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Differential Tolerance in Sweet Corn to Wild-proso Millet (*Panicum miliaceum*) Interference

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Crop tolerance (CT), the crop's ability to endure or avoid competitive stress from weeds, varies between old and modern dent corn hybrids; however, this hypothesis has not been tested in sweet corn. Three modern sweet corn hybrids, known to vary in canopy density, were subjected to a range of wild-proso millet densities under irrigated conditions in Washington and primarily rain-fed conditions in Illinois. A path analysis was used to identify relationships among CT and specific canopy properties important to competitive interactions. Crop tolerance varied among hybrids in three of four site–years. Sweet corn hybrid 'Spirit' suffered higher yield losses than hybrids 'WHT2801' and 'GH2547'. Generally higher yield loss parameter estimates in Illinois, compared with Washington, suggests CT may have more to offer for weed management in the north-central than north-western United States. Path analysis indicated that wild-proso millet biomass and seedling population density were both important factors driving yield loss in canopy-sparse Spirit, whereas only early season wild-proso millet population density contributed to yield loss of canopy-dense WHT2801 and GH2547. Differential tolerance to weed interference exists among commercially available sweet corn hybrids.

Nomenclature: Wild-proso millet, *Panicum miliaceum* L. PANMI, sweet corn, *Zea mays* L. 'GH2547', 'Spirit', 'WHT2801'.

Key words: Competition, path analysis, risk, weed density, yield loss.

Crop tolerance (CT) is a nonchemical weed management tactic that relies on the neutral effect that plants have on their neighbors (Jordan 1993). Crop tolerance is defined as the ability of the crop to endure or avoid competitive stress from the weed without substantial yield reduction. Considerable variation in CT exists between old and modern dent corn hybrids (Lindquist and Mortensen 1998; Tollenaar et al. 1997). The CT of agronomic crops can be enhanced through genetic approaches, such as breeding (Jannink et al. 2000), or cultural approaches, such as crop-row spacing (O'Donovan et al. 2006). The primary goal of using CT as one tactic in an integrated weed management plan is to reduce risk of crop yield loss.

A majority of research on CT in corn has been conducted in dent corn and may have limited application to sweet corn. Sweet corn is differentiated from other types of corn by genes affecting starch synthesis in the endosperm, emergence, and growth (Azanza et al. 1996; Tracy 2001), as well as by crop husbandry, such as lower seeding rates and an extended planting period (Anonymous 2003a,b). The United States ranks first in global sweet corn production; approximately 172,000 ha are grown for processing, and 106,000 ha are grown for fresh market (Anonymous 2006). Of sweet corn grown for processing, over 90% of the production is grown under primarily rain-fed conditions in the north-central United States and under irrigation in the north-western United States (Anonymous 2006).

Weed management systems in sweet corn rely heavily on PRE applications of atrazine (Anonymous 2003b). Swanton et al. (2007) discussed the environmental and political issues surrounding use of atrazine and argued for research that enables atrazine use reduction in North America. Despite extensive use of several herbicides in sweet corn, weeds persist and yield loss due to weed interference appears common (Williams et al. 2006b). Development of herbicide-resistant sweet corn cultivars has lagged in comparison to other agronomic crops in the United States, and few nonchemical weed management tactics have been evaluated (Davis and Liebman 2001; Mohler 1991).

Wild-proso millet, a weedy race of domesticated proso millet, infests much of the sweet corn in the northern United States and southern Canada. Because of natural tolerance to most herbicides used in sweet corn, high competitive ability, and prolific seed production before crop harvest, wild-proso millet is considered one of the most difficult weeds to manage in North America sweet corn production (Kleppe and Harvey 1991; Williams and Harvey 2000). Recent surveys of weeds in sweet corn in Illinois, Minnesota, and Wisconsin documented wild-proso millet as one of the densest, most frequent, and most fecund species observed (Williams et al. 2006b).

