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WEED ABOVEGROUND AND SEEDBANK COMMUNITY RESPONSES TO AGRICULTURAL MANAGEMENT SYSTEMS

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Abstract. The development of integrated weed management programs requires a clear understanding of the factors and mechanisms conditioning weed community dynamics in agroecosystems. This study evaluated the effect of different agricultural management systems on the aboveground and seedbank weed communities in annual row crops at the Long Term Ecological Research project in agricultural ecology at the W. K. Kellogg Biological Station, Michigan, USA. Weed biomass and species composition were sampled for six years over two corn–soybean–wheat sequence cycles in four agricultural management systems: (1) conventional (high external chemical input, moldboard plowed); (2) no-till (high external chemical input, no tillage); (3) low-input (low external chemical input, moldboard plowed); and (4) organic (no external chemical input, moldboard plowed). A greenhouse germination study assessed variation in the abundance and composition of the weed seedbank across the studied systems in the first and sixth year of this study.

Aboveground weed biomass, species density, and diversity were lowest in the conventional system, intermediate in the no-till system, and highest in the low-input and organic systems, but there were significant year-by-system interactions. Monocot and dicot species were equally common in the conventional system, whereas annual grasses, such as *Digitaria sanguinalis* (large crabgrass) and *Panicum dichotomiflorum* (fall panicum), dominated the no-till system. Two perennial weed species (*Trifolium pratense* [red clover] and *Elytrigia repens* [quackgrass]) and one annual dicot (*Chenopodium album* [common lambsquarters]) dominated the low-input and organic systems. A multivariate ordination of all four systems revealed close associations between the conventional and no-till systems and between the low-input and organic systems. Separate ordinations of the four management systems revealed a crop effect in the low-input and organic systems, but no differentiation in the conventional and no-till ones.

The seedbank study revealed a significant increase in the number of weed seeds and species, mainly of annual grasses such as *D. sanguinalis* and *P. dichotomiflorum,* in the conventional and no-till systems over the six years of study. During the same period, the number of weed seeds declined in low-input and organic systems. Three annual dicots (*Stellaria media* [common chickweed], *Veronica peregrina* [purslane speedwell], and *C. album*) dominated the seedbank of the low-input and organic systems. Weed aboveground and seedbank community composition were more constant over time in the low-input and organic systems than in the conventional and no-till systems over the study period. These results demonstrate that agricultural management systems can have both immediate and long-term effects on weed species density, abundance, and diversity. The differences observed among management systems in weed biomass, species composition, diversity, and community constancy indicate challenges that exist for the development of ecologically based weed management systems in row crop agriculture.

Key words: agroecosystems; annual row crops; diversity; Long Term Ecological Research (LTER); management systems; temporal patterns; weed community dynamics.

INTRODUCTION

Despite the wide-scale use of herbicides, tillage, crop rotation, and field cultivation, weed infestation and weed control in USA agriculture currently has an estimated cost of more than $\$15 \times 10^9$ per year (Bridges 1994). Although chemical and mechanical approaches for weed control have increased crop productivity and farm labor efficiency, they have also resulted in erosion, ground and surface water contamination, development of herbicide resistance, and soil degradation (Pimentel et al. 1992, Tilman 1998). Increasing concern about these environmental and economic costs has led

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to a growing consensus for the need to develop an integrated approach to weed management that achieves three goals. First, weed management should be aimed at the reduction of dependence on off-farm inputs. Second, it should increase reliance on ecological processes such as resource competition through cover- or intercropping, postdispersal weed seed predation, mortality due to pathogens, and soil solarization. Finally, weed management programs should be designed as one component in the development of integrated agricultural systems that maintain or improve crop productivity, farm revenues, and environmental quality (Liebman and Gallandt 1997, Buhler et al. 2000, Liebman and Davis 2000, Mortensen et al. 2000). Clearly, the design of alternative management programs for weed control requires an understanding of the different factors and mechanisms that influence the short-, mid-, and long-term dynamics of weed communities in agricultural systems.

Recent studies have increased our understanding of the importance of management practices in determining the composition of weed aboveground (Dale et al. 1992, Derksen et al. 1993, Swanton et al. 1993, 1999, Thomas and Frick 1993, Buhler et al. 1994, Buhler 1995) and seedbank community composition (Roberts and Neilson 1981, Cardina et al. 1991, Ball 1992, McCloskey et al. 1996, Hoffman et al. 1998, Mayor and Dessaint 1998, Buhler 1999). Also, several population-level studies have shown a close linkage between shifts in weed aboveground and seedbank abundance (Forcella and Lindstrom 1988, Mulugeta and Stolenberg 1997, Buhler 1999). Despite these studies, the extent to which aboveground and seedbank community dynamics are interrelated under different management systems is largely unknown.

In this paper, we report the results of a 6-yr study investigating the impact of different management systems on aboveground and seedbank weed community abundance and composition in annual row crops. Specifically, we address the following questions: (1) Do management systems and crop sequence influence aboveground and seedbank weed community composition? (2) Do the diversity and constancy of the weed community vary with management systems? (3) Are shifts in the readily germinable weed seedbank reflected in the aboveground weed community?

Materials and Methods

Description of the experiment

This study was conducted as part of the Long Term Ecological Research (LTER) project in agricultural ecology at the W. K. Kellogg Biological Station (KBS), Michigan, USA (Kalamazoo County; 85°22′ W, 42°24′ N). The site was principally in continuous corn (*Zea mays* L.) production for >20 yr prior to the establishment of the LTER research project in 1989. Strip-cropping of wheat (*Triticum aestivum* L.) and corn occurred for 2 yr in the 1970s and alfalfa (*Medicago sativa* L.) was grown on the western side of the study area for 4 yr in the 1980s. Soils at the LTER site are primarily well-drained Kalamazoo silt loam (Typic Hapludalf, sandy to silty clay loam) with moderate fertility (Robertson et al. 1997).

The experimental design of the KBS LTER site consists of seven experimental systems arranged in a randomized block design with six replications (plot size = 1 ha). Plots are separated by 10-m wide grassy strips that are periodically mowed. The experimental systems include four agronomic management systems in a corn–soybean [*Glycine max* (L.) Merill]–wheat 3-yr sequence, a poplar (*Populus* × *euramericana cv.* Eugenei) monoculture system, a continuous alfalfa system, and a successional system that was abandoned from agricultural cultivation in spring 1989. This study focused on the weed component of the four annual management systems: (1) conventional (high external chemical input, moldboard plowed); (2) no-till (high external chemical input, no tillage); (3) low-input (low external chemical input, moldboard plowed); and (4) organic (no external chemical input, moldboard plowed). In all four annual systems, corn was planted in 1993 and 1996, soybean in 1994 and 1997, and wheat in 1995 and 1998. The systems differed in tillage, source of nitrogen, amount and type of off-farm chemical inputs, and method of weed control. Details of the agronomic protocols and management used to establish and maintain these systems are presented in the Appendix. Additional information concerning agronomic practices as well as the data set used in this study are available at the KBS-LTER home page.[5]

The conventional and no-till systems had been planted in a 2-yr crop sequence (corn–soybean) for 4 yr prior to this study (1989–1992), but were shifted to a 3-yr crop sequence (corn–soybean–wheat) in 1993 when this study was initiated. In contrast, the low-input and organic systems had been in the 3-yr crop sequence since the LTER project was initiated (1989). In this study, only one phase of the crop sequence is planted each year, and year and crop type cannot be considered as independent variables. To reduce the impact of confounding effects in the interpretation of our results, two complete 3-yr corn–soybean–wheat cycles were analyzed. This approach allowed us to assess a potential legacy of the different crop sequences established prior to initiation of this study.

