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Weed seedbank and community shifts in a long-term cropping systems experiment

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Characterizing the long-term effect of agricultural management systems on weed communities will aid in developing sustainable weed management practices. Weed seedbanks and aboveground biomass were measured within a corn–soybean–wheat crop sequence from 1990 through 2002 at Hickory Corners, MI. Four management systems were compared: conventional (CONV; full rates of N fertilizer and herbicides, moldboard tillage), no till (NT; same as CONV with no primary tillage), reduced input (RI; reduced rates of N fertilizer and herbicides, moldboard tillage, mechanical weed control, wheat underseeded with red clover), and organic (ORG; same as RI but no synthetic inputs). Multivariate ordinations of weed seedbanks showed a divergence of the CONV and NT systems from the RI and ORG systems. The CONV and NT seedbanks were dominated by grass species (mainly fall panicum and large crabgrass), whereas the RI and ORG systems were dominated by common lambsquarters and common chickweed. Within a single growing season, weed seedbanks in the RI and ORG systems were positively correlated with weed biomass whereas seedbanks in the CONV and NT system had little predictive value. Weed biomass from 1990 through 2002 showed a strong association of grass weed species with the corn phase of the CONV and NT system and common lambsquarters and redroot pigweed with the corn and soybean phases of the RI and ORG systems. Weed biomass diversity measures were negatively correlated with soybean yields in RI and ORG and wheat yields in NT, RI, and ORG. It is not clear whether crops were less competitive in the NT, RI, and ORG treatments, allowing new weed species to enter the plots, or whether less effective weed management in the NT, RI, and ORG treatments resulted in increased species richness, causing reduced crop yields. Mechanistic studies are needed to elucidate the relationship between weed community diversity and crop performance.

Nomenclature: Common chickweed, *Stellaria media* (L.) Vill. STEME; common lambsquarters, *Chenopodium album* L. CHEAL; fall panicum, *Panicum dichotomiflorum* Michx. PANDI; large crabgrass, *Digitaria sanguinalis* L. DIGSA; redroot pigweed, *Amaranthus retroflexus* L., AMARE; corn, *Zea mays* L. 'Pioneer 3573'; red clover, *Trifolium pratense* L. 'Michigan Mammoth Red'; soybean, *Glycine max* (L.) Merr. 'Pioneer 9172'; wheat, *Triticum aestivum* L. 'Pioneer 2552'.

Key words: Cropping systems, density, diversity, interference, multivariate analysis, richness, seedbank, weed community.

Weed seedbanks can be regarded as the "memory" of a weed community, especially for those communities dominated by annual weed species (Cavers 1995). Because most weed seeds tend to persist in the soil seedbank for more than a year (Thompson et al. 1997), the species composition and physiological states of the weed seeds present in a soil seedbank are integrated over a range of environmental and management conditions confronting a particular agricultural system. One of the fundamental challenges for improving weed management is to determine whether the information stored in the weed seedbank can help predict the nature of future weed infestations and effects on crop yield (Buhler et al. 1997; Cardina and Sparrow 1996; Wilson et al. 1985).

The density and species composition of below- and aboveground components of weed communities both vary in response to underlying environmental variation (Albrecht and Auerswald 2003; Dieleman et al. 2000) and shifts in agricultural management practices such as tillage (Anderson et al. 1998; Ball 1992; Buhler 1995; Clements et al. 1996; Dorado et al. 1999; Tuesca et al. 2001), crop rotation (Cardina et al. 1998, 2002; Moonen and Barberi 2004; Thomas and Leeson 2001), and weed management (Barberi et al. 1998; Mayor and Dessaint 1998; Menalled et al. 2001). In contrast to the thorough documentation of weed community shifts in response to changes in management practices, less has been written regarding the correspondence between below- and aboveground weed communities (Cardina et al. 1996; Mulugeta and Boerboom 1997; Tørresen 2003). Much of the current study to predict weed seedling populations from the weed seedbank focuses on the relationship between the dormancy status of seeds of a single species and the germination behavior of that species (Benech-Arnold et al. 2000; Dekker and Hargrove 2002; Forcella et al. 1997; Leon et al. 2004; Roman et al. 2000). When dealing with multiple species, characterizing the relationship between weed seedbanks and emergent communities is subject to several confounding factors. Only a small percentage of the seeds in a soil seedbank will ever germinate (Zhang et al. 1998), seed and species distributions within fields are spatially very heterogeneous (Luschei 2003), and the large

amount of spatial and temporal variability in growing conditions will cause different fractions of the weed seedbank to germinate out of proportion with their actual representation (Cardina and Sparrow 1996).

In this study, we attempted to overcome the abovementioned obstacles to linking weed seedbanks and emergent communities through sheer force of numbers: large sample sizes replicated over many years. The precursor to this study (Menalled et al. 2001) examined effects of contrasting agricultural management practices on weed seedbanks and emergent weed communities at the Long Term Ecological Research (LTER) agricultural ecology site at Michigan State University's W. K. Kellogg Biological Station in Hickory Corners, MI. Two years of seedbank data and 6 yr of biomass data were analyzed by Menalled et al (2001). In this article, we analyze 5 yr of seedbank data and 12 yr of biomass data from the LTER at Kellogg Biological Station to revisit and extend the analyses in Menalled et al. (2001). In addition to using the expanded data set to determine the effect of agricultural management practices on below- and aboveground weed communities, we included two new research questions: can weed seedbank community species composition be used to predict the species composition of the aboveground community? How is the structure of below- and aboveground communities related to crop yield?

Materials and Methods

Cropping Systems

This study was conducted as part of the LTER agricultural ecology project at Kellogg Biological Station at Hickory Corners, MI, from 1990 through 2002. Before the establishment of the LTER in 1989, the site had been managed primarily in continuous corn for more than 20 yr. The dominant soil type at the LTER site is a Kalamazoo silt loam (Typic Hapludalfs), with 43% sand, 40% silt, 17% clay, a pH of 6.68, and 1.08% soil organic carbon (Robertson et al. 1997).

Each plot within the LTER cropping systems study is 1 ha, with six replications per management system in a randomized complete block design. The present study focused on four row-crop systems represented at the Kellogg Biological Station LTER: conventional (CONV), no till (NT), reduced input (RI), and organic (ORG). The RI and ORG systems were maintained from 1990 onward in a corn–soybean–wheat crop sequence, in which the wheat phase of the sequence was underseeded with red clover at a rate of 13 kg ha^{-1}. The CONV and NT systems were in a corn–soybean crop sequence from 1990 to 1993 and then switched to a corn–soybean–wheat crop sequence in phase with RI and ORG. Soybeans were planted in the CONV and NT systems in 18.75-cm rows, whereas in the RI and ORG systems, they were planted in 76-cm rows to facilitate cultivation. Wheat straw was baled and burndown herbicides applied after harvest in the CONV and NT systems. Only one entry point of the crop sequence was represented in each year of the study.

Primary tillage in CONV, RI, and ORG consisted of moldboard plowing in the spring, whereas the NT treatment received no primary tillage. The CONV and NT treatments received N fertilizer at planting (as NH_4NO_3 through 1995 and 28% UAN from that point on) at a rate of 123 kg N ha^{-1} in the corn phase and 56 kg N ha^{-1} in the wheat phase. The RI treatment received 34 kg N ha^{-1} at planting in wheat and 28 kg N ha^{-1} at planting in corn followed by a sidedress application of N fertilizer, subject to presidedress soil test results. The only source of N in the ORG treatment was from the legume green manure in the wheat phase. Weed management in the ORG treatment consisted of multiple passes with a cultivator and rotary hoe, as deemed necessary by the farm manager. The RI treatment received the same number of cultivator and rotary hoe passes as ORG and also received reduced- to full-rate postemergence (POST) herbicide applications on the basis of scouting data (Table 1). Herbicide-resistant crop varieties were not planted at the LTER site. The CONV and NT treatments received full rates of herbicides in each of the crop phases (Table 1). Complete field crop management information for the LTER may be obtained at http://lter.kbs.msu.edu/Data/LTER_Metadata.jsp?Table= KBS004-001.

