 1984 and 1985, respectively. Early stress reduced plant height by 7% in 1984 and by 22% in 1985. Reductions in plant height due to MDMV were 4% in 1984 and 23% in 1985. Sugar content of kernels was not affected by drought stress or MDMV. Titer of MDMV was not affected by drought stress.

Additional keyword: sugars

Yield, plant height, and grain fill of corn (*Zea mays* L.) can be reduced by infection of plants with maize dwarf mosaic virus (MDMV) (8,11,15,16,18) and by drought stress (5,6,14). The effects on corn of MDMV infection and drought stress have been documented individually, but relatively few researchers have investigated interactions between the two stresses. Such interactions may be important in drought years (such as 1988 in the United States corn belt) because of possible increases in MDMV inoculum caused by higher populations of viruliferous vectors associated with drought.

The results from previous studies of drought and MDM are varied. Lindsey and Gudauskas (12) observed that leaves of corn plants infected by MDMV have lower rates of water transpiration and higher water potentials than leaves of noninfected plants. Also, leaves of infected plants that were drought stressed remained turgid longer than leaves of stressed healthy plants, which may indicate that MDMV infections reduce the severity of drought stress. Kuhn and Jellum (11) suggested that the combined effects of MDM and drought stress on

the vegetative growth of dent corn were less than additive; however, Nelms et al (19) observed infection by MDMV and drought stress to be additive in their effects on yield of sweet corn.

In addition to yield, sweetness of kernels is an important element of the quality of sweet corn. Carey et al (4) determined that infection by MDMV did not affect the sugar content of sweet corn kernels. Similarly, Maranville and Paulsen (13) observed that drought stress did not affect sugar levels in corn leaves. However, the effects of drought stress on sugar content of kernels have not been determined.

In this study, we examined yield, vegetative growth of plants, sugar content of kernels, and titer of MDMV to determine whether infection by MDMV and drought stress interacted in their effects on sweet corn.

MATERIALS AND METHODS

Seed was hand-planted on 28 May 1984 and 17 May 1985 at the University of Illinois Sand Farm at Kilbourne. The soil was a Plainfield sand (97% sand) with low water-holding capacity, which ensured that drought stress could be managed. In 1984, we grew three "sugary" sweet corn hybrids (Sundance, Cherokee, and Gold Cup) that are homozygous-recessive for the *sugary-1* (*su*) endosperm mutation and one "supersweet" hybrid (Florida Staysweet) that is homozygous-recessive for the *shrunken-2* (*sh2*) endosperm mutation. Previously, Sundance and Cherokee were classified tolerant to MDMV, and Gold Cup and Florida Staysweet were

considered susceptible (15). Cherokee and Gold Cup were grown in 1985.

Treatment designs were $3 \times 4 \times 2$ and $3 \times 2 \times 2$ factorials of drought-stress treatments $\times$ hybrids $\times$ viral treatments in 1984 and 1985, respectively. Treatments were arranged in a split-split plot experimental design with four replications. Drought-stress treatments were applied to main plots. Hybrids were grown in subplots. Viral treatments were applied to sub-subplots. Main plots were arranged in a randomized complete-block design. Each experimental unit (sub-subplot) consisted of three 6.1-m rows. Data were collected from the middle row of each experimental unit; the outer two rows were borders. Plants were spaced about 30 cm apart in rows and there was approximately 76 cm between rows.

Irrigation was supplied by a 1.8-m overhead sprinkler system. One sprinkler was placed in the middle of each main plot in 1984. Four sprinklers were placed in the corners of each main plot in 1985. We used three drought-stress treatments: no drought stress (adequate water throughout the growing season), early drought stress (drought stress during the vegetative phase of plant growth), and late drought stress (drought stress during the reproductive phase of plant growth) (Table 1). Irrigation was withheld from the early-stress treatments six times between 13 June and 15 July 1984 and three times between 6 June and 11 July 1985. Irrigation was withheld from the late-stress treatments 10 times between 16 July and 22 August 1984 and four times between 12 July and 9 August 1985. During the first 2 wk after planting, all plots were irrigated six or seven times to ensure good seed germination and seedling vigor. Two samples of soil in each main plot were taken at random with soil augers about every 7 days between 21 June and 8 August 1984. Soil moisture was calculated as the percent dry weight of the samples by drying the soil in an oven at 105 C until a constant weight was reached. The average percentage of moisture loss per day was determined for the periods 21 June to 19 July and 20 July to 8 August 1984. Soil moisture was not measured in 1985.

