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Maize Dwarf Mosaic Can Reduce Weed Suppressive Ability of Sweet Corn

Martin M. Williams II and Jerald K. Pataky*

Maize dwarf mosaic (MDM) stunts corn growth, delays development, and is the most prevalent viral disease of sweet corn grown in many regions of North America and Europe. Although some weeds escape control in most sweet corn fields, the extent to which MDM influences the weed suppressive ability of the crop is unknown. Field studies were conducted over a 3-yr period to characterize the influence of variable MDM incidence in sweet corn on growth, fecundity, and germinability of wild-proso millet, a common weed in the crop. Treatments included five levels of MDM incidence (0, 25, 50, 75, and 100% of plants infected) in two MDM-susceptible hybrids differing in weed suppressive ability. Previous research showed that hybrid 'Legacy' had greater weed suppressive ability than 'Sugar Buns'. Wild-proso millet biomass and fecundity depended largely on the hybrid in which the weed was growing. Wild-proso millet growing in Sugar Buns weighed 45 to 117% more than wild-proso millet in Legacy. Incidence of MDM in sweet corn affected wild-proso millet biomass and fecundity, but only under high weed population densities. When wild-proso millet was observed at 122 plants m^{-2}, weed biomass increased 9 g m^{-2} for each additional 10% incidence of MDM of sweet corn. Weed suppressive ability of the competitive and less competitive hybrids were influenced to the same extent by MDM. Coupled with a lack of resistance to MDM in two-thirds of commercial sweet corn hybrids, the disease could be an additional factor perpetuating weed growth and fecundity in sweet corn, particularly in fields with high population densities of wild-proso millet.

Nomenclature: Wild-proso millet, *Panicum miliaceum* L.; sweet corn, *Zea mays* L., 'Legacy', 'Sugar Buns'.
Key words: Competition, disease susceptibility, germination, maternal environment, weed suppressive ability.

Despite extensive use of broad-spectrum residual herbicides in sweet corn, weed growth and fecundity are common. Field surveys at the time of crop harvest showed weedy plants in nearly every field, with a majority of sweet corn fields suffering yield loss from weed interference (Williams et al. 2008b). Weed interference reduces sweet corn yield and adversely affects ear traits important to processing and fresh markets. For instance, crop losses because of giant ragweed (*Ambrosia trifida* L.) cost $0.86 to $8.75 per giant ragweed plant, depending on sweet corn market type (Williams 2010). Moreover, inadequate weed control in sweet corn exacerbates problems in succeeding vegetable crops, such as snap bean (Davis and Williams 2007). Limiting fecundity is critical because weed control failure has been shown to reduce effectiveness of tillage systems (Hartzler and Roth 1993), and most rotational vegetable crops have few herbicides registered for use (Fennimore and Doohan 2008).

Historically, the ability of a crop to suppress weed emergence, growth, and fecundity (i.e., weed suppressive ability) has been an important component of weed management in many crop production systems. Before the development and adoption of selective herbicides, weed suppressive ability, along with crop rotation, tillage, and hand weeding were major components of weed management (Cox et al. 1931). Weed suppressive ability is largely the result of asymmetric resource capture by the crop. An initial size advantage of the crop confers the ability to capture a disproportionally large share of resources, thus suppressing smaller neighbors (McDonald et al. 2010; Place et al. 2011; Schwinning and Weiner 1998; Weiner et al. 2010). Over time, a positive feedback cycle is created, which increases the size disparity between the crop and weed (Connolly and Wayne 1996). Although rarely used as a conscious attempt to manage weeds, weed suppressive ability continues to play an important role in field crops. For example, poor corn stands increased the size and dormancy level of velvetleaf (*Abutilon theophrasti* Medik.) seedbanks (Nurse and DiTommaso 2005). Initial corn canopy height, relative to the weed, was a major predictor of season-long weed growth potential (McDonald et al. 2010). In sweet corn, weed suppressive ability varies among commercial hybrids (So et al. 2009), influences herbicide performance (Williams et al. 2011), and alters germinability of wild-proso millet (Williams et al. 2012).

