Variation in Wild Proso Millet (*Panicum miliaceum*) Fecundity in Sweet Corn Has Residual Effects in Snap Bean

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Bioeconomic models are predicated upon the relationship between weed fecundity and crop yield loss in consecutive growing seasons, yet this phenomenon has received few empirical tests. Residual effects of wild proso millet (WPM) fecundity in sweet corn upon WPM seedling recruitment, weed management efficacy, and crop yield within a subsequent snap bean crop were investigated with field experiments in Urbana, IL, in 2005 and 2006. WPM fecundity in sweet corn showed strong positive associations with WPM seedbank density, seedling recruitment, and demographic transitions within snap bean. A negative exponential relationship between WPM initial seedling density and seedling survival of a single rotary hoe pass indicated that the rotary hoe was ineffective at low weed population densities, but its efficacy increased with increasing weed population density to a maximum of 75% seedling mortality. Efficacy of postemergent chemical control of WPM was unaffected by WPM population density. Path analysis models demonstrated dependence between WPM fecundity in sweet corn, WPM seedling recruitment in snap bean, and reductions in snap bean yield in subsequent growing season, mediated by negative impacts of WPM seedling establishment on snap bean stand. These results underscore the importance of expanding integrated weed management programs to include management of annual weed populations both at the end of their life cycle, by reducing fecundity and seed survival, and at the very beginning of their life cycle, by reducing seedling recruitment and establishment.

Nomenclature: Wild proso millet, *Panicum miliaceum* L.; sweet corn, *Zea mays* L., 'GH2547', 'Spirit', 'WHT2801'; snap bean, *Phaseolus vulgaris* L., 'Caprise' and 'Charon'.

Key words: Density dependence, population dynamics, integrated weed management, weed suppressive hybrids, interference, path analysis, soil seedbank, safe sites, early season control.

The old maxim ''One year's seeding, seven years' weeding'' summarizes generations of farmer experience with long-term consequences of weed management failures within a given year. Likewise, population dynamics simulation models predict that conditions resulting in substantial inputs to the weed seedbank should have effects that propagate well into the future (Bussan and Boerboom 2001; Davis et al. 2004; Heggenstaller and Liebman 2006; Mertens et al. 2006; Rasmussen and Holst 2003). Bioeconomic models making use of thresholds indicate that, if impacts of present inputs to the seedbank on yield loss and management cost in subsequent growing seasons are considered, tolerance for seed production should be close to zero (Norris 1999). Preventative weed management may be especially relevant for low external-input production systems or crops that are particularly sensitive to weed infestations, such as horticultural crops (Jordan 1996). Given the potential importance of the link between present weed management outcomes and future weed interference with crop yield, empirical tests of this concept under field conditions are surprisingly rare.

Experimental manipulations of weed populations to create large gradients in density have demonstrated density-dependent plant survival (Dieleman et al. 1999) or density-dependent reductions in herbicide efficacy (Taylor and Hartzler 2000). Such results demonstrate the potential hazards associated with permitting weeds to produce seed and also provide an explanation for the self-perpetuating nature of dense weed patches (Mortensen and Dieleman 1998). Under conditions that more closely resemble commercial crop production systems, with smaller density gradients, density-dependent signals are less clear. A long-term study of cropping system effects on above- and belowground community structure and crop yield (Davis et al. 2005) indicated that the association among seedbank density, seedling density, and crop yield varied with management system. For cropping systems with little or no herbicide use, including reduced input or organic systems, large seedbanks resulted in large seedling populations and lower crop yields. In contrast, intensively managed systems tended to disrupt the connection between previous year's management outcomes, mediated through seedbank density, and current year's weed populations and crop yield.

Sweet corn is a commercially important U.S. vegetable crop (NASS 2006) with stringent weed management requirements to maintain crop yield and quality. Because of a shortage of herbicides registered for use in sweet corn and sensitivity of some hybrids to registered products (Williams et al. 2005), integrated weed management strategies incorporating other tactics are critical to successful long-term weed management in sweet corn. In recent work, we demonstrated that variation in sweet corn canopy characteristics (Williams et al. 2006) can make significant contributions to weed management through crop tolerance to weed interference (Williams et al., unpublished data), weed suppressive ability (Williams et al. 2007), and reductions in herbicide use (Williams and Boydston 2007). Differential suppression of WPM by contrasting sweet corn hybrids resulted in large variations in WPM fecundity (Williams et al. 2007). The current study builds upon the previous investigations by testing the hypothesis that management-related variation in WPM fecundity has residual effects upon (1) WPM population density, (2) weed management efficacy, and (3) crop yield in the following phase of a vegetable crop sequence.