Data collection

Aboveground weed community.—Aboveground weed biomass and species composition were sampled each year from 1993 to 1998 at the time of peak biomass from 1993 to 1998 (late August to early September in corn and soybean; mid-July in wheat). Plants were sampled from five 1-m² (2.0 × 0.5 m) quadrats per plot.

[5] URL: ⟨http://lter.kbs.msu.edu⟩

Quadrats were placed perpendicular to the rows at predetermined sampling stations located at fixed (15 m) intervals, for a total of 30 quadrats per year and system. The location of sampling stations was shifted each year to avoid clipping previously harvested areas. All weeds rooted within each quadrat were clipped at ground level, sorted by species, dried at 60°C to constant mass and weighed to the nearest 0.01 g. Species names are presented according to the classification of Gleason and Cronquist (1991).

Germinable weed seedbank.—The weed seedbank present in the four systems was determined prior to the initiation of this study (May 1993) and at its end (May 1999). Each year before corn planting, 10 cores (2.5 cm diameter × 15 cm depth) were collected from a 25 × 25 cm area located 1 m to the southwest of each of the five aboveground sampling quadrats in each plot. For each sampling location, the 10 cores were split by depth (0–5 cm and 5–15 cm) and composited. In the laboratory, the sample was split in half by mass with one half of the sample stored for elutriation analysis of the soil seedbank and the other half used for a direct greenhouse germination analysis (Gross and Renner 1989, Gross 1990).

In this study, we utilized data from the direct germination study because we were interested in making comparisons between the readily germinable fraction of the seedbank and the aboveground weed community. The direct germination study requires a considerable amount of time and space, but provides a more complete listing of species present in the seedbank than elutriation (Gross 1990). Because most agricultural weeds germinate and emerge from the first centimeters of soil (Buhler 1995), only the data from the 0–5 cm samples are reported here. Exposing the soils to a range of treatments (e.g., cold or heat stratification, alternating temperatures) might have provided a more complete inventory of the soil seedbank in these treatments (Gross 1990). However, because our samples were all taken at the end of the cold period (early May) and emergence was monitored for up to 6 mo, we expect that this provides an unbiased estimate of differences in seedbank composition across systems.

Soil samples were spread in a thin layer (<0.5 cm) onto a 4 cm deep layer of soilless seedling mix (Sunshine Germinating Mix #3, Sun Gro Horticulture, Bellevue, Washington, USA) in a 25 × 50 cm plastic tray divided into equal thirds. Samples were randomly assigned to each third of the tray, with ''no soils added'' controls included as a treatment. Trays were placed on a bench in a temperature-controlled greenhouse where they were kept well watered under natural light from mid-May until early November. Temperatures in the greenhouse typically ranged between 20° and 30°C, though in midsummer daytime temperatures were higher (30–40°C). The positions of the trays on the benches were randomized every 1–2 wk over this period. Initially, seedlings emerging in these trays were censused at weekly intervals, but the census interval was increased later as fewer new seedlings emerged. At each census, new seedlings were counted and either removed (if identifiable to species) or marked with coded plastic picks for later identification. Seedlings that were difficult to identify were marked with unique code names and then transplanted to separate pots until they could be identified. Only 1.5% of the 5104 seedlings that emerged could not be identified to species and unique code names were used to distinguish them in the analysis.

Data analysis

Aboveground weed community.—Total aboveground weed biomass, weed species density (number of species per square meter), and species diversity were calculated for each sampled quadrat and each year. Species diversity was assessed using the Shannon diversity index: $H' = -\Sigma p_i(\log p_i)$, where p_i is the proportion of biomass accounted by species i per 1-m^2 quadrat (Magurran 1988). These three variables were compared across the four systems using a three factor (system, replication, year) repeated measures ANOVA model, with year as the repeated measure (Proc GLM, SAS Institute 1996). To meet the assumptions of the ANOVA model, biomass data were log transformed and species density data were square-root transformed before analysis (Sokal and Rohlf 1995). Also, to reduce the possibility of failing to meet the assumptions of normality and equality in the variance–covariance matrices, the degrees of freedom of the within-subject ANOVA tests were adjusted using the Geisser-Greenhouse correction (Crowder and Hand 1990).

The relative influence of agricultural management systems, crop type, and year of study on weed community composition and abundance was analyzed further with a multivariate detrended correspondence analysis (DCA; Hill and Gauch 1980). For each species, the dry biomass collected in the five quadrats per plot was summed to create a plot level data set on species composition and abundance. Ordination of plot data was performed using the PC-ORD multivariate analysis software program (McCune and Mefford 1997). To reduce the importance of less abundant species, a downweighting of rare species was performed prior to ordination. One outlying observation, sampled during 1995 in replication 6 of the no-till system, was deleted from this analysis. Spearman correlation coefficients were calculated using Proc CORR (SAS Institute 1996) to evaluate the association between replication scores on the first two DCA axis and ecological and management variables such as agricultural management system, crop, year, and number and biomass of monocots, dicots, annual, and perennial species (Quinn et al. 1991, Nygaard and Ødegaard 1999). To further explore the influence of agronomic practices on weed community composition, DCA ordinations were run for each management system individually.

The magnitude of temporal changes in weed communities were assessed by measuring the Euclidean distance separating the position that each plot had at different years. Euclidean distances were measured within the space defined by the first three DCA axes and these temporal shifts were examined for three time intervals: (1) year to year, as an estimator of the impact of crop sequence on weed dynamics; (2) 3-yr periods (1993–1996, 1994–1997, and 1995–1998), as an estimator of the constancy of the weed community associated with a specific crop; and (3) a factorial combination of all 6 yr, as an estimator of the overall system constancy. This approach has been used in other studies to evaluate temporal patterns in the composition of plant (Archer et al. 1987, Gibson 1988) and insect communities (Evans 1988, Quinn et al. 1991). For each time interval, differences in Euclidean distances among agricultural management systems were analyzed using a single factor ANOVA model (Proc GLM, SAS Institute 1996). It should be noted that data from the crop sequence analysis and the factorial combination of all 6 yr might have presented temporal autocorrelation. However, the different sample size of the crop sequence data set (two sets of the corn–soybean and soybean–wheat sequences and one of the wheat–corn sequence) and the possible existence of multiple correlations in the overall constancy analysis precluded utilization of a repeated measures ANOVA model. Therefore, results from these two tests should be interpreted with caution.