Weed Community Sampling

Weed seedbanks were sampled in early spring (late April or early May) in the corn phase of each of the four management systems in 1990, 1993, 1996, 1999, and 2002. At five stations within each replication, ten 1.9-cm diameter cores were taken to a 0–15-cm depth from a 25-cm by 25-cm quadrat. These cores were then split into 0–5-cm and 5–15-cm depths, bulked within station and elutriated using a hydropneumatic elutriator (Gross and Renner 1989). In 1993 and 1999, the samples were split for seedbank determination by both elutriation and direct germination (Menalled et al. 2001). Data from only the 0–5 cm sampling depth are reported in this study. Weed aboveground species density and dry weight were obtained at peak biomass (early July in the wheat phase and late August in the corn and soybean phases) by clipping and sorting to species all weed biomass within a 1-m^2 quadrat at five stations within each replication. Samples were then oven-dried at 60 C to constant mass and weighed to the nearest 0.01 g.

Data Analysis

Because many of the weed species represented at the LTER site occurred infrequently, we combined species counts into four categories to avoid excessive numbers of null entries in the data set. These categories were AMARE, CHEAL, GRASS (comprising mainly fall panicum and large crabgrass, with some giant foxtail [*Setaria faberi* L.]), and OTHER (comprising mainly common chickweed, velvetleaf [*Abutilon theophrasti* L.], yellow woodsorrel [*Oxalis stricta* L.], purslane speedwell [*Veronica peregrina* L.], and mouse-ear cress [*Arabidopsis thaliana* (L.) Heynh.]).

Multivariate analysis of variance (MANOVA) was used to analyze weed seedbank composition and weed biomass because the four weed species categories, AMARE, CHEAL, GRASS, and OTHER, did not vary independently (Scheiner 2001). To meet MANOVA assumptions of homoschedastic error terms, all seed and biomass data were $\log_e(x + 1)$ transformed before analysis. For both weed seedbanks and biomass data, MANOVA models included terms for year, replication, management system, and year by Management system, with AMARE, CHEAL, GRASS, and OTHER as dependent variables. MANOVA was conducted using the

Table 1. Herbicide treatments applied to conventional (CONV), no till (NT), and reduced input (RI) plots at the Long Term Ecological Research site in Hickory Corners, MI, from 1990 to 2002.

Year	Crop[a]	Date	Treatment (application type)[b]	Rate	Plots
				g ai ha^{-1}	
1990	Soybean–corn	May 8	Glyphosate (burndown)	1,800[c]	NT
		May 31	Metribuzin (PRE)	480	CONV, NT
			Metolachlor (PRE)	2,280	CONV, NT
1991	Corn–soybean	May 7	Glyphosate (burndown)	1,800	NT
		May 24	Dicamba (POST)+	260	CONV, NT
			Atrazine (POST)	500	CONV, NT
		June 7	Bentazon (POST)	960	CONV, NT
		June 7	Bentazon (POST)	140	RI
			Acifluorfen (POST)	240	RI
1992	Soybean–wheat	May 15	Glyphosate (burndown)	1,800	NT
		May 18	Metribuzin (PRE)	480	CONV, NT
			Metolachlor (PRE)	2,300	CONV, NT
		August 11	Glyphosate (burndown)	1,800	RI
1993	Corn	May 6	Glyphosate (burndown)	1,800	NT
		June 3	Dicamba (POST)+	260	CONV, NT
			Atrazine (POST)+	500	CONV, NT
			Nicosulfuron (POST)	35	CONV, NT
1994	Soybean	May 14	Glyphosate (burndown)	1,800	NT
		May 20	Flumetsulam (PRE)+	70	CONV, NT
			Metolachlor (PRE)	2,700	CONV, NT
		June 9	Thifensulfuron (POST)+	4.5	RI
			Quizalofop (POST)	530	RI
1995	Wheat	May 6	2, 4-D amine (POST)	480	CONV, NT
		September 15	Glyphosate (burndown)	2,500	CONV, NT
1996	Corn	May 13	Glyphosate (burndown)	830	NT
		June 11	Nicosulfuron (POST)	35	RI
		June 14	Bromoxynil (POST)+	290	CONV, NT
			Nicosulfuron (POST)	35	CONV, NT
		June 26	Bromoxynil (POST)	290	RI
1997	Soybean	May 17	Glyphosate (burndown)	830	NT
		May 20	Flumetsulam (PRE)+	72	CONV, NT
			Metolachlor (PRE)+	2,700	CONV, NT
			Chlorimuron (PRE)+	23	CONV, NT
			Metribuzin (PRE)	140	CONV, NT
		June 17	Sethoxydim (POST)	110	RI
		June 18	Bentazon (POST)+	340	RI
			Acifluorfen (POST)+	77	RI
			Thifensulfuron (POST)	4.5	RI
1998	Wheat				
1999	Corn	May 9	Glyphosate (burndown)	420	NT
		May 19	Flumetsulam (PRE)+	72	NT
			Metolachlor (PRE)+	2,700	NT
			s-Metolachlor (PRE)	22	NT
2000	Soybean	May 9	Glyphosate (burndown)	420	NT
		June 23	Sethoxydim (POST)	110	CONV, NT
		June 18	Bentazon (POST)	340	CONV, NT
2001	Wheat	April 28	2,4-D amine (POST)	480	CONV, NT
2002	Corn	April 26	Glyphosate (burndown)	340	NT
		May 11	*s*-Metolachlor (PRE)+	580	CONV, NT
			Mesotrione (PRE)+	85	CONV, NT
			Atrazine (PRE)	1,100	CONV, NT

[a] For the first three years of the study, crop sequences were as follows: CONV and NT, soybean–corn–soybean; RI and ORG, corn–soybean–wheat.
[b] Abbreviations: PRE, preemergence; POST, postemergence.
[c] Glyphosate application rates are expressed in acid equivalents.

General Linear Model (GLM) subroutine of SYSTAT® 9.0 (Wilkinson 1999). After MANOVA, protected analysis of variance (ANOVA) models (Scheiner 2001) and 1 df contrasts were performed for individual weed categories.

Two diversity measures were calculated for below- and aboveground weed communities: species density and the Shannon diversity index, $H' = -\Sigma p_i \log(p_i)$, where p_i is the proportional abundance of species i per 1-m^{-2} quadrat (Begon et al. 1986). ANOVA was performed on $\log_e(x + 1)$–transformed data using the GLM subroutine of SYSTAT® 9.0 (Wilkinson 1999).

Multivariate ordinations of weed seedbank and biomass

TABLE 2. Multivariate analysis of variance of the effects of site heterogeneity, management system, and time on weed community composition[a] within the Long Term Ecological Research plots at Kellogg Biological Station, Hickory Corners, MI.

Community type	Source	Pillai trace	*F*	df	P value
Seedbank	Rep	0.55	3.01	20, 380	< 0.001
	Management (M)	0.93	10.49	12, 282	< 0.001
	Year (Y)	1.32	11.77	16, 380	< 0.001
	MY	0.88	2.23	48, 380	< 0.001
Aboveground	Rep	0.27	3.05	20, 84	< 0.001
	Management (M)	0.83	20.10	12, 627	< 0.001
	Year (Y)	1.33	10.49	40, 840	< 0.001
	MY	1.52	4.28	120, 840	< 0.001

[a] Within each weed community type (seedbank or aboveground biomass), community composition comprised four dependent variables: ln $(x + 1)$–transformed seed abundance per meter square of redroot pigweed, common lambsquarters, grass species, and other species.

community composition (Benoit et al. 1992) were performed using Detrended Correspondence Analysis (DCA). DCA minimized the arch distortion present in our data by dividing ordination axes into many segments and rescaling to equalize the average within-sample dispersion of species scores (Gauch 1982). Ordinations were performed using the PC-ORD® 3.0 multivariate analysis software program (McCune and Mefford 1997), with down weighting of rare species. The relationship between ordination scores for the first two DCA axes and environmental variables was examined using Spearman correlations (Albrecht and Auerswald 2003) with the CORR subroutine of SYSTAT® 9.0 (Wilkinson 1999). Weed community constancy over time was determined by calculating Euclidean distances between years for all combinations of DCA scores within replications of each of the four management systems (Menalled et al. 2001). Euclidean distances for the four treatments were compared using ANOVA models containing terms for replication and management system and Bonferroni-corrected post hoc comparisons (Neter et al. 1996).

