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Interactions between maize dwarf mosaic and weed interference on sweet corn

Martin M. Williams II[a,*], Jerald K. Pataky[b]

[a] Global Change & Photosynthesis Research, USDA-ARS, University of Illinois, 1102 S. Goodwin Ave., Urbana, IL 61801, USA
[b] Department of Crop Sciences, University of Illinois, 1102 S., Goodwin Ave., Urbana, IL 61801, USA

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ABSTRACT

Maize dwarf mosaic (MDM) and weed interference are two economically important stresses to sweet corn; however, a fundamental understanding of the extent to which the crop is affected by combinations of these stresses is lacking. The objective of this study was to quantify the extent to which MDM incidence and weed interference influence the sweet corn canopy, phenological development, and yield. In field research, five levels of MDM incidence (0, 25%, 50%, 75%, and 100% of the plant population) were established in two sweet corn hybrids that also were grown in the presence or absence of wild-proso millet. During the vegetative phase of crop growth, the crop's ability to tolerate these multiple stresses was largely additive. For instance, incidence of MDM decreased crop growth and delayed development by as much as five days, and wild-proso millet added to those detrimental effects by an extent that was determined by the severity of weed interference. In contrast during the reproductive phase, MDM incidence and weed interference interacted in their effect on the crop. Moreover, differences in hybrid responses to the multiple stresses indicated that the benefit of improved crop tolerance to weed interference was not lost when the crop is infected with MDM. Use of hybrids with high levels of MDM resistance and improved competitive ability with weeds reduces the risk of losses from MDM and weed interference, two commonly occurring stresses in sweet corn.

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1. Introduction

Maize dwarf mosaic (MDM) is the most prevalent viral disease of sweet corn (*Zea mays* L.) in the continental U.S. and is caused by *Maize dwarf mosaic virus* (MDMV). *Sugarcane mosaic virus* (SCMV) causes Sugarcane mosaic (SCM) and frequently co-occurs with MDM in sweet corn. Both pathogens overwinter in the southeastern U.S. and are vectored by dozens of species of aphids. Once transmitted to sweet corn, the viruses infect systemically causing symptoms to occur on newly developing plant tissues. The most prominent symptoms are a mosaic or mottled pattern on leaf surfaces. The disease stunts plant growth, delays silking up to four days, and causes up to 70% yield loss (Gregory and Ayers, 1982; Mikel et al., 1981a,b). Yield losses from MDM are the result of a combination of a reduction in photosynthetic rate due to chlorophyll loss, and an elevation in respiration rate due to virus replication (Gates and Gudauskas, 1969; Tu and Ford, 1968; Tu et al., 1968). Little is known about corn canopy responses to the viral diseases, such as the dynamics of the crop's ability to compete for light.

Resistance to MDM and SCM is mostly qualitative (i.e., resistant or susceptible phenotypes) although some intermediate phenotypes occur occasionally. A single gene or extremely closely linked genes on the short arm of maize chromosome six convey resistance to both MDMV and SCMV although modifier genes also appear to influence resistant and susceptible phenotypes (Jones et al., 2007). For brevity, infections by MDMV and SCMV hereafter will be referred to as simply MDM. Nearly two-thirds of all commercial sweet corn hybrids have no resistance to MDM (Pataky et al., 2011). Symptomatic plants also occur sporadically among MDM-resistant hybrids when plants are infected at very early growth stages (e.g., 2–3-leaf stages). Yield losses up to 10% have been observed in MDM-resistant sweet corn hybrids in response to inoculation at early growth stages that results in a low incidence of systemically infected, symptomatic plants (Kerns and Pataky, 1997). The preponderance of MDM-susceptible sweet corn hybrids and the limited use of MDM-resistant hybrids creates the potential for sporadically occurring, severe, localized epidemics of MDM in sweet corn.

Weed interference is common in North American sweet corn production. Based on recent surveys of Midwestern sweet corn growers, nearly all sweet corn fields have weeds that escape control and a majority of fields harbor weed communities sufficiently large enough to cause yield losses (Williams et al., 2008a). Although no single weed species is problematic in every field, wild-proso millet (*Panicum miliaceum* L.) has become prevalent throughout the upper continental U.S. and southern Canada. A weedy race of

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* Corresponding author. Tel.: +1 217 2445476; fax: +1 217 3335251.
E-mail address: mmwillms@illinois.edu (M.M. Williams II).

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domesticated proso millet, wild-proso millet appears to have had multiple introductions into North America (Colosi and Schaal, 1997). First reported in field crops in the 1970s (Harvey, 1979), wild-proso millet is now ranked as the third most abundant weed in fields of sweet corn grown for processing in the Midwest (Williams et al., 2008a).