Germinable weed seedbank.—Data from the 1993 and 1999 germination studies were expressed as number of emerged weed seedlings per square meter, weed species density (number of species per sample), and species diversity (H') per sample. These values were compared using a three-factor (system, replication, year) ANOVA model with a repeated measure on the last factor (year; Proc GLM, SAS Institute 1996). The number of weed seedlings per square meter and number of weed species per sample were square-root transformed prior to the analysis. Because only two within-subject levels were compared in this analysis, a multivariate ANOVA test was used to assess the influence of system, time, and replication as well as second- and third-order interactions. We again used a multivariate analysis to assess variation in weed seedling abundance and composition as a function of system and time. For this analysis, the number of seedlings of each species sampled across the five quadrats from a plot were summed and subjected to a multivariate DCA using the PC-ORD software program (McCune and Mefford 1997). To compare weed seedbank constancy among systems and years, the Euclidean distance separating the position of each plot in 1993 and in 1999 was measured within the space defined by the first three DCA axes. Euclidean distances were compared using a single-factor (agronomic management system) ANOVA model.

TABLE 1. Aboveground weed biomass, species density, and Shannon diversity index (means ± 1 SE) observed over the study period (1993–1998) in four agricultural management systems of the W. K. Kellogg Biological Station Long Term Ecological Research site in Michigan, USA.

Management system	Weed biomass (g/m^2)	Species density (no. species/m^2)	Shannon diversity index
Conventional	18.20 ± 2.96	2.36 ± 0.12	0.18 ± 0.02
No-till	57.76 ± 8.45	2.88 ± 0.19	0.18 ± 0.02
Low-input	69.34 ± 9.33	4.69 ± 0.18	0.28 ± 0.13
Organic	108.52 ± 6.50	6.24 ± 0.21	0.32 ± 0.14

RESULTS

Aboveground weed community analysis

Total weed biomass, species density, and diversity were lowest in the conventional system, intermediate in the no-till system, and highest in the low-input and organic systems (Table 1). However, the between-subjects repeated-measures ANOVA indicated that over the 6 yr of this study there were significant replication × system interactions for these three variables (Table 2). Closer inspection of these results showed that weed biomass, species density, and diversity varied across years and management systems (Fig. 1). Thus, the within-subject ANOVA showed significant second- and third-order interactions (Table 2). There also did not appear to be a common pattern to the temporal variations among the three analyzed variables. Although weed species density was relatively low in all systems in the years in which soybean was planted (1994 and 1997), this was not reflected in lower species diversity or biomass (Fig. 1). Also, although all four systems had high species density and diversity in 1998 (wheat), weed biomass varied by >100-fold across systems in this year (1.2 ± 0.2 g/m^2 in the conventional system vs. 135.8 ± 11.3 g/m^2 in the organic system [means ± 1 SE]).

The combined DCA ordination of all four systems indicated that weed community composition varied as a function of management system with neither crop nor year of study playing a significant role in differentiating weed associations (Fig. 2A). The first DCA axis had a total length of 4.22 SD (standard deviation) units and an eigenvalue of 0.891, reflecting a high floristic variation along this axis. Many variables contributed to the distribution of plots along this axis, the most important of these being management systems, species density, the number and biomass of perennial species, and the number of dicot species (Table 3). Plots from the conventional and no-till systems had low species density (2.36 ± 0.12 and 2.88 ± 0.19 species/m^2, respectively) and were located primarily at high values of the first DCA axis (Fig. 2A). The second DCA axis had an eigenvalue of 0.457 and a gradient length of 3.20 SD units. Whereas plots sampled in the low-input

TABLE 2. Repeated-measures ANOVA for the effect of agricultural management system on weed biomass, species density, and Shannon diversity index.

Variable	df	Weed biomass	Species density	Shannon diversity index
Between-subjects source				
Replication (Rep)	5	6.67**	1.54	0.11
System (Sys)	3	152.14***	116.74***	4.29***
Rep × Sys	15	13.52**	15.83***	0.99**
Error	96	36.18	17.95	2.41
Within-subjects source				
Year	5	88.59***	62.00**	4.61***
Year × Rep	25	12.78**	6.73**	1.022**
Year × Sys	15	57.30***	34.75***	2.90***
Year × Rep × Sys	75	43.97***	25.76***	3.36***
Error	480	110.64	58.37	9.22

Notes: The degrees of freedom, Type III sums of squares, and significance levels of effects are shown for each variable. Biomass comparisons were carried out on log-transformed data. Species density data were square-root transformed before analysis. Within-subject analysis used Geisser-Greenhouse adjusted probabilities. System means and standard errors are shown in Fig. 1.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

and organic systems were clustered in the space of DCA axis 2, those from the conventional and no-till systems were spread across the second DCA axis. This pattern was reflected by a significant, but relatively low, Spearman correlation coefficient of $r = 0.455$ between year of sampling and plot scores along the second DCA axis, suggesting larger year-to-year differences in weed community composition in the conventional and no-till systems than in the low-input and organic systems.

The joint multivariate ordination of the data set indicated an association between functional groups of species and management systems. Whereas monocot and dicots species were equally represented in the conventional systems (46.7% and 53.3%, respectively of the 2601.5 g sampled), annual monocot species represented 78.9% of the 7681.5 g sampled in the no-till systems. Despite these differences in functional group abundance, the species ordination graph indicates an association between annual monocot species and plots from the conventional and no-till systems (Fig. 2B). Overall, annual monocot species comprised 70.1% of the total (10 283.0 g) of dry weed biomass sampled in the conventional and no-till systems, with *Panicum dichotomiflorum* Michx. (fall panicum, PANDI) and *Digitaria sanguinalis* (L.) Scop. (large crabgrass, DIGSA) accounting for 48.5% and 10.8% of the total dry biomass sampled, respectively. In contrast, annual dicots, particularly *Chenopodium album* L. (common lambsquarters, CHEAL) and perennials such as *Elytrigia repens* (L.) Nevski (Synonyms *Agropyron repens*, quackgrass, AGGRE) and *Trifolium pratense* L. (red clover, TRFPR) dominated the low-input and organic systems. These species accounted for 38.9%, 15.4%, and 12.8%, respectively, of the total weed biomass (30 710.2 g) from the low-input and organic systems and had low scores on the first DCA axis (Fig. 2B).