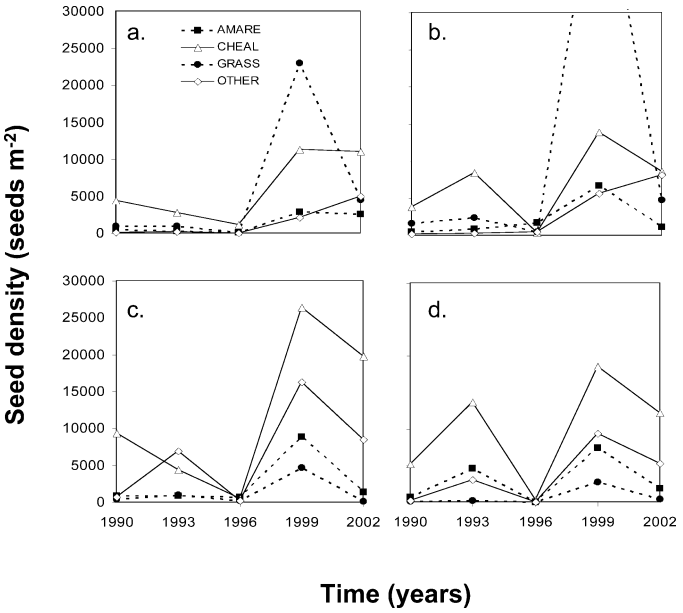

FIGURE 1. Weed seedbank density from the 0- to 5-cm soil depth in (a) conventional (CONV), (b) no till (NT), (c) reduced input (RI), and (d) organic (ORG) production systems at the Long Term Ecological Research site at W. K. Kellogg Biological Station in Hickory Corners, MI, from 1990 through 2002.

Results and Discussion

Weed Community Composition

Seedbank

MANOVA (Table 2) indicated that heterogeneity of the study site, agricultural management practices, and time influenced the composition of the weed seedbank in the LTER cropping systems study. The initial MANOVA was followed by three 1 df multivariate contrasts (data not shown): CONV − NT = 0, RI − ORG = 0, and (CONV + NT/2) − (RI + ORG/2) = 0. These contrasts showed that there were significant differences in seedbank composition between the CONV and NT systems ($P < 0.01$), the RI and ORG systems ($P < 0.001$), and between the high-input (CONV and NT) and low-input (RI and ORG) systems ($P < 0.001$). Differences in seedbank composition because of management showed a strong interaction with time ($P < 0.001$).

Inspection of the changes in seed abundance of the four major seedbank categories over time in each of the agricultural management systems (Figure 1) shows fundamental similarities between the CONV and NT systems and between the RI and ORG systems. All four systems were dominated by CHEAL in 1990. Before the initiation of the experiment, the study site had been managed primarily in continuous corn, with heavy dependence on atrazine for weed control. The CHEAL population at the site was largely triazine resistant (K. A. Renner, unpublished data), possibly explaining its domination of the weed community. Although CHEAL continued to be an important component of the seedbank for each of the systems for the next 12 yr, GRASS and OTHER species became an increasingly important part of the CONV and NT seedbanks whereas OTHER, but not GRASS, increased in abundance in the RI and ORG seedbanks. A multivariate ordination using DCA supported this distinction between the CONV and NT treatments and the RI and ORG treatments (Figure 2). The vertical and horizontal ellipses on the DCA ordination graph contain more than 75% of the observations for the RI and ORG systems and CONV and NT systems, respectively. The tight clustering of these points demonstrates that within each pair, the two systems changed in similar manners over time. The two ellipses share a common "hinge," CHEAL, representing the initial dominance of all seedbanks by this species. However, most variation within the CONV and NT seedbanks takes place along DCA Axis 1, from

TABLE 3. Spearman correlations between plot scores for Detrended Correspondence Analysis (DCA) Axes 1 and 2 of Long Term Ecological Research weed community species composition and selected environmental variables.

Environmental variable	Weed community ordination Axes			
	Seedbank		Aboveground biomass	
	DCA1	DCA2	DCA1	DCA2
%Sand	− 0.17	0.23*[a]	0.11	0.08
%Silt	0.17	− 0.22*	− 0.11	− 0.09
%Clay	0.11	− 0.15	− 0.05	− 0.03
Bulk density	− 0.01	0.16	− 0.20*	0.02
pH	− 0.11	− 0.36*	0.10	0.02
Replication	0.23*	0.25*	0.21*	− 0.13
Management	0.07	− 0.02	0.28**	0.09
Year	0.22†	0.33**	− 0.23*	0.07

[a] †, *, and ** denote significant correlations at the $P < 0.1$, $P < 0.05$, and $P < 0.01$ levels, respectively.

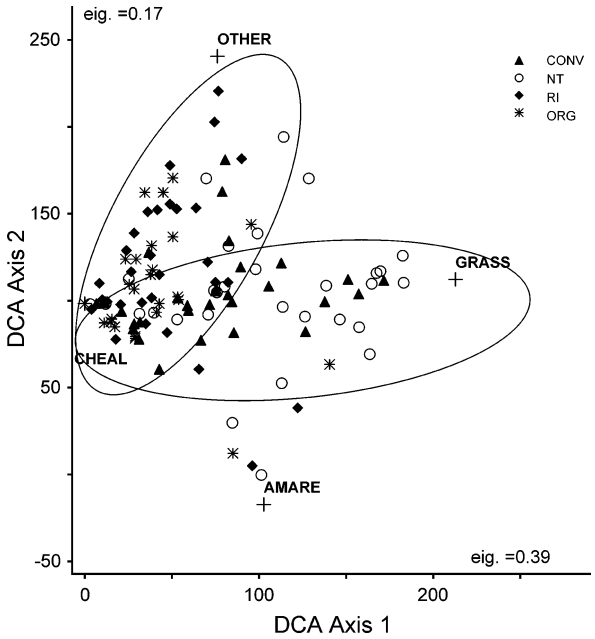

FIGURE 2. Plot scores for first two axes of Detrended Correspondence Analysis of weed seedbank composition in conventional (CONV), no till (NT), reduced input (RI), and organic (ORG) production systems at the Long Term Ecological Research site at W. K. Kellog Biological Station in Hickory Corners, MI, from 1990 through 2002. Crosses represent species scores for the four weed species categories used in the ordination.

CHEAL to GRASS, whereas most variation within the RI and ORG seedbanks takes place along Axis 2, between CHEAL and OTHER. These results support those of Menalled et al. (2001), who found a clear distinction between the CONV and NT systems and RI and ORG systems. Menalled et al. (2001) compared direct germination estimates of the seedbank to estimates obtained through elutriation.

The first two DCA axes explained 39 and 17% of the total variation in seedbank composition over time in the four management systems, respectively. DCA Axis 1 was positively correlated with replication ($r = 0.23$, $P < 0.05$) and year ($r = 0.22$, $P < 0.10$) and negatively correlated with management system ($r = -0.42$, $P < 0.001$) (Table 3). DCA Axis 2 was positively correlated with percent sand ($r = 0.23$, $P < 0.05$) and replication ($r = 0.25$, $P < 0.05$) and negatively correlated with percent silt ($r = -0.22$, $P < 0.05$) and pH ($r = -0.36$, $P < 0.05$). With the clearly visible distinction between management systems, it is not surprising that the strongest correlation between DCA ordination scores and concomitant variables was because of management. The importance of percent sand and silt in study soils reflects the large amount of heterogeneity in soil texture at the study location (Robertson et al. 1997). Albrecht and Auerswald (2003) found that as overall heterogeneity of soil properties increased in study locations, the correspondence between weed seedbanks and soil properties became more pronounced.