Considerable variation exists among the ability of different sweet corn hybrids to endure competitive stress from weeds without loss in growth or yield, hereafter called crop tolerance (So et al., 2009b; Williams et al., 2008b). Of 18 phenomorphological traits measured among 23 hybrids, So et al. (2009b) identified seven traits associated with a large, late-maturing canopy as the primary factor influencing crop tolerance among commercial sweet corn. Those traits included five measured at silking (plant height, leaf area index (LAI), intercepted photosynthetically active radiation (IPAR), plant biomass, and plant leaf area) and two measures of development (thermal time to silking and thermal time to harvest). Crop tolerance to weed interference and resistance to MDM are presumed to be unrelated. Conceivably, reductions in the sweet corn canopy due to MDM incidence would favor weed growth, potentially reducing crop tolerance.

A large proportion of the genetic improvement in corn has been attributed to increased tolerance to multiple stresses (Duvick, 2005; Tollenaar and Wu, 1999). Weed interference and MDM are two economically important stresses in sweet corn that frequently co-occur. A fundamental understanding of the extent to which sweet corn is affected by combinations of these stresses is lacking. The objective of this study was to quantify the extent to which MDM incidence and weed interference influence the sweet corn canopy, phenological development, and yield. Tests were conducted in two MDM-susceptible hybrids that differed in crop tolerance. We hypothesized that hybrid, MDM incidence, and weed interference interacted in their effects on sweet corn.

2. Materials and methods

Field experiments were conducted three years in Urbana, IL, USA (40°6′35″N, 88°12′15″W, 222 m a.s.l.). Experiments were conducted in separate fields each year. The previous crop was soybean (*Glycine max* (L.) Merr.). The soil was a Flanagan silt loam (fine, smectitic, mesic Aquic Argiudolls) averaging 3.8% organic matter and a pH of 6.6. Fields were cultivated after receiving 135 kg N ha^{-1} and planted 22 May 2008, 21 May 2009, and 25 May 2010 at 83,000 seed ha^{-1} of sweet corn. Rainfall was supplemented with sprinkler irrigation as needed to ensure crop/weed establishment and avoid drought conditions.

2.1. Experimental approach

The treatment design was a 2 × 5 × 2 factorial of hybrid × MDM incidence × weed level. Treatments were arranged in a split–split block experimental design with five replications (Lentner and Bishop, 1993). Each block consisted of horizontal strips of two hybrids and vertical strips of MDM treatment factors (i.e., level of incidence) with horizontal strips perpendicular to vertical strips. Each of 10 hybrid × MDM plots was split into two subplots to which weed treatments (i.e., presence or absence of wild-proso millet) were randomly assigned. The two sweet corn hybrids, ‘Sugar Buns’ (Crookham Company, Caldwell, ID) and ‘Legacy’ (Harris Moran, Modesto, CA), have similar susceptibility to MDM (Pataky et al., 2011); however Sugar Buns exhibits lower tolerance to weed interference than Legacy (So et al., 2009a). Within each replication, each hybrid was grown in horizontal strips measuring 6.1 m wide (eight 0.76 m-spaced rows) and approximately 41 m in length. MDM incidence levels of 0, 25%, 50%, 75%, and 100% infected plants were randomly assigned to vertical strips of 16 rows of corn (eight rows of each hybrid) measuring 6.1 m in length. A 1.5 m alley was maintained between MDM levels. Subplots assigned presence or absence of wild-proso millet were four rows by 6.1 m. Since the field had no history of wild-proso millet, seed was shallowly planted at approximately 100 seed/m of row directly into the center two rows of appropriate subplots using a cone planter immediately after planting sweet corn. Wild-proso millet seed was collected in the year preceding each experiment from a local population and stored at room temperature. Prior to planting, germination assays indicated germinability was 40–60%. Selective herbicides, interrow cultivation, and handweeding were used as needed to keep the study area free of all weeds except wild-proso millet. Two weeks after emergence, sweet corn was thinned by hand to 66,000 plants ha^{-1} (five plants per meter of row).