The comparison of the Euclidean distances separating the same plot in consecutive years (Fig. 3A) assessed the impact of crop sequence on weed community composition. Both the corn–soybean and wheat–corn sequence produced larger changes in weed communities in the conventional and no-till systems than in the low-input and organic ones. The transition from soybean to wheat caused a similar magnitude shift in weed species composition in all systems (Fig. 3A). Moreover, during the years in which corn (1993 and 1996) or soybean (1994 and 1997) were planted, the weed communities were less similar (greater Euclidian distance among plots) in the conventional and no-till systems than in the low-input and organic ones (Fig. 3B). Across all years, the constancy of weed communities was significantly lower in the conventional and no-till systems than in the low-input and organic systems (Fig. 3C).

More insight into the impact of management systems on weed communities was revealed when the four management systems were analyzed individually. In the conventional and no-till systems, there was again no clear distinction in the weed communities associated with different crops or years (Fig. 4A and B). Although plots from the no-till systems were scattered along DCA axis 2, it was not possible to detect a clear association with either year or crop (Fig. 4B). However, in the low-input and organic systems, weed communities occurring when wheat was planted (1995, 1998) were clearly distinguishable from the corn and soybean crops (Fig. 4C and D). Red clover (*T. pratense*), a perennial dicot, comprised 51.2% of the total weed biomass when wheat was planted in these systems. In contrast, when corn (1993, 1996) or soybean (1994, 1997) were planted, *C. album* (an annual dicot) accounted for 48.8% and 54.4%, respectively, of the total weed biomass sampled in the low-input and organic systems. As a result, plots from the wheat low-input

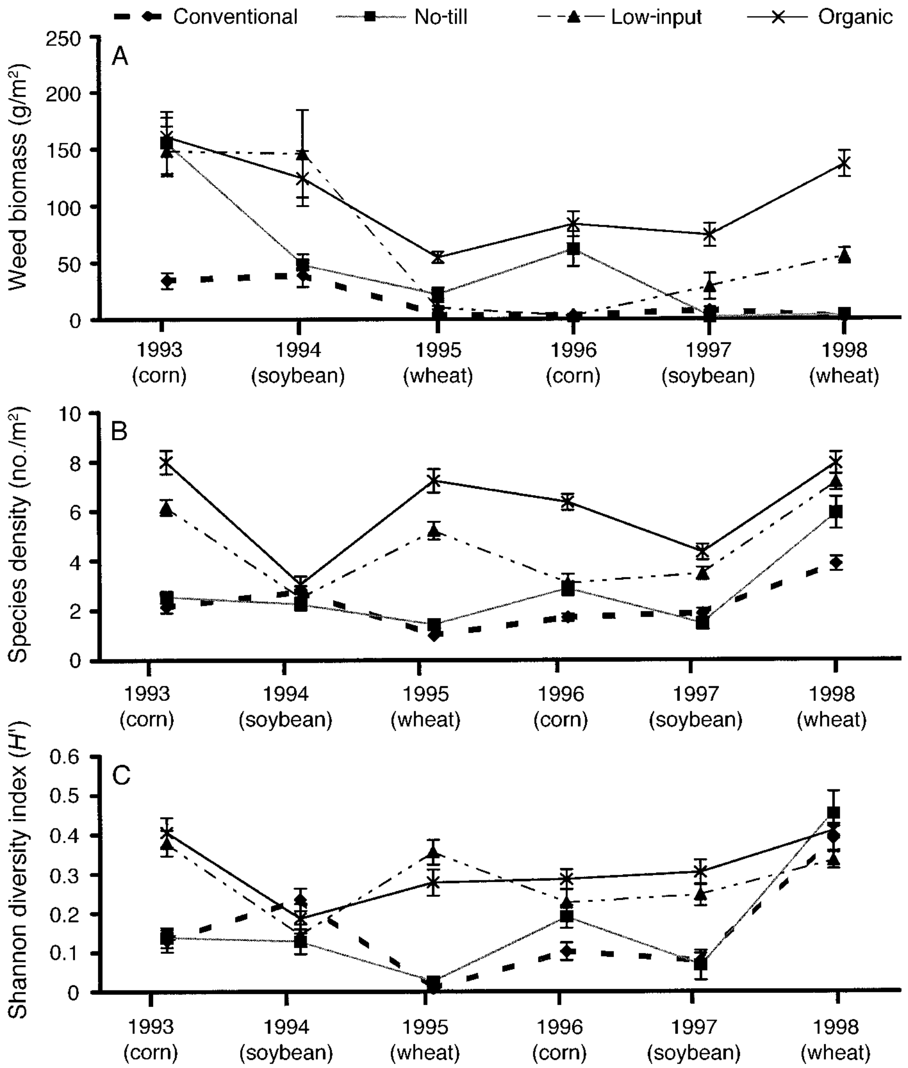

FIG. 1. (A) Weed biomass, (B) species density, and (C) Shannon diversity index in the four studied agricultural systems of the Long Term Ecological Research project in agricultural ecology at the W. K. Kellogg Biological Station, Michigan, USA between 1993 and 1998 (means ± 1 SE).

and organic systems formed a distinct cluster in the positive values of the first DCA axes (Fig. 4C and D).

Germinable weed seedbank community

The seedbank study revealed differences in the potential weed communities among the four management systems. In 1993, more seedlings emerged from soil cores sampled from the low-input and organic systems than from the conventional and no-till ones (Fig. 5A). Species density and diversity were also higher in 1993 in the low-input and organic systems than in the conventional and no-till ones (Fig. 5B and C). Between 1993 and 1999 there was a significant increase in the mean number of weed seedlings and species that emerged in soil cores sampled in the conventional and no-till systems (Fig. 5A and B). In contrast, seedling numbers and mean number of species per sample declined in the low-input and organic systems. These differences accounted for the significant year × system interaction in the within-subject ANOVA test for the number of seedlings and species density comparison (Table 4). These shifts in numbers of species and seedlings had no effect on diversity as measured by the Shannon index (Fig. 5C). While a system effect in the between-subject ANOVA showed that weed seedling species diversity was lower in the conventional and no-till systems than in the low-input and organic systems, the within-subject ANOVA indicated no temporal change in weed seedling diversity across all systems (Table 4).