Modern sweet corn hybrids may vary in CT; however, that hypothesis has not been tested. Factors influencing CT among dent corn hybrids include leaf area index (LAI) (Lindquist and Mortensen 1998), intercepted light (Lindquist and Mortensen 1998), crop maturity (Begna et al. 2001), and other traits that are often intercorrelated (Duvik 2005). Williams et al. (2006a) found significant variation in weed-free canopy properties among three sweet corn hybrids and hypothesized that hybrids varied in competitive ability. If, indeed, hybrids differentially tolerate weed interference, then that knowledge merits consideration in the development of weed management systems for sweet corn.

Using the same hybrids tested by Williams et al. (2006a) for canopy characteristics, we subjected the crop to varying levels of wild-proso millet population density and evaluated responses using a simple mechanistic model. The objectives were to quantify the tolerance of sweet corn hybrids to wild-proso millet interference and to identify potential relationships between the crop and weed.

Materials and Methods

Site Description. Field experiments were conducted in 2004 and 2005 at the University of Illinois, Crop Sciences Research

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and Education Center, near Urbana, IL (40°4′N, 88°12′W), and the Washington State University, Roza Unit, near Prosser, WA (46°15′N, 119°44′W). The soil at Illinois was a Flanagan silt loam (fine, smectitic, mesic Aquic Argiudoll) with 3.6% organic matter and a pH of 6.4, and the soil at Washington was Warden sandy loam (coarse-silty, mixed, superactive, mesic Xeric Haplocambid) with 0.9% organic matter and a pH of 6.5. Experiments were located in different fields in each year. The previous crop was alfalfa (*Medicago sativa* L.; 2004 field) and soybean [*Glycine max* (L.) Merr; 2005 field] at Illinois and dent corn at Washington (both years). Fields in Illinois received 129 kg N ha^{-1}, 113 kg P ha^{-1}, and 135 kg K ha^{-1} on March 23, 2004, and March 16, 2005. Fields in Washington received 319 kg N ha^{-1}, 79 kg P ha^{-1}, and 168 kg K ha^{-1} on May 10, 2004, and 224 kg N ha^{-1}, 59 kg P ha^{-1}, and 186 kg K ha^{-1} on May 2, 2005. The experimental area was chisel-plowed in the fall or spring, followed by one pass each of a disk harrow and a field cultivator before planting.

Experimental Approach. The experimental design was a split plot with four replications, where the main plot factor was sweet corn hybrid and subplot factor, represented in each main plot, was wild-proso millet population density. Sweet corn hybrids 'Spirit', 'WHT2801', and 'GH2547' were planted in 76-cm rows with a four-row planter. All hybrids were *sugary1* endosperm mutants; however, Spirit is an earlier-season hybrid compared with midseason hybrids WHT2801 and GH2547. Fields were planted at 70,400 seeds ha^{-1} in Illinois and 77,800 seed ha^{-1} in Washington, using a seeding depth of 3.2 to 3.8 cm. As needed, sweet corn was thinned to achieve similar population density. Four wild-proso millet seeding rates were assigned to subplots, measuring 12.2 m in length and four rows wide, with the intent to establish a range of 0 to 130 plants m^{-2} over which sweet corn responses could be determined. Wild-proso millet was not previously observed at experimental sites; therefore, within 3 d of crop planting, wild-proso millet was seeded 1.3 cm deep in the center two crop rows of each subplot using a cone planter. Planting dates in 2004 were May 24 and May 19 in Illinois and Washington, respectively. Planting dates in 2005 were May 23 and May 9 in Illinois and Washington, respectively; however, abnormally dry conditions resulted in a poor crop stand in Illinois, and the site was cleared with an application of 1.3 kg ae glyphosate ha^{-1} + 2% v/v ammonium sulfate and replanted with seed of sweet corn and wild-proso millet June 20. In 2004, each location used wild-proso millet seed from populations found in the region; however, Washington seed was used in Illinois during replanting in 2005.