2.2. MDM inoculation

Levels of MDM were established by hand-inoculating specific corn plants in each plot. All plants were inoculated in the 100% MDM incidence. Three of every four plants were inoculated in the 75% MDM incidence treatment. Every other plant was inoculated in the 50% MDM incidence treatment. Every fourth plant was inoculated in the 25% MDM incidence treatment. Plants in the 0 MDM incidence were not inoculated. Inoculum was a combination of strain A of MDMV (MDMV-A) which was maintained on Johnsongrass (*Sorghum halepense* (L.) Pers.) in the greenhouse and strain MB of SCMV (SCMV-MB) which was maintained on sweet corn plants. Inoculum was increased in isolated field plots on susceptible sweet corn. Sap of infectious leaves from inoculum increase fields was extracted by blending equal quantities of MDMV-A and SCMV-MB-infected tissue in 0.1 M potassium phosphate buffer at pH 7 for 30 s. Homogenate was filtered through a 3.8 l paint strainer (Trimaco 11311/25, Trimaco LLC, Durham, NC). Inoculum was prepared by mixing 3.8 l of filtered sap extract with 7.6 l of 0.1 M potassium phosphate buffer. In timing inoculation and data collection, growth stages were determined by the number of visible leaf collars and appearance of reproductive organs (Ritchie et al., 2003). At the three-leaf stage (V3), plants were mechanically inoculated by the pinprick method frequently used to inoculate maize with *Pantoea stewartii* (Chang et al., 1977). The method delivers inoculum into leaf tissue through pinholes made by hand. Plants were inoculated two consecutive days. One week after the first inoculation, asymptomatic target plants, which were identified by wounds from previous inoculations, were inoculated a third time.

2.3. Data collection

All data were recorded from the center two rows of each plot. Wild-proso millet population density was determined three weeks after emergence. Incidence (%) of plants symptomatic of MDM infection was recorded at the V6 stage, approximately 17 days after the first inoculation. Sweet corn leaf area index and intercepted photosynthetically active radiation were measured at V5 and silk emergence (R1) at five locations in each weed-free plot. Sweet corn LAI was measured under full-sun conditions within 2 h of solar noon at three locations in each plot using a linear ceptometer (AccuPAR Linear Ceptometer; Decago Devices, Pullman, WA). Ceptometer measurements of incident light above and below the canopy were used to estimate IPAR. Specifically, IPAR was estimated as unity minus the fraction of the below-canopy to above-canopy measurements, averaged for each plot. Sweet corn height, measured from the soil surface to uppermost leaf, was recorded at V5 and R1 in both weedy and weed-free plots.

Cumulative growing degree days (GDD) were determined beginning with crop emergence using a base temperature of 10 °C and daily temperature data from a weather station within 1 km of the study site (Illinois State Water Survey, Champaign, IL). At the onset of anthesis, the number of plants with emerged silks was counted daily until at least 50% of plants had silked; herein identified as the mid-silk date. Each hybrid was harvested approximately 18 days after mid-silk of weed-free, 0 MDM plots. Marketable ears, measuring ≥4.5 cm in diameter, were hand-harvested over the length of each plot. Ear number and mass were recorded.

2.4. Data analysis

Wild-proso millet establishment differed greatly across years; therefore, analyses were performed within each year. All data were examined with diagnostic tests of residuals to ensure compliance with ANOVA assumptions of homoschedasticity and normality. To evaluate the significance of hybrid, MDM incidence, and weed interference effects on height, thermal time to mid-silk, and yield, data were analyzed using general linear models fit by restricted maximum likelihood. Similar models were used to quantify the significance of hybrid and MDM incidence effects on crop LAI and IPAR. Since treatment factors and interactions often were significant at the $\alpha = 0.05$ level, regression analyses were used to quantify relationships between crop responses and MDM incidence. Sweet corn height at mid-silk, thermal time to mid-silk, and ear mass were fitted to linear or quadratic models as functions of MDM incidence within each hybrid × weed level combination using least-squares regression. Lack of fit was assessed by reporting the coefficient of determination (r^2) and plotting predicted values against means and standard errors of observed values. All analyses were performed in SYSTAT software (SYSTAT, 2004).

3. Results

3.1. Environmental conditions and wild-proso millet

Establishment of wild-proso millet varied considerably among years. Weed population density three weeks after planting averaged 6, 93, and 36 seedlings per meter of row in 2008, 2009, and 2010, respectively. The low weed population density observed in 2008 was the result of excess rainfall early in the season. In the first week after planting in 2008, the experiment received 14.8 cm of rainfall. Although crop emergence was sufficient, excessive soil moisture may have flooded emerging wild-proso millet seedlings or comprised their resistance to soil-borne pathogens. In contrast, high seedling recruitment (i.e., >90%) in 2009 suggested environmental conditions shortly after planting released most of the seedbank from secondary dormancy.

The 2008 season was cool early and wet for an extended period until harvest (Table 1). Conditions in 2009 also were characterized by above-normal water supply and near- or below-normal temperatures. In contrast, 2010 had above-normal temperatures and, with the exception of above-normal precipitation in June, was abnormally dry the rest of the season.