Materials and Methods

Experimental Approach. Field experiments were conducted at the University of Illinois Crop Sciences Research Center in

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Table 1. Schedule of field operations in Urbana, IL, from 2004 to 2006. Separate fields were used in 2004/2005 and 2005/2006 experiments.

Rotation phase[a]	Crop	Month	Field operation	Data collection[b]
S_1	Sweet corn	August	Harvest sweet corn	Quantify WPM fecundity (F)
S_2	Fallow	March	Apply fertilizer and cultivate	Sample WPM seedbank (S)
		April		Census WPM seedlings (P0)
	Snap bean		Glyphosate burndown	
			Plant snap bean	
		May		Census WPM seedlings (P1)
			Rotary hoe	
				Census WPM seedlings (P2)
		June		Census WPM seedlings (P3)
			Apply sethoxydim	
		July		Census WPM seedlings (P4)
				Harvest snap bean
				Final WPM census and biomass

[a] S_1, phase 1, in which three sweet corn hybrids were grown in competition with varying densities of wild proso millet (WPM); S_2, phase 2, in which snap bean was grown in plots that had received varying WPM seed inputs within the sweet corn crop in S_1.

[b] F, fecundity in sweet corn; S, soil seedbank prior to snap bean; P0, WPM plant population density prior to snap bean; P1, WPM plant population density prior to rotary hoeing; P2, WPM plant population density after rotary hoeing; P3, WPM plant population density prior to sethoxydim; P4, WPM plant population density after sethoxydim.

Urbana, IL, from 2004 to 2006. The soil at this site was a Flanagan silt loam (fine, smectitic, mesic Aquic Argiudoll) averaging 3.6% organic matter and pH of 6.4. The experimental system consisted of two consecutive crop phases (Table 1): S_1, in which WPM was grown in competition with three sweet corn hybrids that had contrasting canopy characteristics and differential weed suppressive ability (Williams et al. 2007); and S_2, in which snap bean was grown in plots from the S_1 phase that had received varying inputs of WPM seed to the soil seedbank. Experiments were located each year in different fields. The S_1 phase was comprised of 48 experimental units assigned to plots 12 m in length by 3 m wide. The S_2 phase used the same plots to quantify the impact of residual WPM seedbanks within a following snap bean crop.

With the exception of measuring WPM fecundity in S_1 (Williams et al. 2007), all measurements of WPM population density were made within S_2. One month prior to planting, in late March, fertilizer was incorporated with cultivation, using 129 kg N ha^{-1}, 113 kg P ha^{-1}, and 135 kg K ha^{-1} in 2005 and 90 kg N ha^{-1} in 2006 (see Table 1 for schedule of field operations). Winter annual weed populations were controlled prior to planting with an initial burndown application of glyphosate at 0.35 kg ae ha^{-1}. In early April of 2005 and 2006, WPM soil seedbank density was estimated for each plot by taking six 10-cm-diameter soil cores in to a depth of 5 cm and bulking the cores, within plots, to form a composite sample. Seeds were recovered from soil samples with a mechanical elutriator (Wiles et al. 1996).

In late April of each year, WPM seedling recruitment was censused within a 0.76-m-wide strip running along the center of each plot for its entire length. This census area was used for all subsequent measurements of WPM population density. Immediately following the census, snap bean was planted in 76-cm rows at 126,400 seeds ha^{-1}on April 28, 2005 (‘Caprise’) and April 24, 2006 (‘Charon’).