A PRE application of 2.2 kg ai ha^{-1} atrazine (Illinois) or 1.12 kg ai ha^{-1} atrazine (Washington) was applied to the entire study area within a day of planting, whereas a separate PRE application of 1.78 kg ai ha^{-1} *S*-metolachlor was made to weed-free plots only. Weeds other than wild-proso millet were removed by hand, and lambda-cyhalothrin at 26 g ai ha^{-1} or permethrin at 168 g ai ha^{-1} was applied as needed to control Western corn rootworm (*Diabrotica virgifera* LeConte) beetles. Experimental sites in Washington were furrow-irrigated an average of 44 cm each year. The experimental site in 2005 in Illinois was sprinkler-irrigated twice (July 2 and August 8), and each irrigation event totaled 2.5 cm of water to offset abnormally low rainfall.

Data Collection. Wild-proso millet population density was determined by counting the number of seedlings in three, 1-m sections of row per plot within 3 wk of initial emergence. Using the same sampling pattern at the time of harvest, wild-proso millet shoot biomass was determined by clipping plants at the soil surface, oven-drying at 65 C, and weighing.

LAI was characterized near harvest, a phenological time highly related to weed-free sweet corn yield (Williams et al. 2006a), wild-proso millet suppression by sweet corn (Williams et al. 2007), and dent corn tolerance and weed suppressive ability (Lindquist and Mortensen 1998; Lindquist et al. 1998). Two crop plants were clipped at the soil surface, leaves were separated, and green leaf area was measured using an area meter.[1] LAI was estimated as the product of mean leaf area per plant and number of plants per square meter.

Marketable ears in weedy and weed-free plots were hand-picked 18 to 21 d after anthesis from the center two rows over 6.1 m of row. Ears were considered marketable if kernels were full and had a moisture content of 75 ± 3%, which occurred 18 to 22 d after anthesis. Ears (including silks + husks) meeting these criteria exceeded 4.4 cm in diam. Total mass of marketable ears was recorded.

Statistical Analyses. Mass of marketable ears in each plot was divided by mass in the weed-free plot of each replicate to determine relative yield. Percentage yield loss was calculated as unity minus relative yield. A rectangular hyperbola equation (Cousens 1985) was fit to yield loss in each year and location:

$$Y_l = (I \times N)/[1 + (I \times N/A)] \qquad [1]$$

where Y_l is percentage yield loss, N is wild-proso millet population density (expressed in plants m^{-2}), I is percent yield loss as weed density approaches zero, and A is maximum predicted yield loss. Parameter estimates were determined using an iterative least-squares procedure (SYSTAT).[2] The extra sum of squares principle for nonlinear regression analysis (Ratkowsky 1983) was employed to evaluate the similarity of parameter estimates among hybrids. Comparisons were made by calculating a variance ratio of individual and pooled residual sums of squares (Lindquist et al. 1996).

Potential links between sweet corn LAI, wild-proso millet population density and biomass, and sweet corn yield loss due to weed interference were investigated using path analysis (Ball et al. 2001; Jordan 1989; Ogg and Seefeldt 1999). Path analysis is a multiple regression method that specifies potential causal pathways between two or more independent and dependent variables of interest, accounting for correlations between variables and unexplained (latent) sources of error (Mitchell, 2001). The RAMONA subroutine of SYSTAT was used to estimate standardized regression coefficients and latent variables for a single-path analysis model analyzed within sweet corn hybrids but across locations and years.

Results and Discussion

Sweet corn and wild-proso millet emergence coincided at each site from 4 to 10 d after planting. Measured within 3 wk of emergence, wild-proso millet population density included a range of densities with a maximum of 53 to 173 seedlings m^{-2} over all site–years. Abnormally dry conditions during the grain-fill period in 2005 in Illinois resulted in poorer yields compared with the previous year. Although

Table 1. Parameter estimates of Equation 1 for the effect of initial weed density on relative crop yield loss of three sweet corn hybrids grown near Urbana, Illinois and Prosser, Washington. Standard errors of parameter estimates are in parentheses.