The differential change in the number of weed seedlings and species observed in the conventional and no-till systems was reflected in the DCA ordination. Data collected in 1993 was tightly clustered at low values on

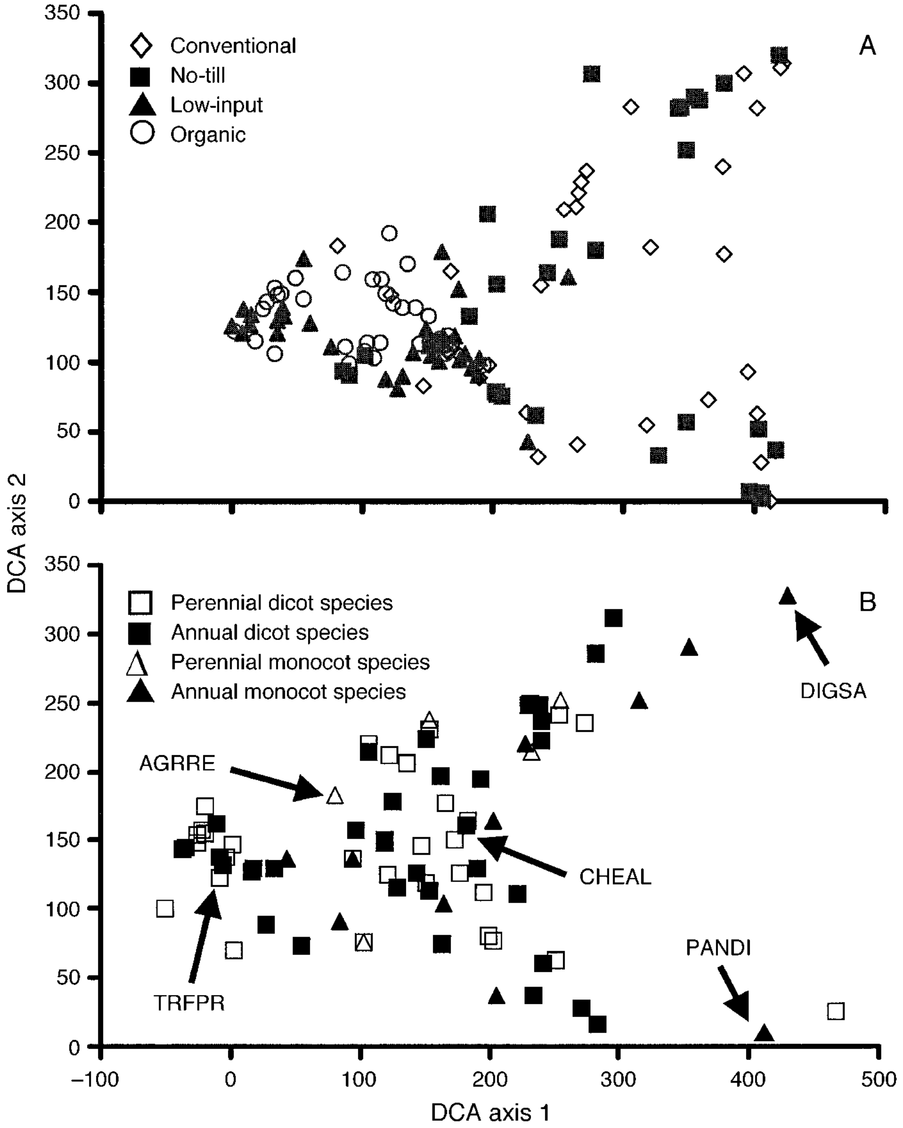

FIG. 2. Detrended correspondence analysis (DCA) ordination of (A) all plots and (B) species scores sampled between 1993 and 1998 in four management systems of the W. K. Kellogg Biological Station Long Term Ecological Research site. Species abbreviations: AGRRE, *Elytrigia repens*; CHEAL, *Chenopodium album*; DIGSA, *Digitaria sanguinalis*; PANDI, *Panicum dichotomiflorum*; TRFPR, *Trifolium pratense* (WSSA 1989).

the first DCA axis, whereas the 1999 seedbank data were differentially distributed along the first two axes (Fig. 6A). Samples obtained in 1999 from the low-input and organic systems had low values on the first DCA axis. In contrast, those sampled from the conventional and no-till systems had higher scores on the first DCA axis and were spread along the second DCA axis. *Panicum dichotomiflorum, Digitaria sanguinalis,* and *Digitaria ischaemum* (smooth crabgrass, DIGIS), accounted for 23.9%, 25.9%, and 21.4%, respectively, of the total seedling emergence observed in the conventional and no-till systems. In the DCA ordination graph, these three annual monocot species were all located at high values on the the first DCA axis (Fig. 6B), confirming their association with the conventional and no-till systems in 1999. The seedbank of the low-input and organic systems was dominated by three annual dicot species. *Chenopodium album, Veronica peregrina* L. (purslane speedwell, VERPG), and *Stellaria media* (L.) Vill. (common chickweed, STEME) accounted for 22.0%, 20.3%, and 16.8%, respectively, of the total seedlings that emerged from soil cores taken at these two systems.

The Euclidean distances separating the position of each plot in 1993 and 1999 evaluated the constancy in the weed seedbank composition over years. The results from this analysis were similar to the patterns observed in the ordination of aboveground weed communities. Between 1993 and 1999, weed seedbank species com-

TABLE 3. Spearman correlation coefficients between plot scores in the first two detrended correspondence analysis axes and agricultural management system, crop type, year of study, and number and biomass of species groups sampled between 1993 and 1998 at the W. K. Kellogg Biological Station Long Term Ecological Research Site.

Variable	Axis 1	Axis 2
Agricultural management system	−0.671***	0.020
Crop type	−0.482***	0.112
Year	−0.236*	0.445***
Species density	−0.610***	0.120
Total weed biomass	−0.312***	−0.274*
Number of dicot species	−0.674***	0.048
Biomass of dicot species	−0.493***	−0.242*
Number of monocot species	−0.197*	0.164
Biomass of monocot species	−0.137	−0.117
Number of annual species	−0.486***	−0.146
Biomass of annual species	−0.016	−0.254*
Number of perennial species	−0.679***	−0.007
Biomass of perennial species	−0.667***	−0.094

* $P < 0.05$; *** $P < 0.0001$; $n = 138$.

position based on emergence from the seedbank samples was more variable in the conventional and no-till systems than in the low-input and organic systems (Fig. 7).

DISCUSSION

This study highlights the importance of a system-oriented perspective in the development of integrated weed management programs. A clear understanding of how different agricultural practices interact with one another in conditioning weed communities is a key component in the development of management practices that will maintain weed abundance at low and consistent values while reducing dependence on herbicides (Mortensen et al. 2000). Several recent studies comparing a range of agroecosystems including organic, low-input, no-till, and conventional farming have shown a significant impact of management systems on weed communities, crop yield, and net returns (Gallandt et al. 1998, Cox et al. 1999, Leeson et al. 2000, Liebman and Davis 2000). Our results demonstrated that crop management systems can have significant impacts on the abundance, diversity, and constancy of the aboveground and seedbank weed communities. In the following sections, we first discuss the aboveground weed community component of this study. Then, we analyze the relationship between germinable seedbank composition and management systems. Finally, we jointly consider our aboveground and seedbank studies to highlight possible implications for weed management.