Plants at the two- to three-leaf stage were inoculated on 15 June 1984 and 6 June 1985 with a mixture of MDMV

strains A and B, which occur naturally in Illinois. Preparation of inoculum and mechanical inoculation were as described by Mikel et al (16). Symptomless plants in inoculated plots and symptomatic plants in noninoculated plots were removed from the experiment throughout the study to ensure that inoculated and noninoculated plots were 100% infected and MDMV-free, respectively, at the time of data collection. Fewer than four plants were removed from any plot.

Plants were sampled on 22 and 26 July and on 2 August 1985 to determine titer of MDMV. Eight symptomatic plants and four symptomless plants were sampled per experimental unit for inoculated and noninoculated treatments, respectively. Five 6-mm leaf disks were collected from the youngest fully expanded leaf of each plant. The samples were analyzed by the enzyme-linked immunosorbent assay (ELISA) protocol described by Romaine et al (20) using antisera to MDMV strains A and B.

Height of plants from the soil surface to the lowest branch of the tassel was measured after anthesis for 15 plants per experimental unit in 1984 and for 10 plants per unit in 1985. Ears were harvested 21 days after midsilk from 15 plants per experimental unit in 1984 and from 10 plants per unit in 1985. Butt blanking (the number of undeveloped kernels in the basal quarter of the ear) was measured for all ears that were harvested. All leaves above the primary ear were removed at harvest from five plants per experimental unit and measured on a Li-Cor model LI 3100 leaf area meter .

To measure the sugar content of kernels at harvest, one ear from each experimental unit was frozen in liquid nitrogen for 1 min immediately after removal from the stalk. The ear was then placed in dry ice, transferred to a freezer, and stored at −80 C until analysis. To extract sugars, frozen kernels were removed from ears using a screwdriver. Five grams of frozen kernels per ear were

dried at 50 C for 2 days to determine the percent dry weight. For sugar analysis, another 5-g sample was placed in a stainless steel Sorvall Omnimixer centrifuge tube to which 25 ml of 80% ethanol was added. The tube was then placed in boiling water until the alcohol began to boil. The boiled kernels were crushed with a large tissue homogenizer and blended in an Omnimixer for 2 min. Tube contents were centrifuged for 6 min at 17,000 rpm in a Sorvall SS-34 rotor, and the supernatant was decanted into a volumetric flask. The pellet was resuspended in 25 ml of 80% ethanol and centrifuged again for 6 min at 17,000 rpm. Two additional resuspensions were done to yield 100 ml of supernatant. The extracts were stirred and then poured into vials, which were sealed with Parafilm and stored at 22 C until chromatographic analysis.

For the chromatographic analysis, 200 μl of ethanol extracts was placed in 250-μl crimp-top Reacti-vials. Most samples were analyzed once, with three or four subsamples per run. Opened vials were dried overnight in a forced-air oven at 50 C and capped immediately upon removal from the oven to prevent condensation. Sugar derivatives were prepared by injecting 50 μl of Stoxoxime internal standard reagent into the samples with a Hamilton syringe and heating for 15 min at 70 C. Samples were vortexed until the sugars were dissolved, then injected with 50 μl of trimethylsilyl imidazole. The samples were vortexed again and allowed to sit for at least 15 min, but not for more than 24 hr. A Hewlett-Packard model HP 5790-A gas chromatograph (gc) was used with the chromatography program described by Ferguson et al (7).

Concentrations of sucrose, glucose and fructose, which spanned the range of the concentrations found in the samples, were prepared as standards. Sugar concentrations of samples were determined from gc peak areas as compared to the standards; they were

expressed as sugar content of kernels on a percent dry weight basis.

All data were analyzed by analysis of variance according to the factorial treatment design and split-split plot experimental design.

RESULTS

Drought stress treatments were effective in both 1984 and 1985, although stress varied between years. The effects of the early-stress treatment were more severe in 1985 than in 1984, although curling and discoloration of leaves and stunting of plants were pronounced in both years. Plants subjected to the early-stress treatment received 47 and 34 cm^3 of water during the early-stress periods in 1984 and 1985, respectively; plants subjected to the no-stress and late-stress treatments received 127 and 71 cm^3 of water during the early-stress periods in 1984 and 1985, respectively (Table 1). Conversely, the effects of the late-stress treatment were more severe in 1984 than in 1985. Plants in late-stress plots had to be irrigated on 7 August 1984 to prevent death of plants. On the other hand, plants in late-stress plots received 84 cm^3 of rain during a 17-day period in 1985. Plants in the the late-stress treatment received 60 cm^3 of water during the late-stress period in 1984 and 94 cm^3 during the 1985 late-stress period. Plants in the the no-stress and early-stress treatments received 241 and 186 cm^3 of water during the late-stress periods in 1984 and 1985, respectively. In 1984, the total amount of water per plot was 404 cm^3 for the no-stress treatments, 324 cm^3 for the early-stress treatments, and 223 cm^3 for the late-stress treatments. In 1985, the water amounts were 314, 277, and 222 cm^3, respectively (Table 1).