3.2. Canopy traits

Crop canopy density at the V5 stage of growth was not affected by MDM, but at the R1 growth stage, canopy density was affected by MDM. Incidence of MDM affected crop LAI at the R1 stage in two (2009 and 2010) of three years and IPAR at the R1 stage in 2010 (Table 2). LAI and IPAR at the R1 stage differed among hybrids. Legacy produced a canopy that, on average, intercepted 22% more photosynthetically active radiation than Sugar Buns at R1.

Incidence of MDM reduced corn growth linearly each year (Fig. 1). Based on slope coefficients of the relationship between crop height and MDM incidence, every additional 10% MDM incidence

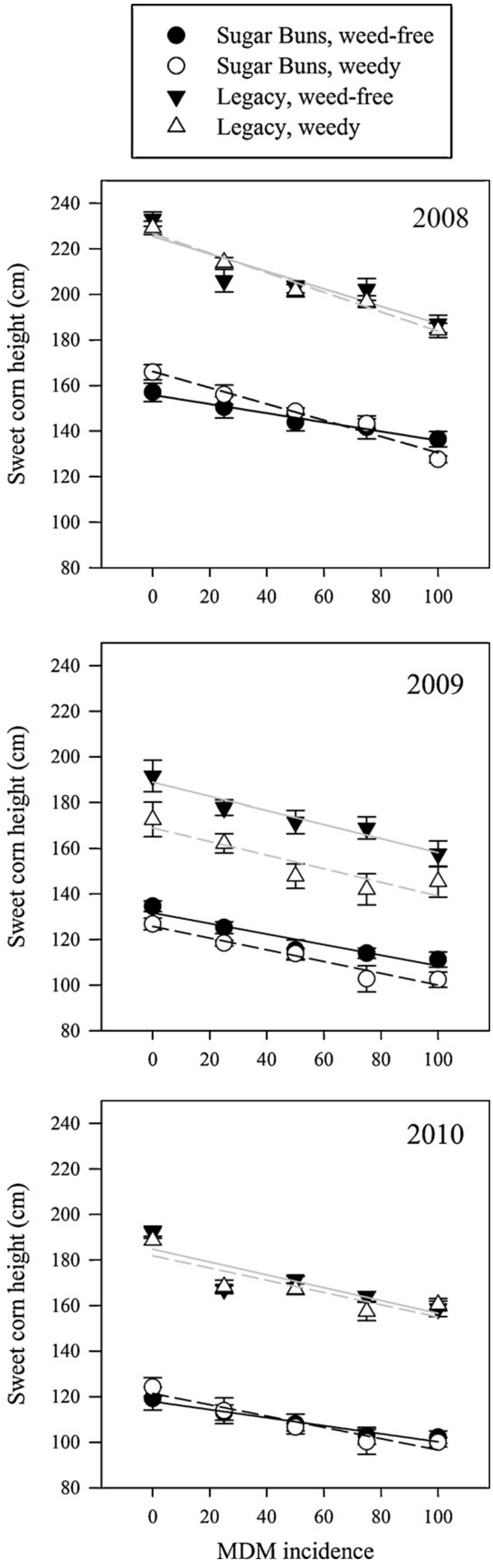

Fig. 1. Sweet corn height at the mid-silk stage as a function of hybrid, weed interference, and MDM incidence. Regression parameter estimates are reported in Table 3.

Table 1
Monthly rainfall and irrigation amounts and minimum, maximum, and mean average daily temperature for the months of May, June, July, and August in 2008, 2009, and 2010 in Urbana, IL. Departure from the 30-yr average precipitation and mean air temperature for these months are included for reference.

Year	Month	Water supply		Ave. daily air temperature			Departure from average	
		Rainfall (mm)	Irrigation (mm)	Minimum (°C)	Maximum (°C)	Mean (°C)	Precipitation (mm)	Temperature (°C)
2008	May	154	0	8.9	20.4	14.6	32.3	−2.5
	June	163	57	17.2	28.6	22.9	55.6	0.8
	July	200	42	17.6	28.8	23.2	81.8	−0.7
	August	20	0	16.5	28.0	22.3	−90.9	−0.6
2009	May	145	12	11.4	23.3	17.4	23.1	0.3
	June	112	17	18.1	29.2	23.7	5.3	1.6
	July	160	33	16.0	26.2	21.1	41.4	−2.8
	August	143	0	15.4	26.9	21.2	31.8	−1.7
2010	May	63	14	12.6	23.7	18.2	−59.2	1.1
	June	212	0	18.6	29.0	23.8	104.6	1.7
	July	95	30	19.4	30.5	25.0	−23.4	1.1
	August	42	0	18.8	31.3	25.1	−69.3	2.3

Table 2
Significance (*P*) of treatments and interactions on leaf area index (LAI), intercepted photosynthetically active radiation (IPAR), sweet corn height, thermal time to mid-silk, and sweet corn yield (ear number and ear mass).