In 2002, after 12 yr of contrasting management practices, weed seedbanks in the LTER cropping systems study differed between treatments in total number of seeds, species density, and species diversity (Table 4). The total number of seeds in 2002 was lowest in ORG, intermediate in NT and CONV, and greatest in RI. The weed seedbank in the RI system was dominated by CHEAL (19,800 seeds m^{-2}) and, to a lesser extent, by OTHER (8,460 seeds m^{-2}), whereas GRASS seeds were scarce (117 seeds m^{-2}) in this system (Figure 1). The weed seedbank in the ORG system followed a pattern similar to the seedbank in RI, but abundance of CHEAL seeds (12,230 seeds m^{-2}) was substantially lower than in the RI system. Both the CONV and NT systems were dominated in 2002 by CHEAL (11,060 and 8,670 seeds m^{-2}), GRASS (4,530 and 4,820 seeds m^{-2}),

TABLE 4. Below- and aboveground weed community composition in the Long Term Ecological Research (LTER) cropping systems study in 2002.

Management system[a]	Weed seedbank			Weed biomass		
	Total seeds	Species density	Shannon diversity index	Total biomass	Species density	Shannon diversity index
	seeds m^{-2}	species m^{-2}		g m^{-2}	species m^{-2}	
CONV	22,600 ab[b]	2.2 a	0.27 b	18.8 a	4.3 a	0.62 a
NT	21,780 ab	3.9 b	0.41 c	13.3 a	5.0 a	0.84 b
RI	29,350 b	1.7 a	0.19 a	37.6 b	6.5 b	0.87 b
ORG	18,540 a	1.8 a	0.22 a	141.2 c	7.7 c	0.98 b
SE	2,800	0.2	0.02	8.4	0.4	0.06

[a] Symbols for agricultural management systems in the LTER are as follows: CONV, conventional; NT, no till; RI, reduced input; and ORG, organic.
[b] Within columns, means followed by different lower case letters were different as determined by a Bonferroni multiple comparison procedure.

and OTHER (4,990 and 8,150 seeds m^{-2}). Weed seedbank species density in study quadrats was more than twice as great in the NT system as in the CONV, RI, and ORG systems. Increased species density in the NT treatment was primarily because of frequent representation in the seedbank of four species in the OTHER category: yellow woodsorrel, common chickweed, purslane speedwell, and mouse-ear cress. Weed seedbank species diversity was greatest in NT, intermediate in CONV, and lowest in the RI and ORG systems. The NT system not only had more species present in the seedbank but these species also were present in the seedbank at higher densities, thereby increasing the sum of proportional species abundances, reflected in the higher values of the Shannon diversity index in the NT system than in the other management systems. The rise of winter annual species in NT indicates that the burndown application of glyphosate in May was not sufficient to erase the temporal niche created in this system by the absence of primary tillage in the fall.

The rise in GRASS and OTHER seeds and overall seedbank diversity within the NT system, compared with the tilled systems, corroborates reports that reductions in tillage are associated with an increase in the prevalence of grass weeds and previously uncommon broadleaf species (Cardina et al. 1998; Tørresen 2003; Tuesca et al. 2001). A more unusual result is the marked decline in the importance of GRASS seeds within the seedbank of the RI and ORG treatments. Both the RI and ORG systems were managed with low N and with repeated passes of a cultivator and rotary hoe, whereas the CONV and NT treatments were managed with high N and herbicides alone. These management differences suggest three possible explanations for the decline in GRASS seeds within the RI and ORG treatments. First, cultivation or cultivation plus herbicides (in the RI system) may have had a stronger negative effect on GRASS weeds than herbicides alone. Second, repeated disturbance of the soil surface because of cultivation may have stimulated germination of GRASS seeds, depleting the GRASS seedbank. Third, reduced external inputs of inorganic N could have reduced grass growth and seed production in the RI and ORG systems. These alternatives are addressed in the next section.

Aboveground Biomass

As with the weed seedbank, MANOVA (Table 2) indicated that replication, agricultural management practices, and time influenced the composition of the aboveground weed community in the LTER cropping systems study. Multivariate contrasts (data not shown) detected significant differences in aboveground weed species composition between CONV and NT ($P < 0.001$), RI and ORG ($P < 0.001$), and the high-input (CONV and NT) and low-input (RI and ORG) systems ($P < 0.001$). Differences in species composition because of management showed a strong interaction with time ($P < 0.001$).

More than twice as many data points exist for the aboveground weed community as for the weed seedbank, and the structure of the biomass data is thus somewhat more complex. A few patterns are evident in the line graphs of LTER weed biomass over time for the four management systems (Figure 3).

First, there is a strong periodicity to changes in biomass

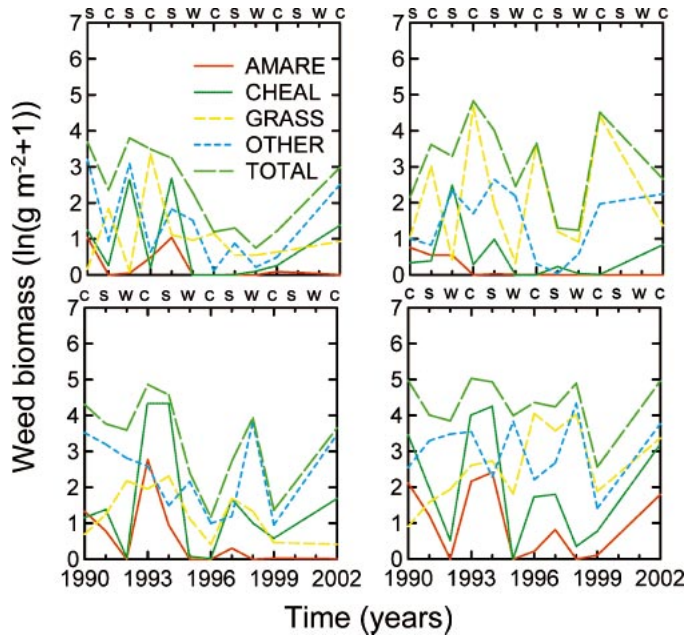

FIGURE 3. Weed biomass in (a) conventional (CONV), (b) no till (NT), (c) reduced input (RI), and (d) organic (ORG) production systems at the Long Term Ecological Research site at W. K. Kellogg Biological Station in Hickory Corners, MI, from 1990 through 2002.

of the different weed species categories. Within the CONV and NT systems, GRASS biomass spiked consistently in the corn phase of the rotation, with lower GRASS biomass in the wheat and soybean phases. This pattern continued through 1996 in CONV and through 1999 in NT system. The biomass of GRASS weeds in CONV corn was reduced greatly when management was shifted in 1999 from POST herbicide applications in corn (Table 1) to an entirely preemergence herbicide program in corn. This change in management practices did not reduce the GRASS problem in NT, for which the increases in GRASS biomass during the corn phase were considerably greater (Figure 3). Running out of phase with the pattern in GRASS biomass, CHEAL and OTHER biomass increased during the soybean phase of the crop rotation in CONV and NT and decreased in importance during the corn phase. Weed biomass was generally lower during the wheat phase of the rotation in CONV and NT than in the corn and soybean phases, particularly in NT.

Second, within the RI and ORG systems, CHEAL and AMARE moved in phase with each other and out of phase with OTHER (Figure 3). Biomass of CHEAL and AMARE spiked in the corn and soybean phases of the rotation in RI and ORG, whereas OTHER spiked during the wheat phase of the rotation. Biomass of GRASS was less predictably periodic in RI and ORG.

Finally, total weed biomass fluctuated strongly over time in the CONV, NT, and RI treatments, ranging from below 3 to above 50 g m^{-2}. Weed biomass in the ORG system also fluctuated but remained consistently higher over time than in the other three treatments, ranging between 48 and 148 g m^{-2} (except in 1999, when drought conditions brought weed biomass down to 12 g m^{-2}).