In 1984, plants in the early-stress plots were not stressed until late in the early-stress period (based on soil moisture data), but plants in the late-stress plots were stressed throughout most of the late-stress period. Average daily moisture loss was 1.6% between 21 June and 19 July in the early-stress treatments and 1.1% between 20 July and 8 August in the late-stress treatments. Soil moisture fluctuated from near saturation after irrigation or rainfall to minimum soil moistures just prior to the next irrigation or rainfall.

Yield. Based on the ANOVA for weight of ears, the main effect of infection by MDMV was significant in both years, the main effect of hybrids was significant in 1985, and the drought stress × hybrid interaction was significant in 1984. Interactions between drought stress and infection by MDMV were not significant. Ears from plants infected by MDMV weighed 16 and 22% less than ears from uninfected plants in 1984 and 1985, respectively (Table 2). Ears from the hybrid Gold Cup weighed

Table 1. Irrigation and rainfall amounts during the study of the effects of drought stress and infection by maize dwarf mosaic virus on sweet corn

Year and plant growth stage	Dates	Total water and events per stress type					
		No stress		Early stress[a]		Late stress[b]	
1984							
Germination	30 May–12 June	36[c]	(8)[d]	36	(8)	36	(8)
Vegetative growth	13 June–15 July	127	(16)	47	(10)	127	(16)
Reproductive growth	16 July–22 August	241	(17)	241	(7)	60	(17)
Total water	30 May–22 August	404		324		223	
1985							
Germination	17 May–5 June	57	(7)	57	(7)	57	(7)
Vegetative growth	6 June–11 July	71	(13)	34	(10)	71	(13)
Reproductive growth	12 July–9 August	186	(15)	186	(15)	94	(11)
Total water	17 May–9 August	314		277		222	

[a] Drought stress during vegetative stage of plant growth.
[b] Drought stress during reproductive stages of plant growth.
[c] Total water (irrigation + rainfall) in cubic centimeters.
[d] Total number of irrigation and rainfall events.

12% less than those from Cherokee in 1985, but ear weight did not differ significantly among any of the four hybrids in 1984 (Table 2). In 1984, when the drought stress × hybrid interaction was significant, reductions in ear weight due to early and late stress were about equal for Cherokee, greater for early stress than late stress for Sundance, and greater for late stress than early stress for Gold Cup (Table 3). In both years, mean weights of ears from early-stress plots were less than those from no-stress plots (Table 2), but the main effect of drought stress was not significant.

Butt blanking. The number of undeveloped kernels in the basal quarter of the ear was significantly affected by drought-stress treatments, hybrids, and infection by MDMV in 1984 and by hybrids and infection in 1985. Interactions between drought stress and MDMV infection were not significant. In 1984, butt blanking was greater on ears from plants subjected to the early-stress treatment than on those in the the no-stress treatment (Table 2). Butt blanking was greatest for Florida Staysweet, intermediate for Cherokee and Sundance, and least for Gold Cup in 1984 (Table 2). In 1985, butt blanking also was less for Gold Cup than for Cherokee. In 1984, plants not infected by MDMV had 19% fewer undeveloped kernels in basal portion of the ear than plants that were inoculated; in 1985, plants not infected had 65% fewer undeveloped kernels (Table 2).

Leaf area. Drought stress, hybrids, and infection by MDMV significantly affected leaf area in both years without there being any significant interactions among these variables. Leaf areas of plants from the early-stress treatment were reduced by 15% in 1984 and by 37% in 1984 compared to plants from the no-stress treatment (Table 2). Leaf areas of plants from the late-stress treatment were reduced by 13% in 1984 but were 8% larger than those from the no-stress treatment in 1985. Infection by MDMV reduced leaf area by 8 and 11% in 1984 and 1985, respectively (Table 2). Differences in leaf area were observed among hybrids in both years (Table 2). In both years, Cherokee had a larger leaf area than Gold Cup. In 1984, leaf area of Florida Staysweet was largest and leaf area of Sundance was smallest.

Plant height. Early stress and MDMV infection reduced the height of plants in both years (Table 2), but there were no drought stress × infection interactions. Plant heights differed significantly among hybrids in 1984 but not in 1985 (Table 2).