Sweet corn is susceptible to several types of diseases that reduce crop growth and development, such as maize dwarf mosaic (MDM) which reduces photosynthetic rate and elevates respiration rate (Gates and Gudauskas 1969). As a result, MDM stunts corn growth, delays reproductive development, and causes up to 70% yield loss (Mikel et al. 1981a,b). The most prevalent viral disease in sweet corn, MDM is caused by *Maize dwarf mosaic virus* (MDMV), *Sugarcane mosaic virus* (SCMV), or both. The pathogens overwinter in the southeastern United States and are vectored by dozens of aphid species. Although genetic resistance to MDM has been identified (Jones et al. 2007), sweet corn hybrids with MDM-resistance genes are not immune to the disease (Kerns and Pataky 1997), and approximately two-thirds of commercial sweet corn hybrids have no resistance (Pataky et al. 2011).

A potential disease-mediated effect on crop competitive ability merits study. Localized epidemics of MDM in sweet corn have been observed throughout North America (Arny et al. 1980; Ayers et al. 1978; Forster et al. 1980), and yield-reducing weed infestations are observed in many sweet corn fields (Williams et al. 2008b). Nonetheless, the extent to which MDM compromises the ability of sweet corn to suppress weeds is unknown. Therefore, the objective of this study was to characterize the influence of variable MDM incidence in sweet corn on growth, fecundity, and germinability of wild-proso millet, one of the most abundant weeds in North American sweet corn production.

Materials and Methods

Field experiments were conducted for three seasons (2008 to 2010) on a Flanagan silt loam (fine, smectitic, mesic Aquic

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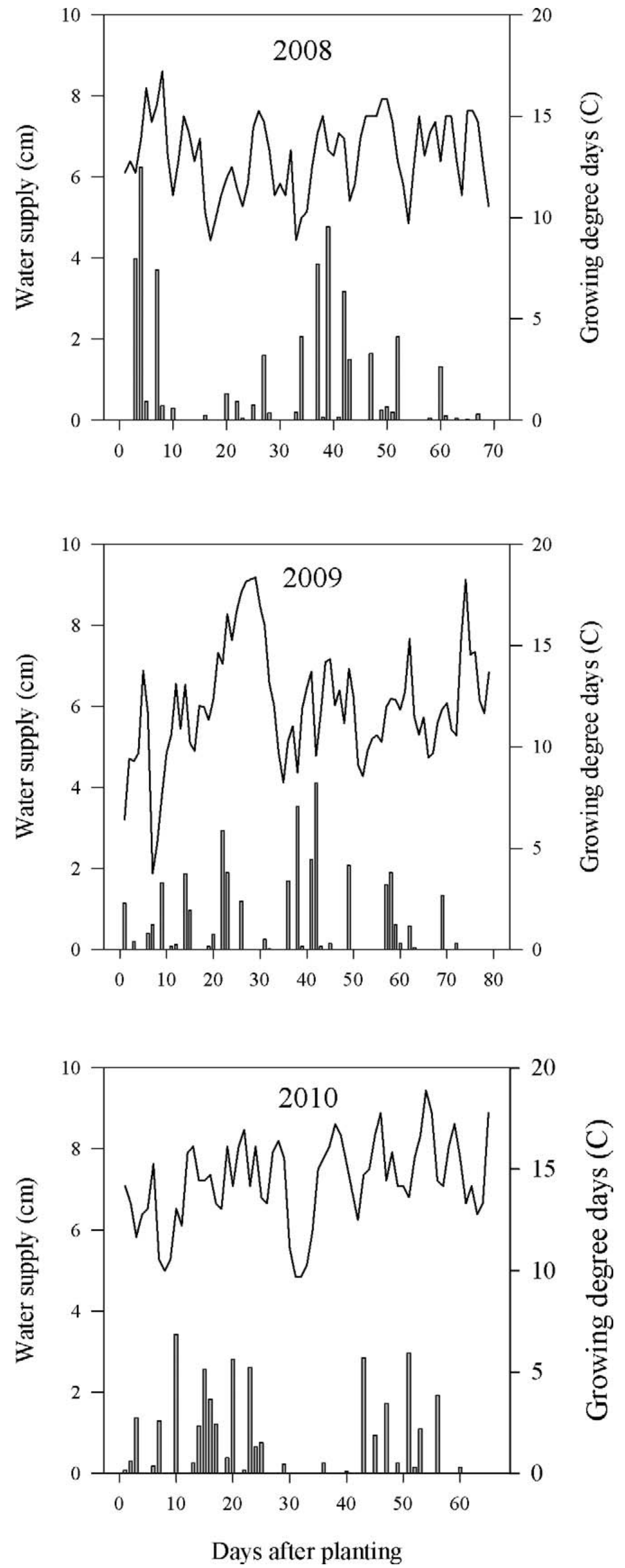