Weed management treatments in snap bean targeted at WPM consisted of one rotary hoe cultivation in the third week of May, followed by a POST application of sethoxydim at 105 g ai ha^{-1} plus 1% v/v crop oil concentrate in the second week of June. In addition to hand-hoeing throughout the season, broadleaf weeds were controlled with a PRE halosulfuron treatment of 53 g ai ha^{-1} and a POST bentazon application of 0.56 kg ai ha^{-1} plus 1% v/v 28% urea-ammonium nitrate on May 31. We did not anticipate any herbicide carryover in snap bean from the sweet corn phase, as broadleaf weeds were controlled during the sweet corn phase with a PRE atrazine treatment of 2.2 kg ai ha^{-1}, followed by hand weeding for the remainder of the growing season. Insect pests in snap bean were controlled with an application of lambda-cyhalothrin at 28 g ai ha^{-1} in the second week of June. WPM population density was measured in census areas before and after each weed management operation (Table 1). Bean stand, final biomass, pod number and pod mass, and WPM final biomass were quantified in early July.

Data Analysis. Levene’s test for homogeneity of variances (Neter et al. 1996) indicated unequal variances between years; therefore, data for the two years of the study were analyzed separately. Within years, data met requirements for analysis of variance, therefore data were not transformed prior to analysis. Changes in WPM population density over time were assessed with linear regression, using the GLM subroutine of SYSTAT 11.0.[1] Influence of WPM population density on rotary hoe and sethoxydim efficacy in controlling WPM in snap bean was analyzed using piecewise nonlinear regression and linear regression, respectively. Piecewise nonlinear regression modeling (Ratkowski 1983) was used after visual inspection of these data indicated that there was a threshold WPM seedling population density, below which there was no relationship between WPM seedling density and rotary hoe efficacy, and above which a negative exponential relationship appeared to apply. This idea was tested through an iterative fitting approach. The independent variable (WPM seedling population density) was incremented between 0 and maximum WPM seedling population density and the response of rotary hoe efficacy to these changes was fit to a negative exponential function (Sit and Poulin-Costello 1994) using the NONLIN subroutine of SYSTAT 11.0. The threshold value was identified as the lower end of the data domain that maximized the adjusted R^2 value (Neter et al. 1996) of the negative exponential fit.

Path analysis models (Mitchell 2001) were fit using the RAMONA subroutine of SYSTAT 11.0. Akaike’s Information Criterion (Burnham and Anderson 2002) was used to identify the most parsimonious path analysis model for each

Table 2. Least squares regression parameters of selected demographic transitions of wild proso millet (WPM) in snap bean following sweet corn.

WPM population density[a]		Regression parameters, by snap bean field season					
		2005			2006		
N_t	N_{t-1}	β_0	β_1	R^2	β_0	β_1	R^2
Census period[b]							
S	F	11.7*	0.003***	0.33	180***	0.11***	0.59
P0	S	0.36	0.009***	0.80	8.0*	0.07***	0.72
P2	P1	0.21	0.49***	0.69	14.2*	0.22***	0.86
P3	P2	24.0*	8.2***	0.37	8.9**	2.73***	0.71
P4	P3	1.6	0.29***	0.49	0.53	0.08***	0.67

[a] N_t and N_{t-1}, WPM population density in at time t and $t-1$, which served as the dependent and independent variables, respectively, in linear regressions. See below for explanation of census times.

[b] F, fecundity in sweet corn; S, soil seedbank prior to snap bean; P0, WPM plant population density prior to snap bean; P1, WPM plant population density prior to rotary hoeing; P2, WPM plant population density after rotary hoeing; P3, WPM plant population density prior to sethoxydim; P4, WPM plant population density after sethoxydim.

* Significant least-squares regression parameters at $P < 0.05$.

** Significant least-squares regression parameters at $P < 0.01$.

*** Significant least-squares regression parameters at $P < 0.001$.

year from several candidate models containing terms for WPM fecundity, population density at several census times and biomass, snap bean stand, biomass and marketable pod number, and physical and chemical weed control efficacy.