Crop management systems and aboveground weed community dynamics

Despite the existence of temporal interactions across systems and replications, our results indicated that differences in management have a major influence in the aboveground weed community of annual crops. Although the system approach employed in this study did not allow us to test hypotheses on the impact of specific management practices on weed community dynamics, it is possible to speculate on the relative importance of major management practices such as tillage and herbicides.

Because reduced tillage systems (''conservation tillage'') represent a very important component in the development of sustainable weed management systems (Swanton et al. 1999), many studies have evaluated the impact of mechanical control practices on weed community dynamics. Although biennial and perennial weeds are predicted to increase their dominance in reduced and no-tillage systems (Phillips et al. 1980, Froud-Williams et al. 1981), observations of weed shifts under different management practices are contradictory. In a review of 12 mid- and long-term studies where the impact of conservation and conventional tillage was compared, Swanton et al. (1993) found no clear tendency towards the increase or decrease of any weed functional group in relation to tillage practices and suggested that tillage, herbicides, and crop rotation might interact in determining weed communities. Confirming this idea, Derksen et al. (1995) observed that herbicide applications inhibited weed community changes among different tillage systems by reducing weed density (number of plants per square meter) without affecting weed species diversity. In accordance with previous studies in which herbicides were applied across different tillage systems (Forcella and Lindstrom 1988, Buhler and Oplinger 1990, McCloskey et al. 1996, Swanton et al. 1999), we observed an increase in the abundance of annual grasses in the no-till system in comparison to a conventional system. The lack of a clear tendency among published results on the impact of tillage and herbicides on weed communities indicates the need for long-term studies aimed at evaluating the existence of synergistic mechanisms by which tillage and herbicides interact in determining weed communities in row crops.

Because herbicide applications tend to reduce the density of susceptible weed species (Hume 1987), organically managed systems are expected to have higher weed diversity than conventional ones (Leeson et al. 2000). In our study, total weed biomass, species density, and diversity were higher in low-input and organic systems than in conventional and no-till systems. Several other studies also have observed that weed biomass and diversity were lower in conservation tillage plots with herbicide use than without herbicides (Mahn 1984, Wicks et al. 1988). In accordance with our results, Moreby et al. (1994) and Van Elsen (2000) reported an increase in the number of weed species sampled in organically managed systems than in conventionally managed ones.

Although the combined multivariate ordination of all four management systems did not reveal any effect of crop on weed community characteristics, separate analysis of these four systems suggested crop type influ-

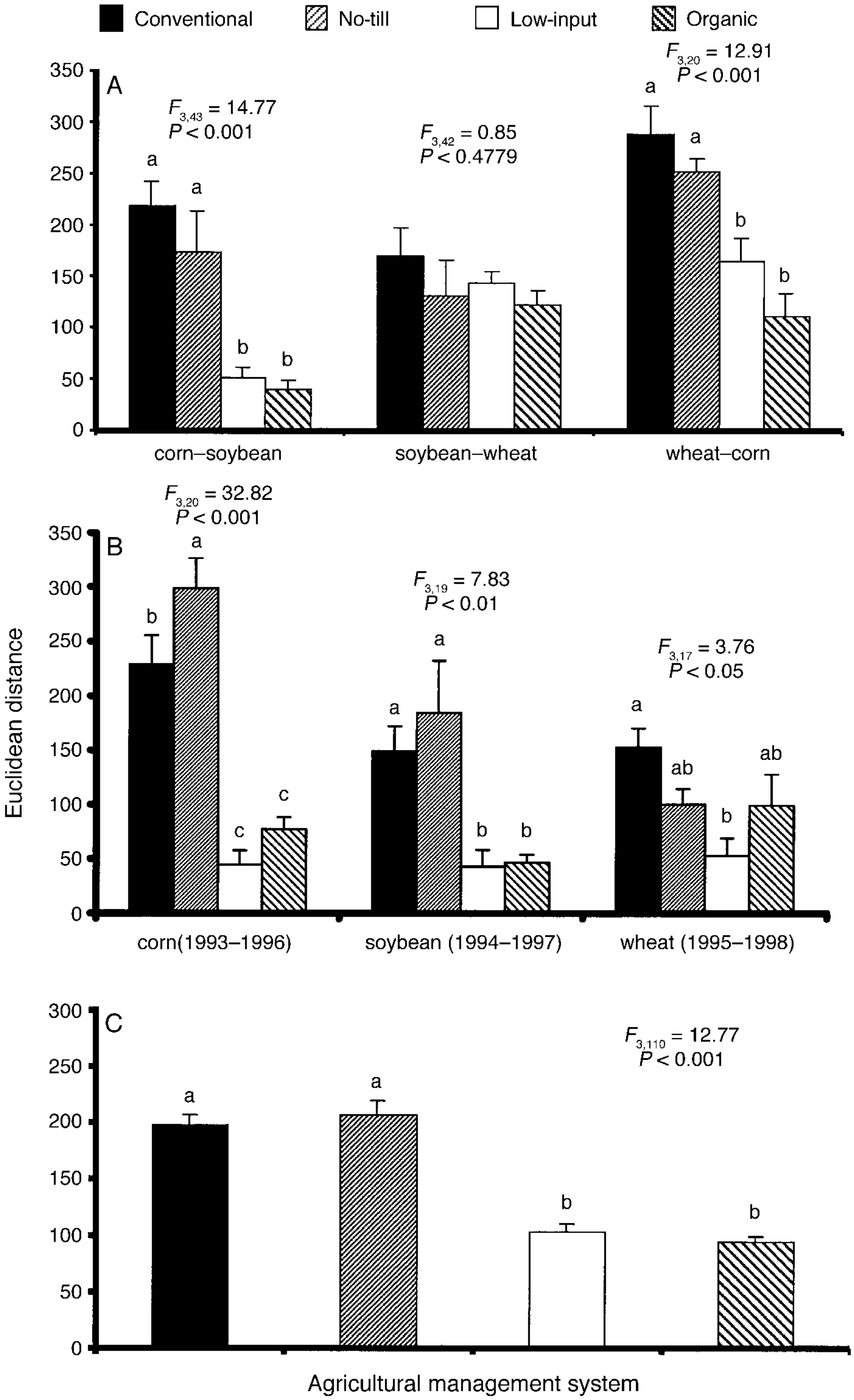

FIG. 3. Agricultural management systems effects on shifts in weed community composition, as estimated by Euclidean distances separating replicates at different times. Euclidean distances were measured within the space defined by the first three detrended correspondence analysis axes and represent: (A) impact of crop sequences in weed community shifts; (B) constancy of the weed community associated with a certain crop; and (C) overall system constancy (means + 1 SE). Systems with the same lowercase letter are not significantly different at $P \leq 0.05$.