Figure 1. Daily water supply (rainfall + irrigation) and growing degree days (base 10 C) at the University of Illinois Vegetable Crop Research Farm near Urbana, IL, in 2008–2010.

Table 1. Significance (P) of sweet corn hybrid, incidence of maize dwarf mosaic (MDM) in sweet corn, and their interaction on wild-proso millet height in five-leaf corn (V5) and at corn midsilk (R1), shoot biomass, fecundity, and subsequent germination.

		Wild-proso millet				
		Height				
Year	Factor	V5	R1	Biomass	Fecundity	Germination
2008	Hybrid	0.856	0.135	0.025	0.003	0.178
	MDM	0.674	0.447	0.770	0.076	0.853
	Hybrid*MDM	0.891	0.575	0.985	0.136	0.851
2009	Hybrid	0.813	0.503	0.008	0.006	0.007
	MDM	0.725	0.084	0.038	0.012	0.804
	Hybrid*MDM	0.708	0.337	0.864	0.100	0.796
2010	Hybrid	0.071	<0.001	0.018	0.012	0.401
	MDM	0.861	0.007	0.903	0.435	0.906
	Hybrid*MDM	0.671	0.535	0.876	0.535	0.829

Argiudolls) at the University of Illinois Vegetable Crop Research Farm near Urbana, IL. Experiments were located in different fields each year. The previous crop each season was soybean. Fields were chisel plowed in the fall and field cultivated in mid-May immediately after receiving a preplant nitrogen application of 135 kg N ha^{-1} as urea. Sweet corn was planted May 22, 2008, May 21, 2009, and May 25, 2010, at 83,000 seeds ha^{-1}. To ensure plant establishment and avoid drought conditions, rainfall was supplemented with 10.0, 6.4, and 4.6 cm of water in 2008, 2009, and 2010, respectively, with a sprinkler irrigation system.

The experimental design was a split block with five replications. The treatment design was a factorial of hybrid and MDM incidence. Each block consisted of horizontal strips of hybrids and vertical strips of MDM incidence, with horizontal strips orthogonal to vertical strips. Two sweet corn hybrids, 'Sugar Buns' (Crookham Company, Caldwell, ID) and 'Legacy' (Harris Moran Seed Company, Modesto, CA), were planted in four 0.76-m-spaced rows. These hybrids were chosen because previous research showed that Legacy was more suppressive of wild-proso millet growth than Sugar Buns (Y. So and M. Williams, unpublished data). MDM infection of plants at incidence levels of 0, 25, 50, and 75% were randomly assigned to vertical strips measuring 6.1 m in length across both hybrids. In 2009 and 2010, the experiment also included a 100% MDM incidence treatment. A 1.5-m alley was maintained between MDM incidence levels. Additionally, a weed-free, 0% MDM incidence treatment of each hybrid was included each year.

Wild-proso millet seed was collected the year before each experiment from a local population and stored at room temperature. Before planting, germination assays indicated germinability was 40 to 60%. The research plot area had no history of wild-proso millet; therefore, seed was shallowly planted at approximately 100 seeds m^{-1} of row directly into the center two rows, 6.1 m in length, using a cone planter immediately after planting sweet corn. Application of 1.78 kg of *S*-metolachlor ha^{-1} 3 wk after wild-proso millet emergence, interrow cultivation, and hand weeding 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} (5 plants m^{-1} of row).