Year	Location	Hybrid	*I*	*A*	R^2
2004	Illinois	Spirit	4.0 (1.8)	100 (42)	0.74
		WHT2801	0.5 (0.5)	100 (> 100)	0.33
		GH2547	8.1 (59)	6.8 (4.8)	0.10
	Washington	Spirit	1.2 (1.4)	20 (8.2)	0.36
		WHT2801	0.1 (0.1)	30 (> 100)	0.16
		GH2547	4.6 (40)	8.6 (4.3)	0.19
2005	Illinois	Spirit	0.7 (0.5)	100 (97)	0.62
		WHT2801	0.9 (0.8)	100 (> 100)	0.42
		GH2547	0.4 (0.6)	100 (> 100)	0.28
	Washington	Spirit	0.4 (0.1)	100 (92)	0.77
		WHT2801	0.1 (0.2)	41 (> 100)	0.22
		GH2547	0.4 (0.2)	29 (9.6)	0.76

season-long cumulative precipitation plus irrigation was similar in both years, drought-stress conditions persisted during much of the grain-fill period in 2005. Weed-free yields in 2004, in Illinois, were 15.5, 13.2, and 16.9 Mg ha^{-1} for Spirit, WHT2801, and GH2547, respectively. Weed-free yields in 2005, in Illinois, were 9.4, 7.2, and 8.5 Mg ha^{-1} for Spirit, WHT2801, and GH2547, respectively. Ear mass yields in Washington were similar across years, averaging 17.5, 22.0, and 23.8 Mg ha^{-1} for Spirit, WHT2801, and GH2547, respectively.

Sweet Corn Tolerance. Overall, sweet corn grown in Washington appeared more tolerant to wild-proso millet interference than sweet corn grown in Illinois. Despite wild-proso millet densities in excess of 140 plants m^{-2}, maximum observed yield loss was less than 41% and, with one exception, maximum predicted yield loss (*A*) was equal to or less than 41% (Table 1). However in Illinois, maximum predicted yield loss was 100% with only one exception in 2004. These results are consistent with McDonald et al. (2004); of 19 site–years of data, they found that warm initial temperatures (> 14.5 C) followed by dry conditions (climatological water balance < 0.6) were associated with highest dent corn yield losses due to velvetleaf (*Abutilon theophrasti* Medic.) interference. In Illinois, where irrigation was limited, such conditions were common and season-long precipitation averaged 55% of rainfall plus irrigation in Washington (data not shown). Sweet corn grown in the arid north-western United States is routinely irrigated, whereas sweet corn grown in the north-central United States is often grown under rain-fed conditions (Anonymous 2003a). Environmental conditions in Washington are typically better for crop growth than Illinois, as evidenced by higher average state-wide yields for sweet corn (Anonymous 2006).

The ability of sweet corn to endure or avoid competitive stress from wild-proso millet varied by hybrid. The *F* test for comparing nonlinear models indicated that crop response to wild-proso millet interference was not consistent among site–years; therefore, data are presented separately for each location and year. Spirit often suffered greater yield loss than WHT2801 or GH2547 (Figure 1). As an example, the *F* test for comparing nonlinear models indicated the yield loss function for Spirit was different from WHT2801 in 3 of 4 site–years, and only in Illinois in 2005 were yield loss relationships similar among hybrids. Fit of the hyperbolic model to yield loss data in Illinois in 2005 was poor for all hybrids (R^2 0.16 to 0.36) and likely due to the yield variation introduced by abnormally low precipitation that year. In contrast, the largest differences in yield loss among hybrids were observed in Illinois in 2004, when maximum predicted yield loss was 100 and 6.8% for Spirit and GH2547, respectively (Table 1).

Few have reported the effect of weed population density on sweet corn yield loss, and this is the first report of differential yield response to weed interference among hybrids. In irrigated dent corn, Wilson and Westra (1991) reported 47 to 67% yield losses from season-long wild-proso millet at densities as high as 380 plants m^{-2}. An unspecified population density of wild-proso millet growing throughout the season caused 80% yield loss in sweet corn in Wisconsin (Williams and Harvey 2000). The *I* parameter of Equation 1 has been used as an index for comparing relative competitiveness among weed species (Swinton et al. 1994) and allows comparison of previously reported *I* values on an equivalent weed-density scale. As an example, *I* values for giant ragweed (*Ambrosia trifida* L.) interference in sweet corn ranged from 97 to 119% (Williams and Masiunas 2006); considerably higher than *I* values reported in Table 1 (0.1 to 8.0%), indicating the lower competitive ability of wild-proso millet relative to giant ragweed.