Year	Factor	LAI V5	LAI R1	IPAR V5	IPAR R1	Height V5	Height R1	Mid-silk	Yield Ear no.	Yield Ear mass
		Growth stage								
2008	Hybrid	0.004	0.000	0.006	0.000	0.001	0.000	0.000	0.000	0.001
	MDM	0.495	0.269	0.374	0.953	0.000	0.000	0.000	0.000	0.000
	Hybrid*MDM	0.927	0.407	0.691	0.920	0.428	0.023	0.318	0.457	0.136
	Weed	–	–	–	–	0.006	0.589	0.035	0.000	0.000
	Hybrid*Weed	–	–	–	–	0.971	0.318	0.324	0.001	0.069
	MDM*Weed	–	–	–	–	0.121	0.110	0.339	0.019	0.005
	Hybrid*MDM*Weed	–	–	–	–	0.241	0.270	0.504	0.539	0.837
2009	Hybrid	0.844	0.004	0.694	0.004	0.009	0.001	0.001	0.010	0.022
	MDM	0.140	0.023	0.156	0.137	0.970	0.000	0.019	0.000	0.000
	Hybrid*MDM	0.790	0.620	0.413	0.876	0.579	0.708	0.826	0.304	0.554
	Weed	–	–	–	–	0.788	0.000	0.000	0.000	0.000
	Hybrid*Weed	–	–	–	–	0.923	0.000	0.003	0.558	0.696
	MDM*Weed	–	–	–	–	0.410	0.422	0.414	0.006	0.000
	Hybrid*MDM*Weed	–	–	–	–	0.281	0.374	0.962	0.001	0.006
2010	Hybrid	0.271	0.000	0.302	0.000	0.001	0.000	0.000	0.000	0.000
	MDM	0.460	0.006	0.376	0.000	0.433	0.000	0.000	0.000	0.000
	Hybrid*MDM	0.709	0.450	0.939	0.066	0.918	0.031	0.710	0.343	0.015
	Weed	–	–	–	–	0.006	0.245	0.000	0.000	0.000
	Hybrid*Weed	–	–	–	–	0.645	0.278	0.000	0.816	0.689
	MDM*Weed	–	–	–	–	0.402	0.362	0.002	0.545	0.224
	Hybrid*MDM*Weed	–	–	–	–	0.476	0.383	0.398	0.013	0.003

resulted in a 2–4 cm reduction in crop height (Table 3). A significant hybrid × MDM interaction in 2008 and 2009 indicated height loss from MDM differed between hybrids. Legacy, which had an average height 65 cm greater than Sugar Buns, lost an average of 3.4 cm of height with every 10% increase in MDM incidence. Sugar Buns lost an average of 2.5 cm of height for every 10% increase in MDM incidence.

Table 3
Sweet corn height at the mid-silk stage as a function of hybrid, weed interference, and MDM incidence. Parameter estimates were obtained by fitting sweet corn height to a linear model $y = a + bx$, where x is MDM incidence.

Year	Hybrid	Weed	a (cm)	b	r^2
2008	Sugar Buns	Weed-free	156	−0.200	0.408
		Weedy	166	−0.357	0.818
	Legacy	Weed-free	227	−0.402	0.676
		Weedy	227	−0.433	0.871
2009	Sugar Buns	Weed-free	132	−0.232	0.597
		Weedy	126	−0.258	0.621
	Legacy	Weed-free	189	−0.307	0.498
		Weedy	169	−0.298	0.382
2010	Sugar Buns	Weed-free	118	−0.177	0.380
		Weedy	121	−0.248	0.504
	Legacy	Weed-free	185	−0.282	0.635
		Weedy	182	−0.269	0.595

Wild-proso millet interference stunted crop height only in 2009 when conditions favored wild-proso millet seedling recruitment. Likely, the intensity of weed interference was higher in 2009 compared to the other two years.

3.3. *Phenological development*

Incidence of MDM delayed sweet corn development as measured by thermal time to mid-silk (Fig. 2). The delay in crop development due to MDM-infection was similar between hybrids as indicated by a lack of hybrid × MDM interactions. Plots with 100% incidence of MDM-infected plants reached the mid-silk stage about one to five days (13–75 GDD) later than plots with no MDM-infected plants.