Levels of MDM incidence were established by mechanically inoculating individual sweet corn plants within all four rows at the three-leaf stage by the pinprick method (Chang et al. 1977). Every fourth plant was inoculated in the 25% level,

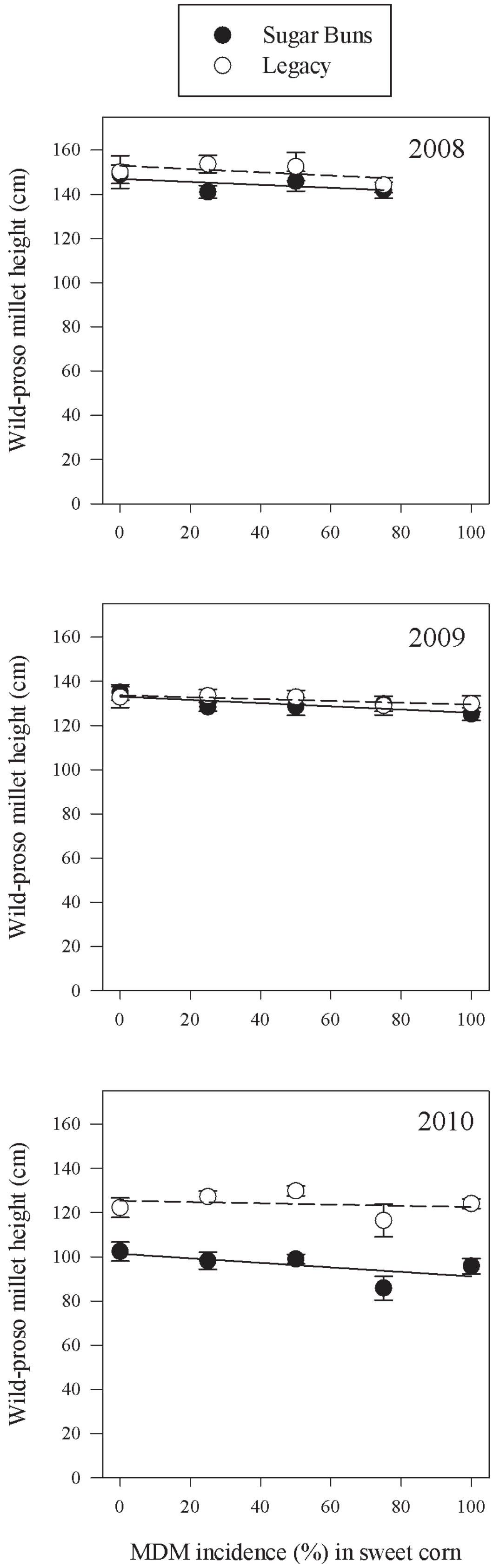

Figure 2. Wild-proso millet height at midsilk (R1) of sweet corn as a function of sweet corn hybrid and maize dwarf mosaic (MDM) incidence in sweet corn. Parameter estimates were obtained by fitting wild-proso millet height to a linear model $y = a + bx$, where x is MDM incidence. Parameter estimates are 2008 Sugar Buns: a = 147, b = −0.067, r^2 = 0.050; 2008 Legacy: a = 153, b = −0.077, r^2 = 0.038; 2009 Sugar Buns: a = 133, b = −0.073, r^2 = 0.128; 2009 Legacy: a = 134, b = −0.042, r^2 = 0.036; 2010 Sugar Buns: a = 101, b = −0.102, r^2 = 0.138; 2010 Legacy: a = 125, b = −0.029, r^2 = 0.011.

every other plant was inoculated in the 50% level, three of every four plants were inoculated in the 75% level, and every plant was inoculated in the 100% level. Plants in the 0% level were not inoculated. Plants were inoculated on two consecutive days. Asymptomatic target plants, identified by wounds from previous inoculations, were inoculated a third time 1 wk later. Inoculum was a combination of strain A of MDMV (MDMV-A), which was maintained on johnsongrass [*Sorghum halepense* (L.) Pers.] in the greenhouse and SCMV (i.e., MDMV-B), which was maintained on sweet corn plants. Inocula of both viruses were increased on field-grown sweet corn plants. Sap of infectious leaves was extracted by blending approximately 500 g each of MDMV-A and SCMV-infected tissue in 3.8 L of 0.1 M potassium phosphate buffer at pH 7 for 30 s. Homogenate was filtered through a paint strainer. Inoculum was prepared by mixing filtered sap extract with 7.6 L of 0.1 M potassium phosphate buffer.