Multivariate ordinations, within management systems, of aboveground weed community composition (Figure 4) supported the patterns identified through visual inspection of

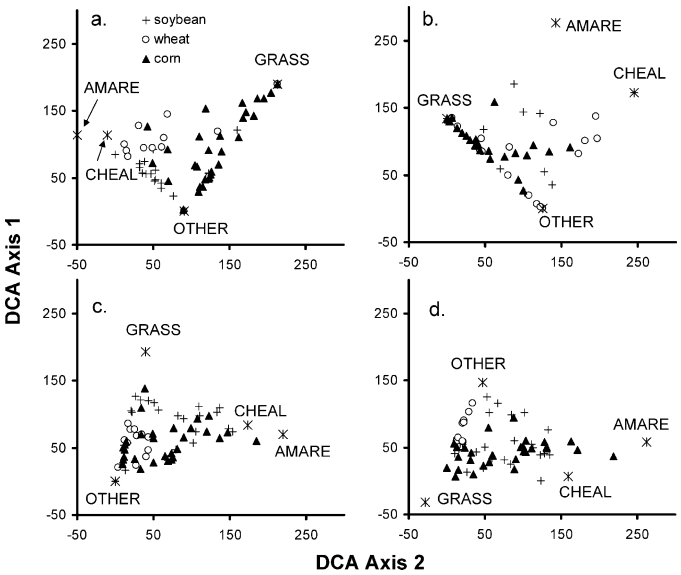

FIGURE 4. Plot scores for first two axes of detrended correspondence analysis of weed biomass composition in (a) conventional (CONV), (b) no till (NT), (c) reduced input (RI), and (d) organic (ORG) production systems at the Long Term Ecological Research site at W. K. Kellog Biological Station in Hickory Corners, MI, from 1990 through 2002. Crosses, circles, and triangles represent soybean, wheat, and corn phases of the crop sequence, respectively. Asterisks represent species scores for the four weed species categories used in the ordination.

Figure 3. Within the CONV and NT systems, GRASS tended to be associated with the corn phase whereas CHEAL and OTHER tended to be associated with the wheat and soybean phases. Within the RI and ORG systems, OTHER was associated with tight clusters of plots in the wheat phase and CHEAL, AMARE, and GRASS were more loosely associated with the corn and soybean phases. When ordinations of weed biomass were performed across management systems, there was no clear clustering of sites associated with different management systems (data not shown), as there was for the seedbank ordination. Weed biomass DCA Axis 1 explained 35% of the variation in the data and was correlated with bulk density, replication, management and year (Table 3). Weed biomass DCA Axis 2 explained 12% of the variation in the data and was correlated only with unexplained environmental variability, as represented by replication.

In 2002, weed biomass was lowest in CONV and NT, intermediate in RI, and greatest in ORG (Table 4). A protected Bonferroni multiple comparison of weed biomass averaged over the entire study period showed the same pattern, with 6 and 8 g m^{-2} in CONV and NT, 11 g m^{-2} in RI, and 29 g m^{-2} in ORG. These relative levels of weed biomass in the four management systems reflect the findings of Menalled et al. (2001).

GRASS biomass across the study period was lowest in the CONV and RI treatments (2.2 and 2.9 g m^{-2}, respectively) and greatest in the NT and ORG treatments (6.8 and 10.8 g m^{-2}, respectively). In the previous section, we hypothesized that (1) cultivation in the RI and ORG treatments helped deplete the GRASS seedbank by stimulating germination of GRASS seeds, (2) low levels of inorganic N in the RI and ORG treatments did not support GRASS growth and seed production, or (3) a combination of cultivation and herbicides gave superior control of GRASS weeds. High levels of GRASS biomass in the ORG treatment compared with the RI treatment indicated that neither cultivation alone nor low N (the only N input to the ORG system was from the red clover green manure in the wheat phase) was enough to suppress GRASS weeds. Despite high GRASS biomass in the ORG system, the GRASS seedbank in ORG remained as low as in the RI system. Either greater seed germination or seed mortality rates would have been necessary in the ORG system compared with the RI system to maintain this disparity, but this question must remain unanswered for the present. The low levels of both GRASS seeds and biomass in the RI system demonstrated that a combination of cultivation and herbicides can be used effectively to reduce a large GRASS seedbank while maintaining low GRASS biomass.

Weed species density in 2002 was consistent with treatment differences identified by the biomass results: the number of species was lowest in CONV and NT, intermediate in RI, and greatest in ORG (Table 4). However, the Shannon diversity index grouped NT, RI, and ORG together, with higher diversity scores than CONV. OTHER biomass in the CONV system was dominated by common chickweed, which accounted for more than 95% of the biomass in this category. In contrast, OTHER biomass in NT was split more evenly between common chickweed, velvetleaf, curly dock (*Rumex crispus* L.), yellow woodsorrel, and dandelion (*Taraxacum officinale* Webber). Important species in the OTHER category for biomass in the RI and ORG systems were common chickweed, velvetleaf, quackgrass [*Elytrigia repens* (L.) Nevski], mayweed chamomile (*Anthemis cotula* L.), and common ragweed (*Ambrosia artemisiifolia* L.). The higher levels of weed species diversity in the RI and ORG treatments than in the CONV and NT treatments are consistent with literature reports of increased weed diversity in low–external input production systems compared with conventional systems (Menalled et al. 2001; Moonen and Barberi 2004).

The species represented in the OTHER category for biomass were somewhat different than those represented in the seedbank, although both biomass and seedbank were dominated heavily by common chickweed. This discrepancy was most likely because of the use of an elutriation technique for seedbank recovery rather than a glasshouse approach. Elutriation tends to more accurately reflect the total number of seeds in the seedbank but underestimate the total number of species in the seedbank (Gross and Renner 1989).

Weed Community Constancy

Developing the ability to predict weed communities in the future on the basis of current community composition is an attractive, but elusive, goal. Such information would potentially benefit weed managers by allowing them to target specific management practices at problem weeds. Paradoxically, such an approach would almost certainly ensure rapid shifts in the weed community away from the species singled out for greater attention.

One approach to studying the constancy of weed communities was developed by Menalled et al. (2001) in a previous study of the LTER weed seedbank. By calculating Euclidean distances between the DCA ordination scores for the same plots at different points in time, they were able to compare the relative stability of the weed community in

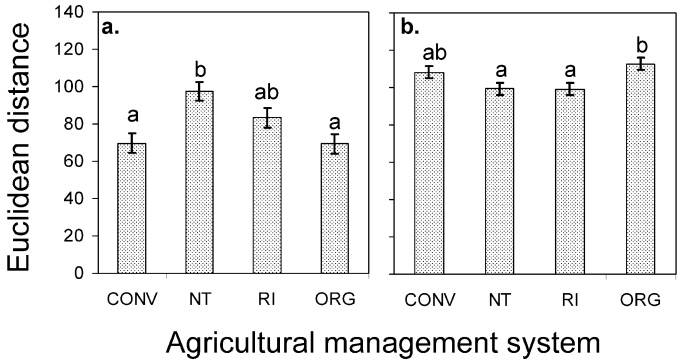

FIGURE 5. Euclidean distances between (a) seedbank and (b) biomass plot scores for individual plots over time within conventional (CONV), no till (NT), reduced input (RI), and organic (ORG) production systems at the Long Term Ecological Research site at W. K. Kellogg Biological Station in Hickory Corners, MI, from 1990 through 2002.

different management systems. Large means for Euclidean distance correspond to more change in DCA scores and lower constancy than small means for Euclidean distance. In the previous study, Euclidean distances were measured for aboveground communities using observations from 1993 through 1998 and for direct germination estimates of the seedbank using observations in 1993 and 1999. For both biomass and seedbank observations, Menalled et al. (2001) found that weed community constancy was lowest in the CONV and NT systems and greatest in the RI and ORG systems.