Path Analysis. Path analysis of sweet corn LAI and wild-proso millet population density and biomass effects on sweet corn yield loss due to interference showed similar results for WHT2801 and GH2547. In these hybrids, sweet corn LAI was negatively correlated, whereas wild-proso millet population density was positively correlated, with wild-proso millet biomass at final sweet corn harvest (Figure 2; Table 2). Wild-proso millet biomass and sweet corn LAI were not correlated with yield loss for these hybrids; therefore, the model did not offer support for either a direct or indirect causal link between sweet corn LAI and sweet corn yield loss. Measurements of LAI taken earlier in the season (see Williams et al. 2006a) were not correlated with yield loss either (data not shown). There was no indirect link between wild-proso millet population density and sweet corn yield loss through wild-proso millet biomass, but there was a direct positive association between population density and yield loss. Results for Spirit were similar to those of GH2547 and WHT2801 with one important exception: there was a strong positive association between wild-proso millet biomass and sweet corn yield loss. Thus, the model showed the interaction of three weed–crop parameters influencing yield loss of Spirit. Variations in sweet corn LAI could either suppress or fail to suppress development of wild-proso millet biomass, which increased in proportion to early season wild-proso millet population density and contributed to reductions in sweet corn yield.

Differences between hybrids in the impact of weed biomass on yield loss due to interference appear to have resulted from WHT2801 and GH2547 dominating the weed–crop canopy thereby preventing substantial growth of wild-proso millet biomass, compared with the weaker and more variable canopy of Spirit. Wild-proso millet biomass was higher when grown in Spirit than wild-proso millet grown in WHT2801 or GH2547 (Williams et al. 2007). Variation in crop canopy density was seen in efficiency of light capture as well. Shortly after anthesis, WHT2801 and GH2547 captured approxi-