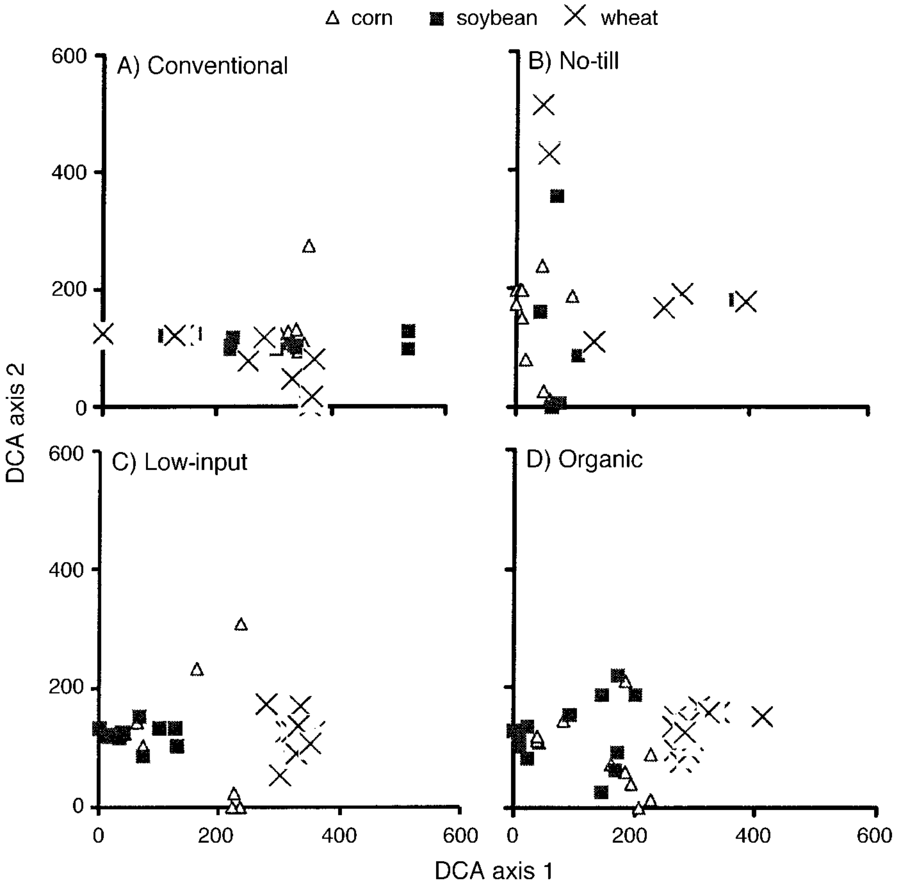

FIG. 4. Individual detrended correspondence analysis (DCA) ordination of replications sampled between 1993 and 1998 at the four agricultural management systems of the W. K. Kellogg Biological Station Long Term Ecological Research site.

enced weed communities in some management systems. Whereas crop did not influence weed community composition in the conventional and no-till systems, weed communities of wheat fields were distinctly different from those in corn and soybean fields in the low-input and organic systems. Similarly, Barberi et al. (1997) observed that the effect of crop rotation on the density and composition of a winter wheat weed flora was evident only in reduced herbicide systems. The systems approach employed in our study precludes us from testing specific hypotheses on the factors responsible for the observed results. Nevertheless, it is possible to speculate on possible causes for the observed differences. First, the environmental conditions at the time of planting and field preparation for winter annual (winter wheat) vs. summer crops (corn and soybean) might create conditions that encourage, or inhibit, certain weed species (Cousens and Mortimer 1995, Liebman and Davis 2000). Second, because of the relatively low selectivity of herbicides, chemical control tactics in conventionally managed systems diminish the importance of environmental factors on weed emergence, thus reducing the importance of crop rotation as an ecological tool for managing weed communities.

The ability to predict shifts in weed communities in response to management practices will facilitate adoption of ecologically based strategies for weed management (Swanton and Murphy 1996). Our analysis of Euclidean distances showed that the constancy of aboveground weed communities was affected by management practices. Although weed communities in conventional and no-till systems had overall lower biomass and fewer species, they were more variable in composition across years than those from the low-input and organic systems.

Influence of crop management systems on weed seedbank characteristics

Over the 3 yr prior to the initiation of this experiment, the conventional and no-till chemically managed systems were in a corn–soybean sequence, whereas the low-input and organic ones had a corn–soybean–wheat sequence. The presence of a different crop in 1992 may have influenced weed species composition, weed seed production, seed dormancy, seed germination, seed decay, and/or post-dispersal seed predation (Ball 1992, Cardina and Norquay 1997, Hulme 1998, Cromar et al. 1999, Kegode et al. 1999). These processes might have

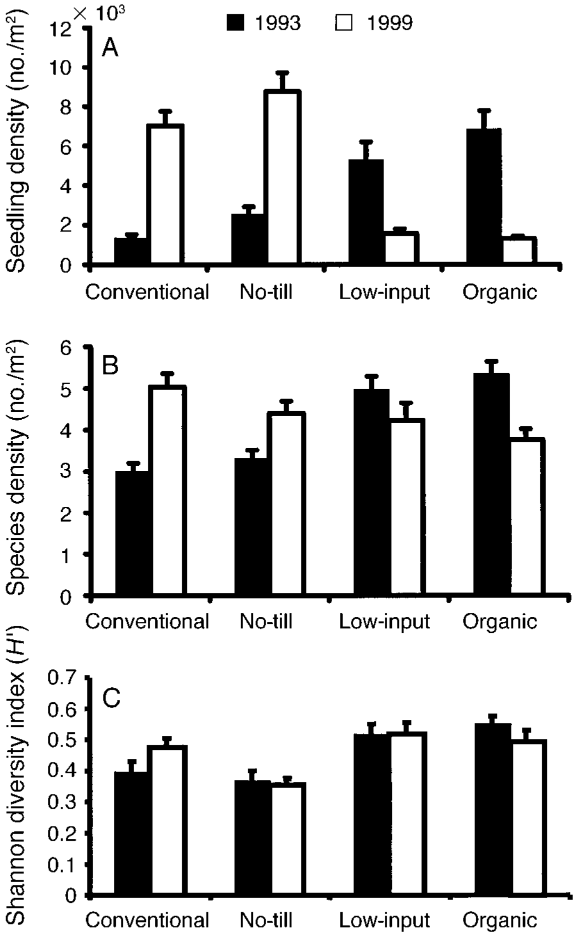

FIG. 5. (A) Seedling density, (B) species density, and (C) Shannon diversity index in the four agricultural management systems of the Kellogg Biological Station Long Term Ecological Research site in 1993 and 1999 (means + 1 SE).

fostered the differences in the seedbank abundance and composition observed in 1993.