Results from this study for weed community constancy differed from those of Menalled et al. (2001). For weed seedbank data from 1990 through 2002, community constancy was greatest in CONV and ORG, intermediate in RI, and lowest in NT (Figure 5). The pattern was reversed when considering biomass data: community constancy was greatest in NT and RI, intermediate in CONV, and lowest in ORG. Because all the management systems showed differing degrees of constancy for seedbank data compared with biomass data, these results indicate low correspondence between below- and aboveground weed communities (Cardina et al. 1996) and suggest that stability measures may have more value for understanding systems retrospectively than for predicting future stability.

Correspondence Between Weed Seedbanks, Weed Biomass, and Crop Yield

Predictive Value of the Weed Seedbank

Attempts to predict future weed population size and composition are confounded by the large amount of spatial and physiological variability in weed seedbanks and the small percentage of the weed seedbank that undergoes recruitment (Cardina and Sparrow 1996). Our results showed little predictive value overall but did demonstrate how management can affect correspondence between the weed seedbank and aboveground community.

For the RI and ORG systems, the number of CHEAL and OTHER seeds at the beginning of a given growing season was strongly correlated to CHEAL and OTHER biomass later in the same growing season (Table 5). This relationship also held for GRASS seeds in the CONV system. The only significant interyear correlations between weed seedbank and weed biomass occurred in the ORG system. CHEAL seed abundance was strongly correlated with CHEAL biomass in the subsequent growing season, and OTHER seed abundance was negatively correlated with OTHER biomass in the previous growing season. The negative relationship between years for OTHER seed abun-

TABLE 5. Pearson correlation coefficients between Long Term Ecological Research weed seedbank abundance and weed biomass and weed seedbank abundance and crop yield.

Weed seedbank category	Management system[a]	Weed biomass at year (n)[b]			Crop yield at year (n)		
		t	t − 1	t + 1	t	t − 1	t + 1
AMARE	CONV	− 0.41	0.01	− 0.27	0.14	0.27	0.09
	NT	0.07	− 0.18	− 0.04	− 0.33	0.30	− 0.02
	RI	0.22	0.11	0.14	0.12	− 0.11	0.07
	ORG	0.51	0.46	0.29	0.72***[c]	− 0.27	0.13
CHEAL	CONV	− 0.07	− 0.02	0.31	0.1	0.63**	− 0.13
	NT	0.45	0.30	− 0.03	0.31	− 0.07	0.19
	RI	0.67*	0.43	0.37	0.49*	0.15	− 0.18
	ORG	0.72**	0.40	0.68*	0.55**	− 0.21	0.09
GRASS	CONV	0.70*	− 0.42	0.32	0.1	0.22	0.29
	NT	0.18	0.16	0.12	− 0.29	− 0.09	0.30
	RI	0.08	0.22	− 0.13	− 0.32	− 0.30	0.31
	ORG	0.19	0.09	− 0.09	0.48*	− 0.40	0.07
OTHER	CONV	0.25	− 0.44	0.38	0.15	0.46*	− 0.04
	NT	− 0.13	− 0.35	− 0.20	− 0.24	0.40	− 0.35
	RI	0.72**	0.37	0.32	0.43*	− 0.18	0.01
	ORG	0.60*	− 0.69*	− 0.21	0.69***	− 0.26	0.13

[a] See Table 4 for explanation of management system symbols.

[b] Time is measured with respect to seedbank abundance estimates, which were obtained in year (t) = {1990, 1993, 1996, 1999, and 2002}. Therefore, year (t) correlations are between below- and aboveground measurements that were both made in 1990, 1993, 1996, 1999, and 2002. Year (t − 1) correlations are between seedbank abundances in year (t) and aboveground measurements made in 1992, 1995, 1998, and 2001. Year (t + 1) correlations are between seedbank abundances in year (t) and aboveground measurements made in 1991, 1994, 1997, and 2000. Year (n) refers to year (t), year (t − 1), or year (t + 1).

[c] Symbols for Bonferroni-corrected probabilities are as follows: *, **, and *** represent the $P < 0.05$, 0.01, and 0.001 levels of probability, respectively.

dance and biomass indicates that plants in the OTHER category may not have been successful in producing much seed in the ORG system, so that germination of OTHER seeds represented a net loss to the OTHER seedbank. Six out of seven significant correlations between the below- and aboveground weed community were found in the RI and ORG systems. No significant correlations between the seedbank and emergent weed community existed for the NT system, contrary to the prediction of Ghersa and Ghersa-Martinez (2000) that the weed seedbank should have better predictive capacity for aboveground weed communities in NT systems because the shallow depth placement of seeds leads to greater proportional recruitment. The consistent use of herbicides in the CONV and NT systems appeared to disrupt the relationship between the weed seedbank and weed biomass, whereas in RI and particularly ORG, the weed seedbank expressed itself more clearly in the weed biomass. Teasdale et al. (2004) also found a significant link between weed seedbanks and weed abundance at maturity in ORG production systems.

If high weed seed abundance leads to large amounts of weed biomass in the same growing season, one would expect a negative relationship between weed seed abundance and crop yield. Our results did not show this. Seed abundance of AMARE, CHEAL, GRASS, and OTHER were all positively correlated with crop yield during the same growing season in the ORG treatment (Table 5). The positive correlation between seed abundance and crop yield may have been because of underlying variations in soil fertility. Because no N other than that mineralized from the legume green manure in the wheat phase was added to the ORG system, N-deficient areas of these plots may have had a negative effect on weed seed production. Conversely, more fertile areas of the ORG plots may have supported higher levels of both weed and crop seed production.

Aboveground Weed Communities and Crop Yield

Weed species density, species diversity, and total biomass showed strong negative correlations with crop yield (Table 6). These correlations were primarily in the soybean and wheat phases of the RI and ORG systems but also occurred in the corn and wheat phases of the NT system and wheat phase of the CONV system. A subsequent analysis of the relationship of species density and species diversity to yield (on the basis of splitting the data into two groups above and below the median biomass) indicated that the negative relationship was significant at both low and high weed biomass (data not shown). The negative relationship between crop yield and weed biomass is well known (Zimdahl 2004), but the effect of weed community diversity on crop yield is not well characterized.

Mohler (2001) predicted that more diverse weed communities should have greater potential to negatively affect crop yield because of the increased chance that one or more members of the community will be able to survive a given control measure. To understand the significance of the yield–diversity relationship in this study, we tested two alternate hypotheses: (1) greater weed species density and diversity were associated with greater amounts of total weed biomass and (2) greater weed species density and diversity were associated with greater biomass for a given component of the weed community. The former hypothesis explains the negative relationship between weed diversity and crop yield in the following manner: more diverse weed communities have greater overall biomass, causing greater interference and crop yield loss. The latter hypothesis offers a different explanation for the decline in crop yield in more diverse weed communities: as weed communities become more diverse, they are more likely to contain species that are highly competitive with crops or resistant to control measures.

TABLE 6. Pearson correlation coefficients between Long Term Ecological Research crop yield and weed aboveground community indices.

		Weed aboveground community indices		
Crop phase	Management system[a]	Species density	Shannon diversity index	Total biomass
Corn	CONV	− 0.45	− 0.22	0.18
	NT	− 0.56**[b]	− 0.56**	− 0.25
	RI	0.20	0.25	0.00
	ORG	− 0.10	0.03	0.13
Soybean	CONV	0.14	0.29	0.19
	NT	− 0.35	0.01	− 0.51**
	RI	− 0.49**	− 0.31†	0.19
	ORG	− 0.50**	− 0.28	− 0.37
Wheat	CONV	− 0.72**	− 0.40	0.42
	NT	− 0.75***	− 0.83**	0.18
	RI	− 0.77*	− 0.57**	− 0.75***
	ORG	− 0.70***	− 0.78***	− 0.57*

[a] See Table 4 for explanation of management system symbols.
[b] Symbols for Bonferroni-corrected probabilities are as follows: †, *, **, and *** represent the $P < 0.10$, 0.05, 0.01, and 0.001 levels of probability, respectively.