Wild-proso millet also delayed sweet corn development as measured by thermal time to mid-silk. Similar to the effect of weed interference on corn height, the greatest delay in thermal time to mid-silk occurred in 2009 when conditions favored wild-proso

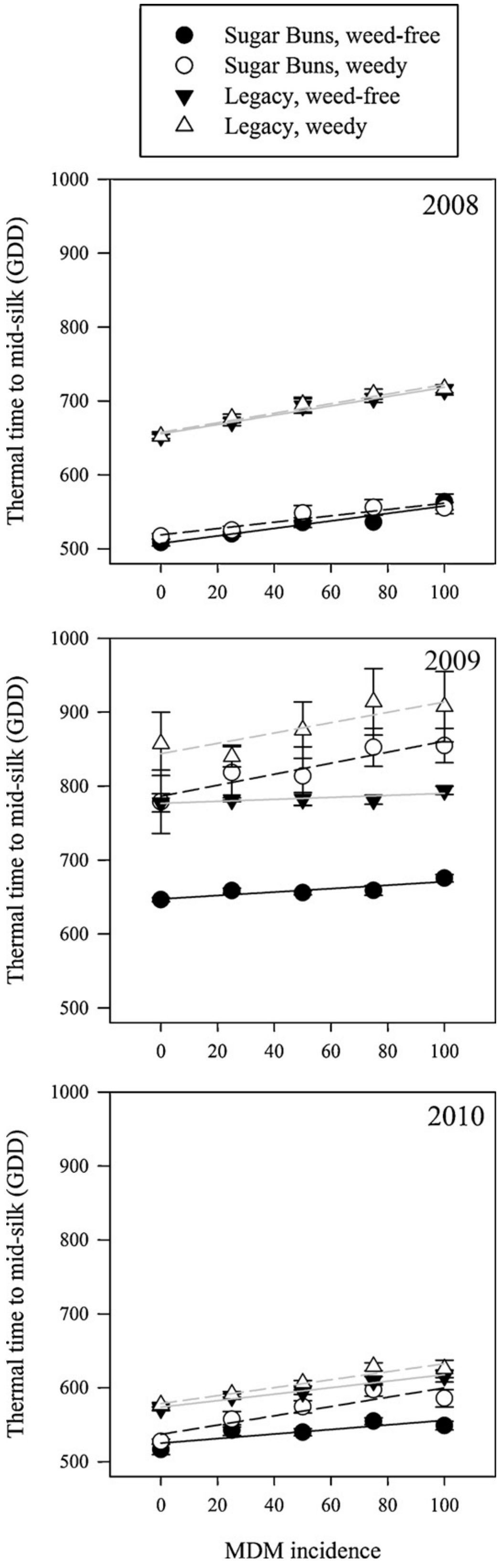

Fig. 2. Thermal time to sweet corn mid-silk as a function of hybrid, weed interference, and MDM incidence. Regression parameter estimates are reported in Table 4.

Table 4
Thermal time to sweet corn mid-silk as a function of hybrid, weed interference, and MDM incidence. Parameter estimates were obtained by fitting thermal time to mid-silk to the linear model $y = a + bx$, where x is MDM incidence.

Year	Hybrid	Weed	a GDD	b	r^2
2008	Sugar Buns	Weed-free	507	0.506	0.649
		Weedy	519	0.429	0.448
	Legacy	Weed-free	656	0.630	0.712
		Weedy	658	0.647	0.728
2009	Sugar Buns	Weed-free	647	0.233	0.415
		Weedy	786	0.745	0.125
	Legacy	Weed-free	777	0.134	0.081
		Weedy	844	0.698	0.087
2010	Sugar Buns	Weed-free	525	0.308	0.376
		Weedy	537	0.628	0.539
	Legacy	Weed-free	574	0.438	0.690
		Weedy	579	0.538	0.653

millet seedling recruitment (Fig. 2). Weed interference delayed development of Sugar Buns more than development of Legacy. Based on 15 GDD per day, weed interference delayed Sugar Buns mid-silk date ~1 day in 2008 and 2010, but delayed mid-silk date ~9 days in 2009 (Table 4). In contrast, weed interference delayed mid-silk date of Legacy minimally (2–5 GDD) in 2008 and 2010, and by ~4 days in 2009. In the absence of MDM and weed interference, Legacy reached the mid-silk stage an average of seven to eight days later than Sugar Buns. These observations provide evidence that Legacy has greater developmental tolerance to weed interference than Sugar Buns, despite a longer vegetative stage than Sugar Buns during which sweet corn plants and weeds compete.