Sugar content. Sugar content of kernels (sucrose, glucose, and fructose) was not affected by drought stress or MDMV infection (Table 2). Florida Staysweet, a *shrunken-2* hybrid, had higher levels of kernel sugars than the

other hybrids, which are *sugary-1* endosperm mutants.

Titer of MDMV. Titer of MDMV was similar for all drought stress treatments at each sampling date (Table 4). Titer of MDMV was similar for Cherokee and Gold Cup on 22 July and 2 August 1985 but was higher for Cherokee on 26 July 1985 (Table 4).

DISCUSSION

Effects of drought stress and infection by MDMV on sweet corn were additive. As a result, the effects of MDM on sweet corn were not affected by drought stress and the effects of drought stress on sweet corn were not affected by MDM. In 1985, for example, leaf area of plants was reduced 167 cm² by MDM and 567 cm² by early stress; thus, an additive model would predict that leaf area would be reduced by 734 cm² in plants that are both infected by MDMV and subjected to early stress. In fact, the leaf areas of uninfected, unstressed plants of Chero-

kee and Gold Cup were 675 and 812 cm² greater, respectively, than leaf areas on infected plants of those hybrids that were stressed early. Similar comparisons can be made for other dependent variables. These results corroborate the nonreplicated, unrepeated findings of Nelms et al (19), in which the effects of MDMV and drought stress on yield and butt blanking of sweet corn were additive.

Inferences made from the statistical analyses of the effects of drought stress on yield may have been affected by our experimental design. In split-plot designs, differences among treatments in subplots are more easily detected than those in main plots. In this study, the major objective was to test drought stress × MDMV interactions, so drought stress treatments were randomized among main plots and MDMV treatments were randomized among sub-subplots. Weights of ears did not differ significantly among stress treatments even though these differences in ear weight

Table 2. Effects of drought stress, hybrids, and infection by maize dwarf mosaic virus on weight of sweet corn ears, butt blanking of ears, leaf area of plants, height of plants, and sugar content of kernels

Year and main effect treatments	Weight of ears (g)	Butt blanking[v]	Leaf area (cm²)	Plant height (cm)	Kernel sugars[w] (%)
1984					
No stress	140	20 a[x]	1,254 a	146 a	25 a
Early stress[y]	122	31 b	1,065 b	136 b	24 a
Late stress[z]	113	24 ab	1,086 b	145 a	22 a
Cherokee	131	21 b	1,141 b	145 b	19 b
Florida Staysweet	118	38 c	1,503 a	139 c	40 a
Gold Cup	128	12 a	1,023 c	148 a	17 b
Sundance	121	29 b	884 d	138 c	18 b
Noninoculated	134 a	22 a	1,179 a	146 a	24 a
Inoculated	113 b	27 b	1,090 b	140 b	24 a
1985					
No stress	152 a	14 a	1,518 b	142 a	21 a
Early stress[y]	122 a	11 a	951 c	111 b	19 a
Late stress[z]	157 a	10 a	1,651 a	135 a	20 a
Cherokee	153 a	14 b	1,518 a	128 a	18 a
Gold Cup	134 b	9 a	1,228 b	132 a	21 a
Noninoculated	161 a	6 a	1,457 a	146 a	20 a
Inoculated	126 b	17 b	1,290 b	113 b	20 a

[v] The number of undeveloped kernels in the basal quarter of the ear.
[w] Sucrose, glucose, and fructose content as the percent dry weight of kernel.
[x] Numbers followed by the same letter are not different statistically for comparison within groups of main effect treatments. Numbers not followed by letters should not be compared as main effects because of significant interactions.
[y] Drought stress during vegetative stage of plant growth.
[z] Drought stress during reproductive stages of plant growth.

Table 3. Weight of ears (g) of four sweet corn hybrids subjected to three drought-stress treatments in 1984

	Hybrid			
Drought stress	Cherokee	Florida Staysweet	Gold Cup	Sundance
No stress	155 a[x]	117 ab	137 a	151 a
Early stress[y]	122 b	139 a	139 a	86 b
Late stress[z]	117 b	98 b	107 b	130 a

[x] Numbers followed by different letters are significantly different for comparisons within hybrids.
[y] Drought stress during vegetative stage of plant growth.
[z] Drought stress during reproductive stages of plant growth.

were similar to those between infected and uninfected plants. For example, differences in ear weight between infected and uninfected plants of 21 and 35 g in 1984 and 1985, respectively, were significant, whereas a 27-g difference between late-stress and no-stress treatments in 1984 and a 30-g difference between early-stress and no-stress treatments in 1985 were not significant. Additional replication of main plots (stress treatments) or reassignment of treatments in the split-split plot design may have caused significant differences in ear weight among stress treatments.