Tests of Hypothesis 1 indicated that this was not the primary explanation for the negative diversity–yield relationship. There was a significant relationship between diversity and total biomass only in the wheat phase of the RI treatment ($r = 0.79$, $P < 0.01$) and in the soybean phase of the ORG treatment ($r = -0.43$, $P < 0.05$).

The positive correlation in RI wheat offered limited support for Hypothesis 1 but did not rule out the possibility (Hypothesis 2) that increasing diversity was associated with an increase in the proportional abundance of one or more weed species in the community that were able to compete effectively with soybean. Accordingly, we determined whether the negative association between weed diversity measures and crop yield could be explained by changes in components of the weed biomass. Within the wheat phase, for all four management treatments, diversity measures were positively correlated with the biomass of weed species that were negatively associated with crop yield. In CONV wheat, species density was positively correlated with CHEAL biomass ($r = 0.47$, $P = 0.06$) and negatively correlated with GRASS biomass ($r = -0.50$, $P < 0.05$). At the same time, CHEAL biomass was negatively correlated with yield ($r = -0.57$, $P < 0.05$) and GRASS biomass was not correlated with yield. The negative relationship between species density and yield in this case was explained by the displacement of a weed that was not having a negative effect on crop yield (GRASS) by a weed that was having a negative effect on crop yield (CHEAL). For NT wheat, diversity was positively correlated with CHEAL biomass ($r = 0.43$, $P < 0.05$) and CHEAL biomass was negatively correlated with wheat yield ($r = -0.80$, $P < 0.001$). For RI wheat, diversity was positively correlated with CHEAL

($r = -0.50$, $P < 0.05$), GRASS ($r = 0.68$, $P < 0.01$), and OTHER ($r = 0.87$, $P < 0.001$) biomass, all of which were negatively correlated with wheat yield (respective correlations were $r = -0.90$, $P < 0.001$; $r = -0.62$, $P < 0.01$; and $r = -0.90$, $P < 0.001$). Finally, for ORG wheat, diversity was positively correlated with GRASS ($r = 0.65$, $P < 0.01$) and OTHER ($r = 0.64$, $P < 0.001$) biomass, both of which were negatively correlated with wheat yield (correlations were, respectively, $r = -0.93$, $P < 0.001$ and $r = -0.73$, $P < 0.001$). These examples offer support for Hypothesis 2; that negative effects of weed diversity on crop yield are mediated through increases in the biomass of one or more competitive, or difficult to control, weeds.

Increases in biomass of competitive weeds did not explain the relationship between weed diversity and crop yield for all treatment–crop combinations. In NT corn, there was a positive correlation ($r = 0.54$, $P < 0.01$) between OTHER biomass and weed diversity. However, there was no relationship between OTHER biomass and corn yield. Similarly, in RI soybean, there was a positive correlation ($r = 0.56$, $P < 0.01$) between OTHER biomass and weed diversity but no relationship between OTHER biomass and corn yield.

To address the cases that did not support Hypothesis 2, we tested a third hypothesis to explain the negative relationship between weed diversity and crop yield: increased weed diversity would reduce the negative effect of environmental heterogeneity on overall weed biomass, leading to lower variance of total weed biomass in replications with greater weed diversity. There was no relationship between diversity measures (species density or diversity) and variance of the weed biomass for either NT corn or RI soybean. Nor was there a relationship between diversity measures and total weed biomass for these treatment–crop combinations. The relationship between diversity and crop yield for these instances must remain unexplained at present.

An additional explanation for the negative weed diversity–crop yield relationship should also be considered. Because the data examined in this study are correlations, they do not assign the direction of causality in the diversity–yield relationship. Hypotheses 1 through 3 operate on the assumption that greater weed diversity was causing lower crop yield. It is also plausible that lower crop yield led to greater weed diversity, perhaps through decreased crop interference with weed recruitment and growth. Path analysis offers one method of testing causal relationships (Mitchell 2001); however, there were not enough experimental units within crop phases to run these analyses. Experimental plant community diversity gradients (Tilman et al. 2001) will be necessary to arrive at a more definitive explanation for the weed diversity–crop yield relationship. These questions are currently being addressed in a biodiversity study at the KBS LTER in which crop yield response to variation in cropping sequence diversity and crop diversity within phases of a crop sequence is being examined.

Future Directions and Weed Management Considerations

The data presented in this study constitute a relatively large-scale effort to characterize cropping system effects on weed communities and to derive the significance of weed community structure for crop performance. We were unable to make strong inferences from the weed seedbank to aboveground weed biomass or crop yield beyond a single growing season. Some of this failure may have been because of the inherent variability in weed seedbanks and growing environment and some to the coarse grain at which the observations were taken (Benoit et al. 1992). Another limitation of our results is that weed seed dormancy was not included in predictive relationships with the aboveground weed community. It has been suggested that the "active fraction" of the weed seedbank, those seeds that are readily germinable in spring, should give the best prediction of aboveground populations (Zhang et al. 1998). We are inclined to believe that for the purpose of elucidating in situ relationships between the weed seedbank, the emergent weed community, environmental factors, and crop performance, fine-scale mechanistic studies may be more fruitful than large-scale observational studies.

Analysis of the emergent weed community also did not allow us to make strong inferences beyond a single growing season but did provide more insight into weed management pros and cons of the cropping systems under consideration. The strong spikes in GRASS biomass within the corn phase of the CONV and NT systems indicated failures in postemergent weed control and largely disappeared when the corn herbicide program shifted to preemergent weed control. When reduced-input POST herbicide applications were complemented by cultivation operations, as in the RI system, GRASS weeds were controlled successfully, as were CHEAL and AMARE. This supports the findings of Buhler et al. (1995) and Mulugeta and Stoltenberg (1997), who demonstrated that combining herbicides with cultivation gave superior weed control in corn compared with herbicides alone, and made reduced herbicide application rates feasible.

Although the ORG system had a slightly lower weed seedbank density than the other systems, it also had the greatest amount of weed biomass by a factor of four. Overall weed biomass was not increasing or decreasing with time in this system, indicating that weed populations were in equilibrium with the weed management practices. Soybean yield was equivalent in all four systems in three out of four cycles (data not shown), but corn yield was lowest in ORG in two out of four cycles, and wheat yield was always lowest in ORG. These results indicate that there is much room for improvements in both fertility management and weed management in ORG production systems beyond cultivation as the sole source of weed mortality.

The strong negative relationship between aboveground weed diversity and crop yield (Table 6) highlights two important management considerations. First, if increases in weed diversity are responsible for declines in crop productivity, then special care should be taken to avoid introducing new weeds to a field (e.g., through contaminated equipment or seed) (Jordan 1996) and weed management efforts against particularly competitive species should be monitored for effectiveness (Mohler 2001). Alternatively, if crop productivity determines weed community diversity, this underscores the value of crop interference for integrated weed management sysstems (Jordan 1993). Mechanistic experiments exploring the relationship between weed diversity and crop performance will help generate greater understanding regarding the relative importance of weed prevention and crop interference to integrated weed management programs.

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Literature Cited

Albrecht, H. and K. Auerswald. 2003. Arable weed seedbanks and their relation to soil properties. Asp. Appl. Biol. 69:11–20.

Anderson, R. L., D. L. Tanaka, A. L. Black, and E. E. Schweizer. 1998. Weed community and species response to crop rotation, tillage and nitrogen fertility. Weed Technol. 12:531–536.

Ball, D. A. 1992. Weed seedbank responses to tillage, herbicides and crop rotation sequence. Weed Sci. 40:654–659.

Barberi, P., A. Cozzani, M. Macchia, and E. Bonari. 1998. Size and composition of the weed seedbank under different management systems for continuous maize cropping. Weed Res. 38:319–334.

Begon, M., J. L. Harper, and C. R. Townsend. 1986. Ecology: Individuals, Populations and Communities. Sunderland, MA: Sinauer Associates. 595 p.