Two permanent quadrats per plot were established by randomly locating 1-m lengths of row in the center two sweet corn rows and marking with wire flags. All wild-proso millet data were taken from plants in permanent quadrats. Three weeks after emergence, wild-proso millet population density was determined from seedling counts. Wild-proso millet height from the soil surface to the plant apex was measured when corn had five fully emerged leaves and at midsilk (R1). At the time of sweet corn harvest, wild-proso millet shoots were clipped at the soil surface, panicles were threshed with a stationary thresher (Seedburo, Chicago, IL), and seeds were cleaned, counted, and stored at room temperature. Shoot biomass was oven-dried at 65 C for 5 d and weighed. Four months after harvest, seeds were tested for germinability in assays using a completely randomized design. In each assay, four 50-seed replicates per plot were incubated on distilled water-moistened filter paper in petri dishes at 25/20 C day/night temperatures with a 12-h photoperiod. Germinated seeds were counted and removed daily for 7 d, after which no additional germination was observed.

Growth variables were measured on both hybrids in the weed-free and 0% MDM treatment after silk emergence. Plant height was measured from the soil surface to the uppermost leaf. Sweet corn leaf area index was measured under full-sun conditions within 2 h of solar noon using a linear ceptometer (AccuPAR model LP-80, Decago Devices, Pullman, WA). Ceptometer measurements of incident light above and below the canopy were used to estimate intercepted photosynthetically active radiation (IPAR). Days from crop emergence to midsilk also were recorded.

Because a MDM incidence level (i.e., 100%) was added to the experiments after the 2008 season and because wild-proso millet establishment differed greatly across years, analyses were performed within each year. Data were examined with diagnostic tests of residuals to ensure compliance with ANOVA assumptions of normality and homoschedasticity. To evaluate the significance of hybrid and MDM incidence on wild-proso millet growth and fecundity, data were analyzed with general linear models fit by restricted maximum likelihood. Regression analyses were used to quantify