Results and Discussion

WPM Population Density. WPM fecundity in sweet corn (S_1 phase) varied from less than 1,000 seeds m^{-2} to more than 30,000 seeds m^{-2}, with significant effects of cultivar and competition (Williams et al. 2007). Variation in WPM fecundity within the S_1 phase created a carryover effect on WPM population density that propagated throughout its life cycle in snap bean (S_2 phase) (Table 2). Overwinter losses from the WPM seedbank (transition of F to S, Table 2) were greater and initial seedling recruitment (transition of S to P0) was lower in 2005 than 2006. Low recruitment in 2005 may have been exacerbated by extremely dry conditions. Precipitation in March and April of 2005 was 30% below the 15-yr average for Urbana; whereas, precipitation for the same period in 2006 was 15% greater than the 15-yr average. In both 2005 and 2006, a second flush of WPM seedling emergence took place during the P2 to P3 transition from late April to mid-May, with greater recruitment in plots with higher WPM population densities (Table 2). All relationships were positive and linear, indicating that WPM densities were low enough that the experimental system was seed rather than safe-site limited (Boyd and Van Acker 2004; Maron and Gardner 2000; Ross and Harper 1972). The observation that variations in WPM fecundity do indeed manifest themselves in demographic transitions in a subsequent growing season demonstrates that, although weed seedbanks can experience a great deal of consumer pressure from seed predators (Carmona et al. 1999; Harrison et al. 2003; Menalled et al. 2006), there are sufficient safe sites in the soil seedbank to preserve the signal from high seed input events and structure future population dynamics.

The spatial layout of the experiment, with many possible combinations of WPM densities in adjoining plots, allowed us to determine how much noise in the relationship between WPM fecundity and recruitment in the following year came from seed movement between experimental plots. When fecundity in adjoining plots to the south, north, east, and west was added to regressions of initial WPM seedling recruitment (P0) on fecundity (F) within a given plot, explanatory power increased for both years. In 2005, the most parsimonious regression model was $P0 = 0.004 * F_{same} + 0.003 * F_{west}$ ($P < 0.001$), explaining 60% of the observed variation, compared to just 33% in the model that contained only F_{same} (Table 2). In 2006, the most parsimonious regression model was $P0 = 11.2 + 0.053 * F_{same} + 0.034 * F_{east} + 0.027 * F_{west}$ ($P < 0.001$), explaining 66% of the observed variation, compared to 59% in the model that contained only F_{same}. Seed movement from west to east accounted for as much as 27% of the experimental variation in P0 in 2005, whereas east–west seed movement accounted for less than 10% of the experimental variation in P0 in 2006. Since all tillage took place in a north–south direction, we can infer from these results that significant movement of seeds between experimental plots was caused primarily by strong west winds that occur in the fall in central Illinois, rather than by movement due to tillage.

Carryover Effects of Weed Fecundity on Weed Management and Performance of Following Crop. Rotary hoe efficacy was influenced by WPM seedling population density such that, above a certain threshold seedling population density, the percentage of WPM seedlings surviving the rotary hoe operation decreased as a negative exponential function of pre-hoeing seedling density (Figure 1). The threshold population density, below which there was no relationship between WPM seedling density and rotary hoe efficacy, was 2.6 and 8.4 seedlings m^{-2} in 2005 and 2006, respectively. This threshold may be seen as representing the population density at which WPM seedlings were so sparsely distributed that seedling survival was essentially unaffected by the rotary hoe since most seedlings were unlikely to encounter a rotary hoe spoon. With increases in WPM population density above the threshold value, safe sites (Ross and Harper 1972) between rotary hoe spoons became filled and the proportion of WPM seedlings killed by the spoons increased until the maximum efficacy of the tool was reached. Maximum rotary hoe efficacy was the same in both years: 25% of WPM seedlings survived, equivalent to 75% control efficacy (Figure 1). There are no reports in the weed science literature to date of weed population density-dependent reductions in the efficacy of physical control methods. This may be due to insufficient weed population densities, or it may simply be that weed seedlings in early growth stages do not provide enough

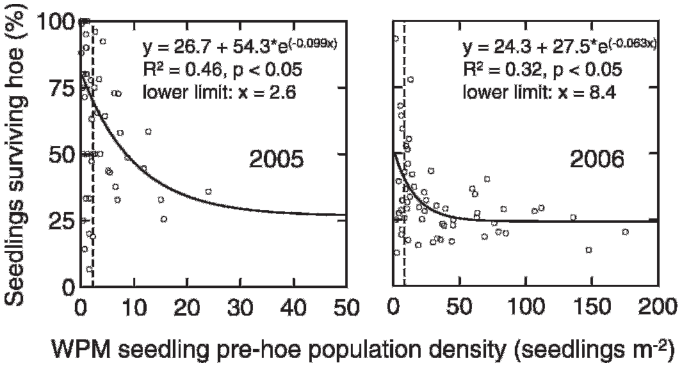

Figure 1. Proportion of wild proso millet (WPM) seedlings surviving a single rotary hoe pass in relation to WPM seedling population density prior to hoeing in 2005 and 2006. The lower limit in each panel refers to the threshold WPM population density, below which, no significant relationship existed between the independent and dependent variables in the regression.