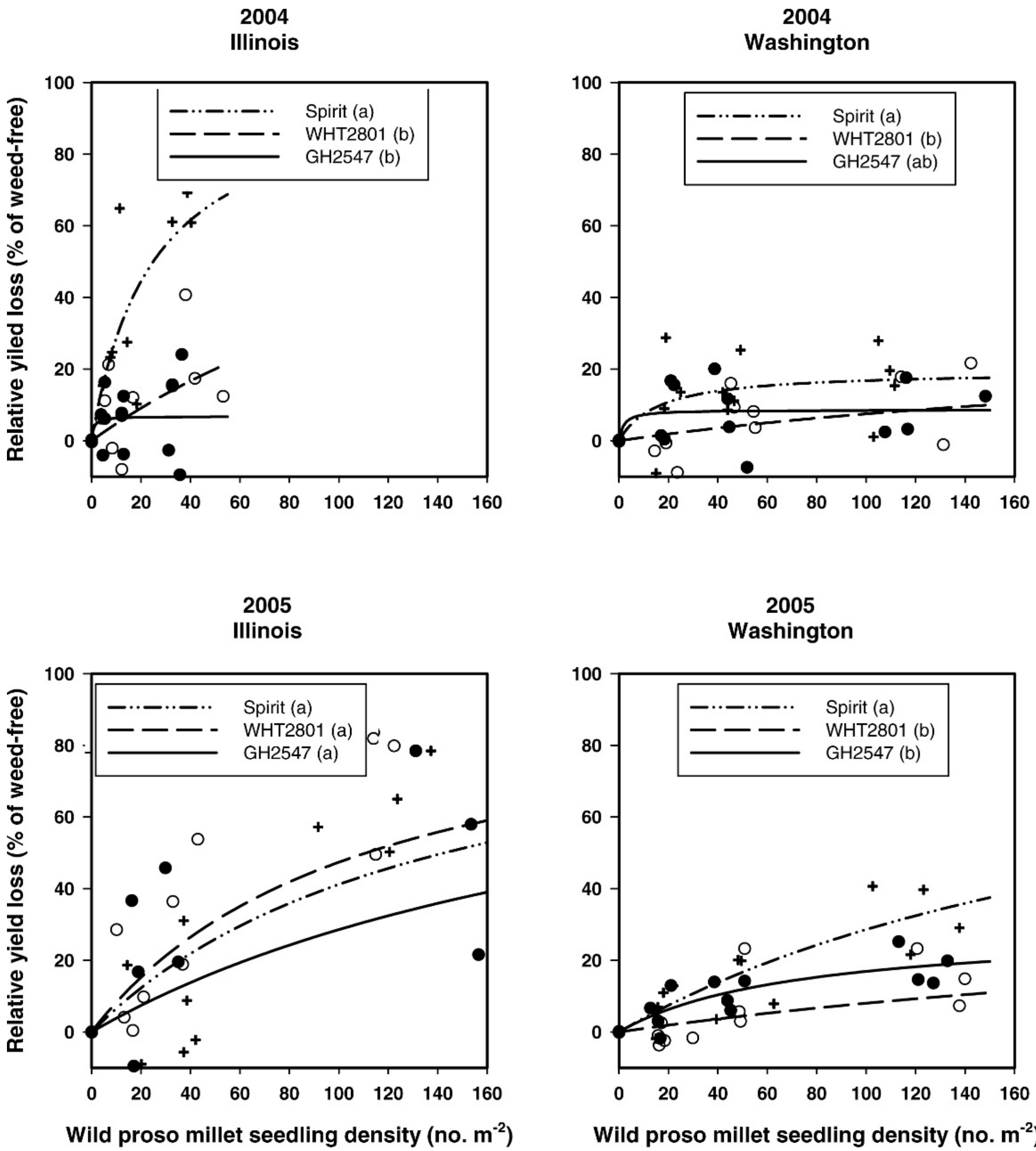

Figure 1. Effect of wild-proso millet population density on relative sweet corn yield loss in field studies conducted in Urbana, IL, and Prosser, WA, in 2004 and 2005. Within each site–year, hybrids followed by the same letter (in parentheses) are similar as evidenced by $P > 0.05$ for the variance ratio of individual and pooled residual sums of squares. Symbols for observed values: +, Spirit; ○, WHT2801; ●, GH2547. Parameter estimates of Equation 1 are shown in Table 1.

mately 92% of photosynthetically active radiation, with a range of only 14 and 17%, respectively, between the lowest (84 and 81%, respectively) and highest levels (98% for both hybrids) of light capture (Williams et al. 2006a). Spirit, in contrast, captured 85% of photosynthetically active radiation on average and had a twofold greater range between the lowest (61%) and highest (97%) levels of light attenuation (Williams et al. 2006a).

Although wild-proso millet biomass was not correlated with yield of GH2547 and WHT2801, the population density of wild-proso millet was strongly associated with yield loss. The V2 stage of growth lies within the critical period of weed control for sweet corn (Williams 2006). One possible mechanism that could explain the negative impact of numerous small weed seedlings on sweet corn yield, yet not through their contribution to weed biomass, is by the influence of weed seedlings on the early season light environment experienced by the crop. Rajcan et al. (2004) found that changes in the red : far-red light ratio due to soil cover by low lying vegetation was sufficient to induce developmental changes in dent corn seedlings resulting in change in carbon allocation (greater shoot : root ratio) and leaf orientation. Thus, the canopy of a more competitive hybrid may help limit sweet corn yield loss due to weed interference by constraining weed growth, but a viable integrated weed management system will also require some form of early season weed control.