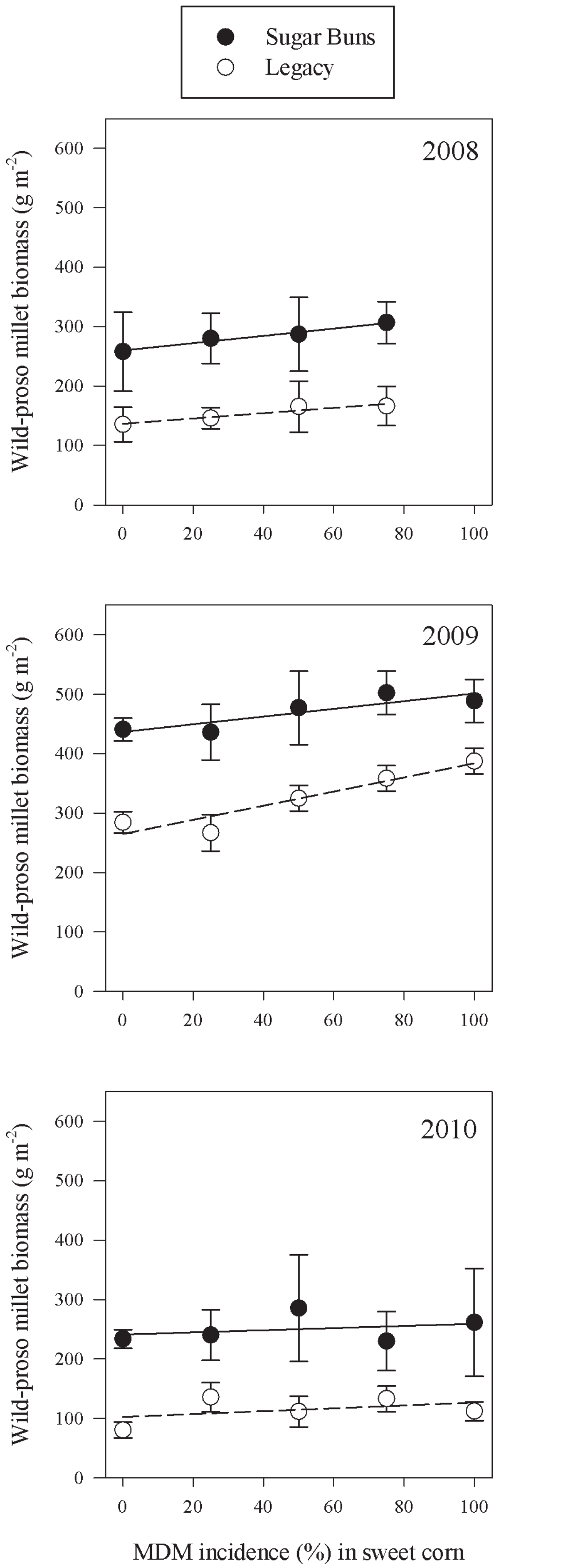

Figure 3. Wild-proso millet shoot biomass at sweet corn harvest as a function of sweet corn hybrid and maize dwarf mosaic (MDM) incidence in sweet corn. Parameter estimates were obtained by fitting wild-proso millet biomass to a linear model y = a + bx, where x is MDM incidence. Parameter estimates are 2008 Sugar Buns: a = 260, b = 0.613, r^2 = 0.025; 2008 Legacy: a = 136, b = 0.441, r^2 = 0.207; 2009 Sugar Buns: a = 437, b = 0.647, r^2 = 0.067; 2009 Legacy: a = 265, b = 1.189, r^2 = 0.428; 2010 Sugar Buns: a = 241, b = 0.181, r^2 = 0.002; 2010 Legacy: a = 103, b = 0.242, r^2 = 0.035.

relationships between wild-proso millet responses and MDM incidence. Even though interactions between the factors were not observed, the effect of MDM incidence on wild-proso millet was plotted separately by hybrid to illustrate both the low variation of the MDM effect and the large hybrid effect. Therefore, wild-proso millet height, biomass, fecundity, and germination were fitted to linear or quadratic models as functions of MDM incidence within each hybrid using least-squares regression. All analyses were performed in SYSTAT (2004) software.

Results and Discussion

Three weeks after planting, wild-proso millet population density averaged 8, 122, and 47 plants m^{-2} in 2008, 2009, and 2010, respectively. Low weed population density in 2008 was largely a result of excessive rainfall immediately after planting. For instance, 14.8 cm of rain fell in the first week after planting in 2008 (Figure 1). Saturated soil conditions appeared to have compromised seedling survival. Weather conditions the remainder of the 2008 season were relatively cool and wet. Generally above-normal rainfall was also observed in 2009. With the exception of above-normal rainfall in June, the 2010 season was characterized as abnormally dry and frequently hot.

Wild-proso millet height was affected ($P \leq 0.007$) by hybrid and MDM incidence in sweet corn only at the R1 sampling date in 2010 (Table 1). The influence of MDM incidence in sweet corn on wild-proso millet height was subtle. For instance, wild-proso millet grew ~ 1 cm shorter with each 10% increase in MDM incidence in 2010 (Figure 2). A decline in weed height with increasing MDM incidence seems logical, in that MDM has been reported to stunt sweet corn growth and reduce canopy density (Mikel et al. 1981a,b; Olson et al. 1990). Therefore, any shade avoidance response of wild-proso millet would be reduced in an MDM-stunted crop.

In the 0% MDM incidence treatment, Legacy was 48, 42, and 61% taller at the R1 growth stage than Sugar Buns in 2008, 2009, and 2010, respectively (data not shown). Nonetheless, wild-proso millet height at the R1 sweet corn growth stage was affected by hybrid only in 2010 (Figure 2). In that year, wild-proso millet growing in plots of Legacy was 28 cm taller than wild-proso millet in Sugar Buns. The increased height of wild-proso millet in the taller hybrid indicated a shade avoidance response; however, this response was not consistent across years despite large height differences between hybrids.