physical resistance to impede cultivation implements, regardless of the seedling population density.

Linear regressions of WPM population density before and after sethoxydim treatments indicated that the herbicide treatment reduced WPM population density by 71 and 92%, respectively, in 2005 and 2006 (Table 2). The first order linear regression function was significant ($P < 0.001$), but higher order linear and nonlinear functions were not, indicating that sethoxydim efficacy did not vary with WPM population density. These results support the findings of Dieleman et al. (1999) who demonstrated that variation in population density of velvetleaf (*Abutilon theophrasti* Medicus) and common sunflower (*Helianthus annuus* L.) did not influence efficacy of foliar-applied herbicides. In contrast, Taylor and Hartzler (2000) found that increasing population densities of velvetleaf and giant foxtail (*Setaria faberi* Herrm.) through seedbank augmentation resulted in decreasing efficacy of soil and foliar-applied herbicides. One factor that may account for the difference between these studies is that weed population densities in the study by Taylor and Hartzler (2000) were more than twice as high as those in the present study and Dieleman et al. (1999). It may be that density-dependent reductions in weed control efficacy do not become an important factor until weed population densities have reached a very high level (Mortensen and Dieleman 1998).

A maximum-likelihood comparison of several candidate models (data not shown) indicated that the most parsimonious path analysis model of the relationship between WPM population density, weed management efficacy, and snap bean performance included terms for WPM fecundity, WPM seedling population density prior to rotary hoeing in mid-May (P1 in Table 2; P0, P2, P3 and P4 were also included as variables in candidate models, but were not selected in the final model), snap bean population at bean harvest, mechanical and chemical weed control efficacy, and snap bean marketable pod number (Figures 2a and 2b). In both 2005 and 2006, three pairs of model components were significantly associated ($P < 0.05$): WPM fecundity in sweet corn was positively associated with WPM seedling recruitment in snap bean, WPM seedling recruitment was negatively associated with snap bean population at harvest, and snap bean population at harvest was positively associated with snap bean marketable pod number. The effect of WPM seedling