Results from this work support the hypothesis that CT varies among modern sweet corn hybrids (Figure 1). Although WHT2801 and GH2547 responded similarly to wild-proso millet interference, Spirit suffered higher yield losses in three of four site–years. Differential CT among

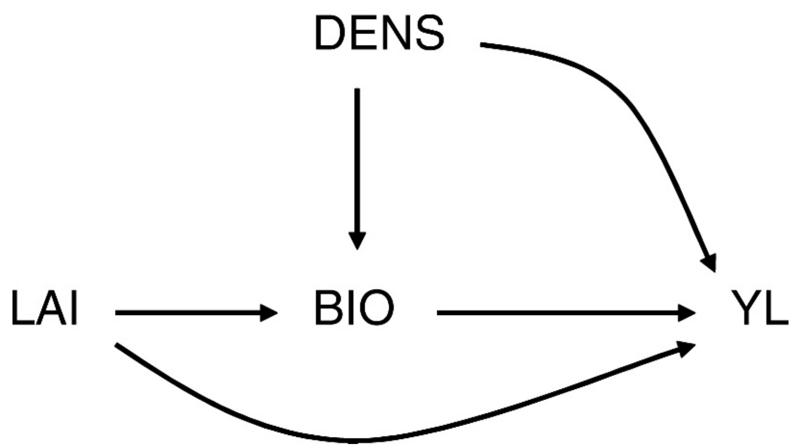

Figure 2. Path-analysis model for comparing sweet corn canopy and wild-proso millet population density contributions to sweet corn yield loss. Abbreviations: DENS, wild-proso millet population density (plants m^{-2}) within 3 wk of emergence; LAI, sweet corn leaf area index (cm^2 m^{-2}) under weed-free conditions near harvest; BIO, wild-proso millet biomass (g ha^{-1}) at time of at harvest; YL, sweet corn yield loss (percentage of weed-free yield) due to wild-proso millet interference.

Table 2. Standardized regression coefficients for path analysis of sweet corn canopy and wild-proso millet population density contributions to yield loss of three sweet corn hybrids grown near Urbana, Illinois and Prosser, Washington in 2004 and 2005.

Sweet corn	Standardized regression coefficients				
hybrid	LAI[a] → BIO	DENS → BIO	LAI → YL	BIO → YL	DEN → YL
Spirit	−0.25*	0.45**	−0.14	0.56**	0.32*
WHT2801	−0.28**	0.61**	−0.02	−0.04	0.48**
GH2547	−0.27**	0.64**	0.12	0.18	0.33*

[a] Abbreviations: DENS, wild-proso millet population density (plants m^{-2}) within 3 wk; LAI, sweet corn leaf area index (cm^2 m^{-2}) under weed-free conditions near harvest; BIO, wild-proso millet biomass (g ha^{-1}) at harvest; YL, sweet corn yield loss (percentage of weed-free yield) due to wild-proso millet interference.

*$P < 0.05$; ** $P < 0.01$ significance of standardized regression coefficients.

commercially available hybrids should be considered in developing integrated weed management systems for sweet corn. Weed management systems developed in the context of competitive hybrids, such as GH2547, may carry a higher risk of failure in less-competitive cultivars. Cultural practices, such as selecting hybrids with greater CT for weedy fields, could reduce risk of yield loss when other tactics are expected to result in incomplete weed control. Efforts at parameterizing decision-support systems for sweet corn are underway (e.g., WeedSOFT[3]); however, current models do not currently account for cultivar differences in CT (Neeser et al. 2004). Though breeding for improved CT has been proposed in some agronomic crops, such efforts do not appear to be a priority among most, if not all, breeding programs, and constraints to this approach in sweet corn are currently undefined. Knowledge of differential CT among commercially available hybrids identifies a unique challenge, and perhaps opportunities, to managing weeds in sweet corn.

Sources of Materials

[1] LI-3100C Area Meter, LI-COR, 4421 Superior Street, Lincoln, Nebraska 68504-0425.

[2] SYSTAT software 2004, Version 11.0, Systat Software Inc., 1735 Technology Drive, Suite 430, San Jose, CA 95110.

[3] WeedSOFT®, University of Nebraska–Lincoln, 3310 Holdrege Street University of Nebraska-Lincoln Lincoln, NE 68583.

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