Wild-proso millet biomass was affected ($P \leq 0.038$) by both the hybrid in which the weed was growing and by MDM incidence in sweet corn in 2009 (Table 1). Averaged across MDM incidence, wild-proso millet growing in Sugar Buns weighed 45 to 117% more than wild-proso millet in Legacy (Figure 3). This difference in growth of wild-proso millet between more competitive and less competitive sweet corn hybrids is comparable to previous research in the Midwest and Pacific Northwest (Williams et al. 2008a). Sugar Buns

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intercepted 17 to 25% less IPAR than Legacy (data not shown). Therefore, more light was intercepted by wild-proso millet growing in Sugar Buns than in Legacy, driving a higher level of biomass accumulation. These results are consistent with previous research on the effect of shading on wild-proso millet biomass (Carpenter and Hopen 1985). Incidence of MDM in sweet corn affected wild-proso millet biomass only in 2009. For each additional 10% incidence of MDM across hybrids, wild-proso millet biomass increased 9 g m^{-2} (Figure 3).

Similar to wild-proso millet biomass, fecundity depended on the hybrid ($P \leq 0.012$ across years) in which the weed was growing and, to a lesser extent, by MDM incidence ($P = 0.012$ in 1 yr) in sweet corn (Table 1). Averaged across MDM incidence, wild-proso millet produced 2,700 to 7,200 more seeds per square meter in plots of Sugar Buns than in Legacy (Figure 4). Also, incidence of MDM in sweet corn affected wild-proso millet fecundity only in 2009, with higher levels of weed fecundity with increasing incidence of MDM in sweet corn.

Wild-proso millet germination was largely unaffected by the maternal environments created by hybrid and MDM incidence treatments (Table 1). In previous research, a relationship was observed between the maternal crop environment and wild-proso millet germination immediately after harvest (Williams et al. 2012). Specifically, maternal environments characterized by short, thin crop canopies resulted in wild-proso millet seed that was more germinable immediately after crop harvest compared with maternal environments consisting of tall, dense crop canopies. Apparently the hybrid and MDM incidence treatments in the present work were insufficient in creating unique maternal environments relevant to wild-proso millet germination. Alternatively, the 4-mo postharvest interval preceding germination tests could have attenuated responses to sweet corn treatments.

Commercial sweet corn hybrid had a larger effect on wild-proso millet growth and fecundity than incidence of MDM in the crop. Averaged over MDM incidence, differences between hybrids in weed biomass was 137 g m^{-2}, averaged over years. In contrast, differences in weed biomass between 0 and 100% MDM incidence treatments was 50 g m^{-2}, averaged over years. Similar trends were observed in fecundity, where differences between hybrids were ~ 2.7 times higher than differences in fecundity between 0 and 100% MDM incidence treatments.

Nonetheless, incidence of MDM in sweet corn could be a contributing factor to weed escapes in certain fields. Incidence of MDM reduced the weed suppressive ability of sweet corn under high weed population densities. For instance, when wild-proso millet averaged 122 plants m^{-2} in 2009, each additional 10% incidence of MDM in sweet corn resulted in an additional 6 to 12 g m^{-2} of weed biomass. Although not significant ($\alpha \leq 0.05$) in years with lower weed population densities, there remained a trend for increased weed biomass and fecundity with increased MDM incidence in sweet corn.