3.4. Yield

Incidence of MDM reduced crop yield substantially (Fig. 3). The relationship between ear mass and MDM incidence was curvilinear as low levels of MDM (e.g., 25–50%) had a greater impact on ear mass than equal increments of MDM incidence at higher levels (e.g., 75–100%). Wild-proso millet interference also consistently reduced crop yield. Legacy consistently yielded more than Sugar Buns. However, specific yield responses often were the result of interactions among hybrid, MDM, and weed factors (Table 2).

In the absence of MDM, Legacy had greater tolerance in ear mass to weed interference than Sugar Buns. For example, weedy ear mass averaged 45% and 73% of weed-free for Sugar Buns and Legacy, respectively (Table 5). With increased incidence of MDM, Legacy generally maintained ear mass better than Sugar Buns. Similar results were observed for ear number (not reported).

Table 5
Mass of marketable sweet corn ears as a function of hybrid, weed interference, and MDM incidence. Parameter estimates were obtained by fitting ear mass to a quadratic model ($y = a + bx + cx^2$), whereby x is MDM incidence.

Year	Hybrid	Weed	a (Mt ha^{-1})	b	c	r^2
2008	Sugar Buns	Weed-free	11.7	−0.123	0.0004	0.808
		Weedy	6.3	−0.106	0.0006	0.665
	Legacy	Weed-free	16.4	−0.182	0.0009	0.801
		Weedy	12.8	−0.163	0.0009	0.720
2009	Sugar Buns	Weed-free	12.1	−0.131	0.0005	0.697
		Weedy	1.8	−0.023	0.0001	0.535
	Legacy	Weed-free	12.0	−0.076	0.0004	0.180
		Weedy	5.3	−0.059	0.0003	0.341
2010	Sugar Buns	Weed-free	11.0	−0.187	0.0010	0.859
		Weedy	7.2	−0.147	0.0008	0.751
	Legacy	Weed-free	18.4	−0.221	0.0014	0.868
		Weedy	17.9	−0.303	0.0020	0.882

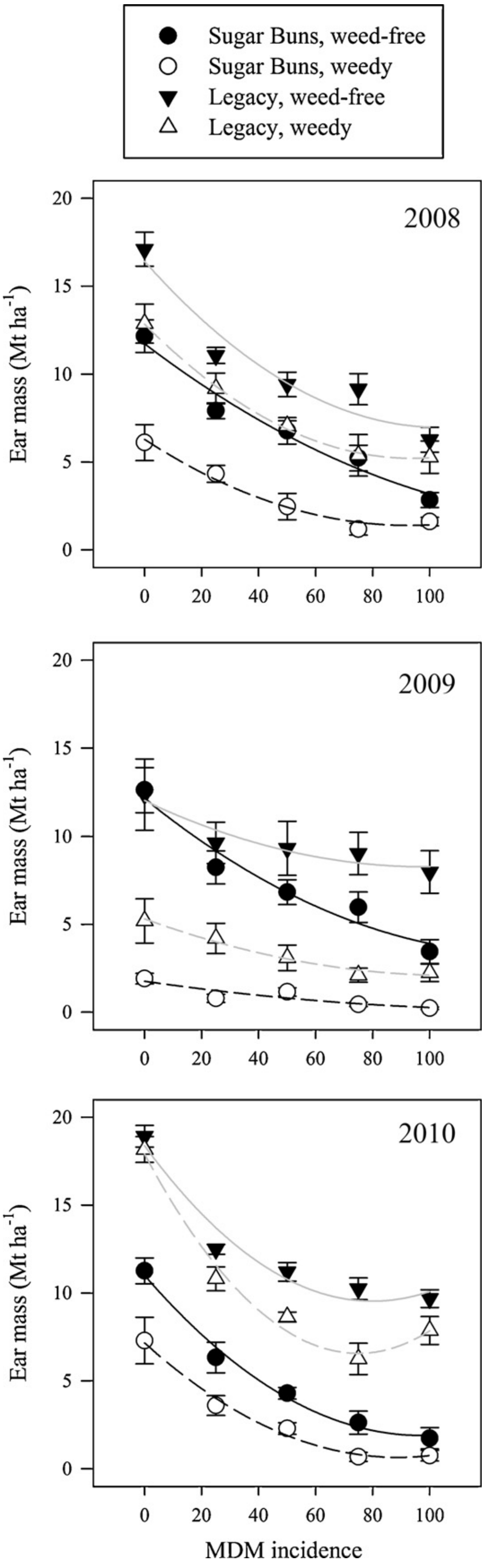

Fig. 3. Mass of marketable sweet corn ears as a function of hybrid, weed interference, and MDM incidence. Regression parameter estimates are reported in Table 5.