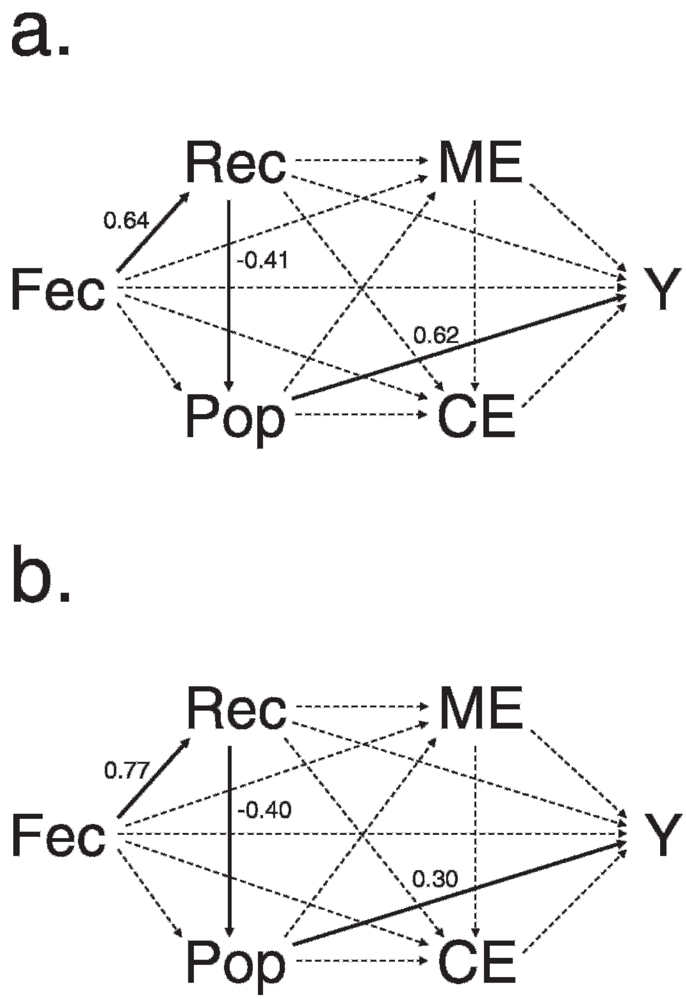

Figure 2. Path analysis model of hypothetical links between wild proso millet (WPM) population density, weed control efficacy, and snap bean performance in (a) 2005 and (b) 2006. Explanation of abbreviations: Fec, WPM fecundity in sweet corn; Rec, WPM seedling recruitment in snap bean in mid-May, prior to rotary hoeing (P1); Pop, snap bean population at harvest; ME, efficacy of mechanical weed control; CE, efficacy of chemical weed control; Y, snap bean marketable pod number. Solid, bold arrows indicate significant associations ($P < 0.05$) between variables, whereas dotted arrows indicate nonsignificant associations. Standardized regression coefficients are reported for significant associations only.

recruitment on snap bean population at harvest may have been due to water stress, as precipitation for the period from May through July was 45 and 38% below average in 2005 and 2006, respectively. As we did not collect soil moisture data for this period, this explanation is speculative.

The pathway of significant associations between model components supports the hypothesis that residual effects of variation in weed population density from one growing season may exert some negative influence upon crop performance in the following growing season, in this case mediated through reduced survival of crop plants over the course of the season. Other possible causal pathways, such as direct effects of WPM fecundity or seedling density upon snap bean yield, or reductions in weed control efficacy due to variation in WPM population density, were not supported by the model. The association between rotary hoe efficacy and WPM seedling population density, although significant on its own (Figure 1), did not contribute significantly to the path analysis model.

Implications for Weed Management. The retention of early-season WPM seedling recruitment in the path analysis model and the significance of this life stage in relating WPM fecundity in S_1 to crop yield loss in S_2 underscore the important effect that weed population dynamics prior to weed management operations can have on crop performance. Previous work by Rajcan et al. (2004) demonstrated that early-season infestations of weed seedlings could alter corn growth patterns, via changes in light quality, in such a way as to reduce crop yield, even in the complete absence of resource competition. Given that weed infestations early in the growing season may create conditions resulting in crop yield losses, early-season weed population dynamics should not be ignored. The critical period of weed control in white bean starts at the appearance of the second trifoliate and lasts from 3 to 5 wk thereafter (Woolley et al. 1993). The results presented here suggest that weed management in snap bean should not be delayed until the appearance of the second trifoliate. Rather, some form of early-season weed control should be used, such as preemergence herbicides with or without early cultivation (Colquhoun et al. 1999) or stale-seedbed techniques and flaming (Boyd et al. 2006; Melander et al. 2005) for low-external-input systems. In crops where the choice of preemergence herbicide is not limited due to crop sensitivity, it should be possible to nearly eliminate this cryptic form of early season competition. Because of the dependence shown here between weed population densities in consecutive growing seasons, an additional layer of protection against crop yield loss may be obtained by reducing inputs to the weed seedbank in the previous crop, either by directly reducing weed fecundity through control measures (fewer weeds) or weed suppressive crop cultivars (smaller weeds), or by reducing the survival of seeds within the soil seedbank through seed predation (Menalled et al. 2006) or microbial attack (Chee-Sanford et al. 2006).

Integrated weed management systems are predicted to be most successful when they make use of tools that spread opportunities for weed management throughout the weed life cycle (Davis and Ngouajio 2005; Liebman and Gallandt 1997; Mohler 1996). This study supports that prediction and highlights the need for new weed management tactics, as well as more timely applications of current tactics, targeted at both the very beginning and end of the growing season.

Sources of Materials

[1] SYSTAT Software Version 11.0, Systat Software, Inc., 501 Canal Blvd., Suite E, Point Richmond, CA 94804.

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