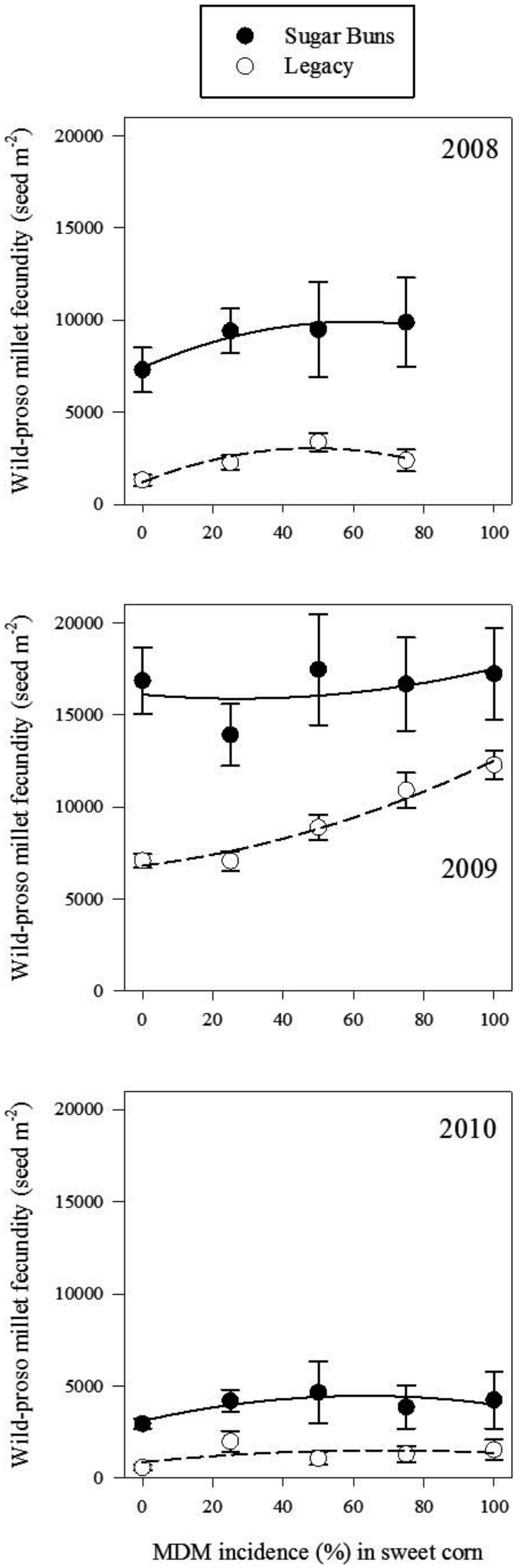

Figure 4. Wild-proso millet fecundity at sweet corn harvest as a function of sweet corn hybrid and maize dwarf mosaic (MDM) incidence in sweet corn. Parameter estimates were obtained by fitting wild-proso millet fecundity to a quadratic model $y = a + bx + cx^2$, where x is MDM incidence. Parameter estimates are 2008 Sugar Buns: a = 7414, b = 83.26, c = −0.6987, ~ r^2 = 0.064; 2008 Legacy: a = 1205, b = 73.41, c = −0.7533, ~ r^2 = 0.353; 2009 ←

Sugar Buns: a = 16108, b = −16.44, c = 0.3047, ~ r^2 = 0.015; 2009 Legacy: a = 6817, b = 23.00, c = 0.3409, ~ r^2 = 0.673; 2010 Sugar Buns: a = 3110, b = 43.09, c = −0.3416, ~ r^2 = 0.038; 2010 Legacy: a = 877, b = 18.56, c = −0.1360, ~ r^2 = 0.052.

Conditions of high weed interference are not uncommon in sweet corn. Weed interference was high enough to cause yield losses in most fields, with moderate to severe levels (i.e., $> 5\%$ and $> 20\%$ crop losses, respectively) occurring in one-quarter of fields surveyed (Williams et al. 2008b).

MDM is problematic throughout North America (Arny et al. 1980; Ayers et al. 1978; Forster et al. 1980). Minimizing the negative effects of the disease requires the use of MDM-resistant hybrids, but approximately two-thirds of commercial sweet corn hybrids have no resistance to MDM (Pataky et al. 2011). Regardless of inherent differences in competitiveness between the two hybrids tested in the present work, the weed suppressive ability of the crop was equally affected by the disease. Given the MDM susceptibility of hybrids grown in North America, the disease might be an additional factor perpetuating weed growth and fecundity in sweet corn, particularly in fields with high weed population densities of wild-proso millet.

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