4. Discussion

Incidence of MDM reduced the density and vertical distribution of the sweet corn canopy, thereby reducing the crop's ability to compete for light. Because light cannot be stored, competition for photons in a mixed canopy favors weed species. Light transmittance in a corn canopy stimulates not only weed growth (McLachlan et al., 1993) and weed fecundity (Lindquist and Mortensen, 1998), but also weed seed germination (Egley, 1986). Lindquist et al. (1998) identified several canopy traits that improve crop tolerance, including greater LAI and height at which leaf area occurred. A reduction in the crop's ability to compete for light and a concomitant increase in weed growth intensifies late-season, weed-crop competition. For instance, in previous research with wild-proso millet, we found that as sweet corn canopy density among hybrids declined, weed biomass became an important influence on crop yield loss (Williams et al., 2008b). Rajcan and Swanton (2001) surmised the reduction in crop LAI from weed interference is a better predictor of crop losses than lower photosynthetic rates of shaded crop leaves. Conceivably MDM also changed the spectral distribution of light penetrating the crop canopy, which could exacerbate the effects of weed interference. Chloroplasts in leaves infected with MDM are reduced in size and number in both mesophyll parenchyma cells and bundle sheath cells (Tu et al., 1968). Chlorophyll content of emerging leaves infected with MDM has been demonstrated to be 19–29% of chlorophyll content of healthy leaves (Gates and Gudauskas, 1969). Light quality, driven by selective absorbance of red light (660–670 nm) of neighboring plants, influences growth and fecundity of important row crop weeds such as common lambsquarters (*Chenopodium album* L.) (Gramig and Stoltenberg, 2009). These morphological changes (i.e., a shade avoidance response), which may precede the onset of competition, generally improves the weed's competitive ability.

During the vegetative phase, the crop's ability to tolerate multiple stresses was largely additive, as evidenced by few MDM × weed interactions for sweet corn height and thermal time to mid-silk. As a result, the effects of MDM on crop growth and development were not affected by weed interference, and the effects of weed interference on sweet corn growth and development were not affected by MDM incidence. One exception was on thermal time to mid-silk in 2010, when the combination of MDM incidence and weed interference delayed crop development more than either factor alone. Olson et al. (1990) found that drought stress and MDM were additive in their effects on sweet corn height and leaf area.

During the reproductive phase, MDM incidence and weed interference interacted in their effect on the crop, as evidenced by significant MDM × weed interactions on crop yield. Ear mass data show Legacy generally maintained ear mass better than Sugar Buns across the range of MDM incidence. Differences between hybrid responses to the multiple stresses appear to have resulted from Legacy dominating the crop-weed canopy, compared to the shorter, weaker canopy of Sugar Buns. Wild-proso millet biomass was approximately two-fold higher in Sugar Buns than Legacy (Williams and Pataky, unpublished data). While both hybrids lost height and leaf area due to MDM, the multiple stresses on Sugar Buns appear to have weakened this hybrid to below a critical threshold, thereby allowing wild-proso millet to intensify its competitive effect on the crop. Increased severity of weed escapes and crop losses in poorly competitive hybrids also can be the result of high weed population density (Williams et al., 2007), reduced herbicide use (Williams et al., 2011), and inadequate mechanical weed control (Boydston and Williams, 2011). Results from the present work indicate that the benefit of improved crop tolerance to weed interference was not lost when the crop is infected with MDM.

5. Conclusion

Although resistance genes for MDM have been incorporated into some sweet corn lines, most commercial hybrids have little or no resistance to the disease. Coupled with the fact that weeds often escape control and cause losses in a majority of sweet corn fields, the crop is likely to experience a combination of stresses from MDM incidence and weed interference. Results from this study confirmed the hypothesis that hybrid, MDM incidence, and weed interference interact in their effects on sweet corn. Incidence of MDM decreased crop growth and delayed development by as much as five days. The presence of wild-proso millet added to those detrimental effects by an extent that was determined by the severity of weed interference. An MDM-mediated reduction in the crop canopy could exacerbate losses due to weeds in hybrids with thin canopies where light is a limiting factor. Hybrids with greater crop tolerance, such as Legacy, may not be immune to the effects of MDM incidence and weed interference; however, crop development and yield may be affected less by the combination of stresses in comparison to poorly competitive hybrids such as Sugar Buns. Use of hybrids with high levels of MDM resistance and improved competitive ability with weeds reduces the risk of losses from these commonly occurring stresses.

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