Benech-Arnold, R. L., R. A. Sanchez, F. Forcella, B. C. Kruck, and C. M. Ghersa. 2000. Environmental control of dormancy in weed seedbanks in soil. Field Crops Res. 67:105–122.

Benoit, D. L., D. A. Derksen, and B. Panneton. 1992. Innovative approaches to seedbank studies. Weed Sci. 40:660–669.

Buhler, D. D. 1995. Influence of tillage systems on weed population dynamics and management in corn and soybean production in the central USA. Crop Sci. 35:1247–2157.

Buhler, D. D., J. D. Doll, R. T. Proost, and M. R. Visocky. 1995. Integrating mechanical weeding with reduced herbicide use in conservation tillage corn production systems. Agron. J. 87:507–512.

Buhler, D. D., R. G. Hartzler, and F. Forcella. 1997. Implications of weed seedbank dynamics to weed management. Weed Sci. 45:329–336.

Cardina, J., C. P. Herms, and D. J. Doohan. 2002. Crop rotation and tillage effects on weed seedbanks. Weed Sci. 50:448–460.

Cardina, J. and D. H. Sparrow. 1996. A comparison of methods to predict weed seedling populations from the soil seedbank. Weed Sci. 44:46–51.

Cardina, J., D. H. Sparrow, and E. L. McCoy. 1996. Spatial relationships between seedbank and seedling populations of common lambsquarters (*Chenopodium album*) and annual grasses. Weed Sci. 44:298–308.

Cardina, J., T. M. Webster, and C. P. Herms. 1998. Long-term tillage and rotation effects on soil seedbank characteristics. Asp. Appl. Biol. 51: 213–220.

Cavers, P. B. 1995. Seed banks: memory in soil. Can. J. Soil Sci. 75:11–13.

Clements, D. R., D. L. Benoit, S. D. Murphy, and C. J. Swanton. 1996. Tillage effects on weed seed return and seedbank composition. Weed Sci. 44:314–322.

Dekker, J. and M. Hargrove. 2002. Weedy adaptation in *Setaria* spp. V. Effects of gaseous environment on giant foxtail (*Setaria faberii*) (Poaceae) seed germination. Am. J. Bot. 89:410–416.

Dieleman, J. A., D. A. Mortensen, D. D. Buhler, C. A. Cambardella, and T. B. Moorman. 2000. Identifying associations between site properties and weed species abundance: I. Multivariate analysis. Weed Sci. 48: 567–575.

Dorado, J., J. P. Del Monte, and C. Lopez-Fando. 1999. Weed seedbank response to crop rotation and tillage in semiarid agroecosystems. Weed Sci. 47:67–73.

Forcella, F., R. G. Wilson, J. Dekker, et al. 1997. Weed seedbank emergence across the corn belt. Weed Sci. 45:67–76.

Gauch, H. G., Jr. 1982. Multivariate Analysis in Community Ecology. Cambridge, UK: Cambridge University Press. Pp. 154–155.

Ghersa, C. M. and M. A. Ghersa-Martinez. 2000. Ecological correlates of weed seed size and persistence in the soil under different tilling systems: implications for weed management. Field Crops Res. 67:141–148.

Gross, K. L. and K. A. Renner. 1989. A new method for estimating seed numbers in the soil. Weed Sci. 37:836–839.

Jordan, N. 1993. Prospects of weed control through crop interference. Ecol. Appl. 3:84–91.

Jordan, N. 1996. Weed prevention: priority research for alternative weed management. J. Prod. Agric. 9:485–490.

Leon, R. G., A. D. Knapp, and M.D.K. Owen. 2004. Effect of temperature on the germination of common waterhemp, (*Amaranthus tuberculatus*), giant foxtail (*Setaria faberi*), and velvetleaf (*Abutilon theophrasti*). Weed Sci. 52:67–73.

Luschei, E. C. 2003. Comparison of the effectiveness of seedbank sampling to seedling counts in reducing the uncertainty in estimates of weed population size. Asp. Appl. Biol. 69:137–142.

Mayor, J. P. and F. Dessaint. 1998. Influence of weed management strategies on soil seedbank diversity. Weed Res. 38:95–105.

McCune, B. and M. J. Mefford. 1997. PC-ORD. Multivariate Analysis of Ecological Data. Version 3.0. Gleneden Beach, OR: MjM Software Design.

Menalled, F. D., K. L. Gross, and M. Hammond. 2001. Weed aboveground and seedbank community responses to agricultural management systems. Ecol. Appl. 11:1586–1601.

Mitchell, R. J. 2001. Path analysis: pollination. Pages 217–234 *in* S. M. Scheiner and J. Gurevitch, eds. Design and Analysis of Ecological Experiments. New York: Oxford University Press.

Mohler, C. L. 2001. Weed evolution and community structure. Pages 444–493 *in* M. Liebman, C. L. Mohler, and C. Staver, eds. Ecological Management of Agricultural Weeds. Cambridge, UK: Cambridge University Press.

Moonen, A. C. and P. Barberi. 2004. Size and composition of the weed seedbank after 7 years of different cover-crop-maize management systems. Weed Res. 44:163–177.

Mulugeta, D. and C. M. Boerboom. 1997. Seasonal abundance and spatial pattern of *Setaria faberi*, *Chenopodium album*, and *Abutilon theophrasti* in reduced-tillage soybeans. Weed Sci. 47:95–106.

Mulugeta, D. and D. E. Stoltenberg. 1997. Weed and seedbank management with integrated methods as influenced by tillage. Weed Sci. 45: 705–715.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied Linear Statistical Models. Chicago, IL: Irwin. Pp. 1096–1097.

Robertson, G. P., K. M. Klingensmith, M. J. Klug, E. A. Paul, J. R. Crum, and B. G. Ellis. 1997. Soil resources, microbial activity, and primary production across and agricultural ecosystem. Ecol. Appl. 7:158–170.

Roman, E. S., S. D. Murphy, and C. J. Swanton. 2000. Simulation of *Chenopodium album* seedling emergence. Weed Sci. 48:217–224.

Scheiner, S. M. 2001. MANOVA: multiple response variables and multispecies interactions. Pages 99–155 *in* S. M. Scheiner and J. Gurevitch, eds. Design and Analysis of Ecological Experiments. 2nd ed. New York: Oxford University Press.

Teasdale, J. R., R. W. Mangum, J. Radhakrishnan, and M. A. Cavigelli. 2004. Weed seedbank dynamics in three organic farming crop rotations. Agron. J. 96:1429–1435.

Thomas, A. G. and J. Y. Leeson. 2001. Residual weed communities. Pages 1–11 *in* A. G. Thomas and S. A. Brandt, eds. Scott Alternative Cropping Systems Project Review: The First Six Years. Chapter 12. Saskatoon, SK, Canada: Agriculture and Agri-Food Canada.

Thompson, K., J. Bakker, and R. Bekker. 1997. The Soil Seed Banks of North West Europe: Methodology, Density and Longevity. Cambridge, UK: Cambridge University Press. 20 p.

Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science 294:843–845.

Tørresen, K. S. 2003. Relationship between weed seedbanks and emerged weeds in long-term tillage experiments. Asp. Appl. Biol. 69:55–62.

Tuesca, D., E. Puricelli, and J. C. Papa. 2001. A long-term study of weed flora shifts in different tillage systems. Weed Res. 41:369–382.

Wilkinson, L. 1999. SYSTAT® version 9.0 for Windows. Chicago, IL: SPSS.

Wilson, R. G., E. D. Kerr, and L. A. Nelson. 1985. Potential for using weed seed content in the soil to predict future weed problems. Weed Sci. 33:171–175.

Zhang, J., I. O. Gardiner, and S. E. Weaver. 1998. Dependence of weed flora on the active soil seedbank. Weed Res. 38:143–152.

Zimdahl, R. L. 2004. Weed-crop Competition: A Review. Ames, IA: Blackwell Publishing. Pp. 27–106.

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