Yield of sweet corn subjected to drought stress depends primarily on two factors: the amount of assimilate the plant is able to produce during grain filling and the total amount of assimilate that the plant is able to store in the stems (2,22). Factors that reduce production or storage of assimilate will reduce yield. Plants stressed to the point of zero photosynthesis during grain filling will mobilize carbohydrate reserves from the stems to compensate for the lack of photosynthate production (22). Most of the storage carbohydrates are produced between anthesis and maturity. Maize plants stressed continually from silking to maturity showed large reductions in yield (22). In our study, weights of ears from plants subjected to drought stress during reproductive stages averaged 27 g less than the control in 1984. Stress occurred throughout this period, so it is probable that production of storage carbohydrates was reduced. Because these plants were also stressed during grain fill, they probably did not produce as much photosynthate as the control and had to draw on reduced reserves during the later portion of the late-stress period. Late stress did not reduce yield in 1985. In 1985, rain fell on late-stressed plants on 15, 26, and 31 July (for a total of 83.8 cm). Possibly, the stress period

during grain fill was not severe enough to limit photosynthesis, in which case grain fill relied upon production of photosynthates rather than upon stored photosynthates.

The drought stress × hybrid interaction for ear weight in 1984 was primarily a result of differences in hybrid maturities. Ear weights were affected most by early stress in the earliest-maturing hybrid, Sundance. Ear weight of Cherokee, the hybrid which matured second, was reduced by early and late stress. Ears from the two later-maturing hybrids, Gold Cup and Florida Staysweet, weighed less for the late-stress treatment.

Reduction in the development of kernels in the basal quarter of the ear (butt blanking) may have resulted from embryo abortion, reduction in the number of spikelets, nonviability of pollen, or lag times between pollen shed and silking (6,9,10,17,18). In 1984, butt blanking was greater in the early-stress plots than in the control plots, although the cause of this reduction in kernel development is unkown. Butt blanking caused by MDMV contributed to reductions in yield in both years. Mikel et al (17) have identified poor growth of pollen germ tubes as the cause for butt blanking due to MDMV. Since reductions in ear weight were much greater than weight loss due to the number of missing kernels, reductions in yield were not caused entirely by butt blanking. Nevertheless, butt blanking caused by MDMV or drought stress may render ears unsuitable for fresh market sale because of their unacceptable quality.

Large reductions in leaf area and plant height occurred after early stress. The reduced leaf area due to early stress is consistent with reports that stress inhibited leaf elongation before it inhibited photosynthesis (1,3,21). In those studies, elongation of leaves was inhibited, leaf turgor was maintained, and photosynthesis continued, all of which were beneficial on a short-term basis. However, those conditions would severely reduce leaf area and photosynthesis later in the season if the stress continued. Also, stem areas were reduced in shorter plants, thus reducing the potential for storage of assimilates. The end result could be reduced yield, as may have occurred with early stress in 1985.

Sugar content of kernels was not affected by MDMV in our study, which agrees with the findings of Carey et al (4). Neither early nor late drought stress had any effect on sugar content of kernels.

Effects of viral diseases on plant performance may be related to virus titer. Since ear weight, butt blanking, leaf area, and plant height of Cherokee and Gold Cup were affected similarly by MDMV infection (i.e., no hybrid × infection interaction), one would expect titer of MDMV to be similar between the two

hybrids. In fact, there were no differences in the titer of MDMV between Cherokee and Gold Cup on two of the three sampling dates, and early-drought and late-drought stress had no effect on titer.

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Table 4. Titer of maize dwarf mosaic virus A and B during reproductive growth stages of two sweet corn hybrids subjected to three drought-stress treatments in 1985

Drought stress or hybrid	Absorbance at 405 nm		
	22 July	26 July	2 August
No stress	0.558 a[w,x]	0.373 a	0.348 a
Early stress[y]	0.595 a	0.351 a	0.327 a
Late stress[z]	0.635 a	0.348 a	0.336 a
Cherokee	0.645 a	0.378 a	0.342 a
Gold Cup	0.548 a	0.337 b	0.332 a

[w]Titer measured by enzyme-linked immunosorbent assay. All OD_{405} values were greater than the means of the noninoculated plants plus four standard deviations.

[x]Numbers followed by the same letter are not different statistically for comparison within groups of main effect treatments.

[y]Drought stress during vegetative stage of plant growth.

[z]Drought stress during reproductive stages of plant growth.

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