The range of seedling densities, species density, and diversity observed in our seedbank analysis were similar to those found in previous studies done across a wide array of agroecosystems. For example, Renner et al. (1998) reported seedbank densities varying from 1873 to 5000 seeds/m^2 in Michigan corn–soybean–wheat fields, closely resembling our observations. High variability in seedbank densities was also observed by Cardina et al. (1991; 400–77 800 seeds/m^2), Mayor and Dessaint (1998; 2765–43 272 seeds/m^2), and Vanasse and Leroux (2000; 957–1625 seeds/m^2). Although these studies differed in the depth to which the seedbank was sampled and the method employed to assess seedbank density, a common result among these and other studies (Roberts and Neilson 1981, Schweizer and Zimdahl 1984) is that conventional tillage, herbicides, and other management practices can reduce seedbank densities.

Our results showed a contrasting pattern among the studied systems. Between 1993 and 1999, seedling emergence and species density increased in the conventional and no-till systems. During the same period, these two variables decreased in the low-input and organic systems. It is unclear if these observations represent long-term patterns resulting from the impact of contrasting management systems and/or short-term oscillations resulting from differences in seed dormancy due to specific weather conditions. Evaluating the percentage of seeds present in different categories (germinable, dormant, and dead) represents a potential study to answer this question, but the magnitude of such analysis precluded us from pursuing it. Despite this limitation, it is possible to speculate that within a given year, any difference among treatments reflects the effect of management systems on the germinable

TABLE 4. Repeated-measures ANOVA for the effect of agricultural management systems on seedling density, species density, and Shannon diversity index.

Variable	df	Seedling density	Species density	Shannon diversity index
Between-subjects source				
Replication (Rep)	5	9313.33**	0.446	0.17
System (Sys)	3	8968.06***	1.29*	1.07***
Rep × Sys	15	15559.37**	3.68	0.84*
Error	96	34819.67	14.56	2.83
Multivariate ANOVA, within-subject source				
Year	1,96	3.99*	1.28	0.01
Year × Sys	5,96	0.79	1.42	2.03
Year × Rep	3,96	108.65***	20.48***	1.92
Year × Sys × Rep	15,96	5.07***	1.58	1.21

Notes: Numbers of seedlings and species data were square-root transformed prior to analysis. The degrees of freedom, Type III sums of squares, and significance levels of effects are shown for each variable in the between-subject comparisons. Wilks' λ F values and degrees of freedom are shown for the multivariate within-subject comparison. System means and standard errors are shown in Fig. 5.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

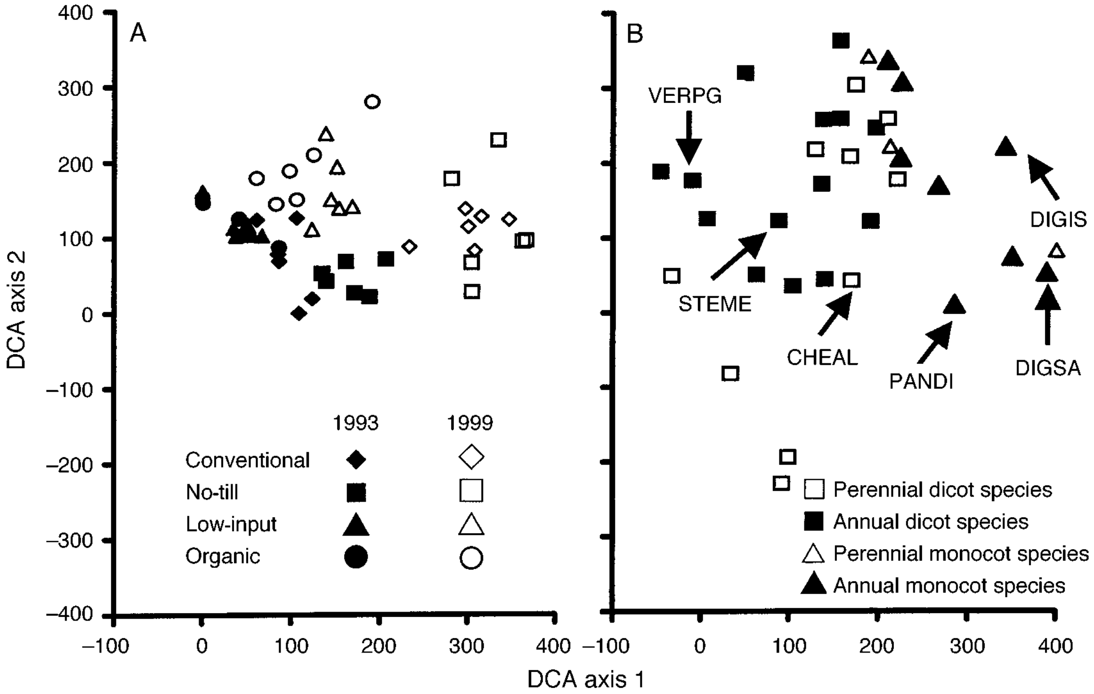

FIG. 6. Detrended correspondence analysis (DCA) for germinable weed seedbank data: (A) plot scores and (B) species scores of the agricultural management systems of the Kellogg Biological Station Long Term Ecological Research site. Species abbreviations: CHEAL, *Chenopodium album*; DIGIS, *Digitaria ischaemum*; DIGSA, *D. sanguinalis*; PANDI, *Panicum dichotomiflorum*; STEME, *Stellaria media*; and VERPG, *Veronica peregrina* (WSSA 1989).

seedbank. In accordance with the hypothesis of a strong environmental influence determining seedbank germination, Mayor and Dessaint (1998) observed that year-to-year variations in seedbank densities may exceed 100%.

Agricultural management systems can not only impact the size of the weed seedbank, but also its composition and relative abundance of species. A consistent result of our seedbank study was the relationship

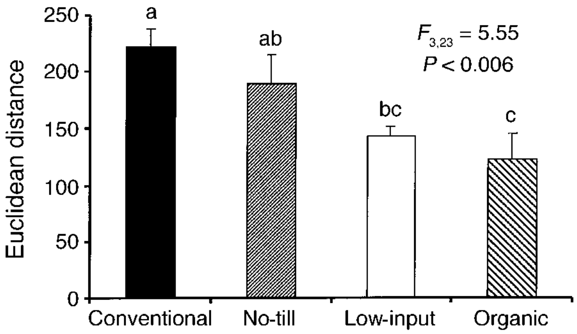

FIG. 7. Effect of agricultural practices on temporal changes in the germinable weed seedbank composition, as estimated by the Euclidean distance separating the position of each plot in 1993 and 1999 (means + 1 SE). Euclidean distances were measured within the space defined by the first three DCA axes. Systems were compared with a one-way ANOVA. Systems with the same lowercase letter are not significantly different at $P \leq 0.05$.

between management systems and weed species diversity. In the systems where herbicides were a major weed management tool (conventional and no-till systems), species diversity in the seedbank was consistently lower than in the low-input and organic systems. Although the Shannon diversity index is sensitive to variation in species density (Magurran 1988), the low diversity values observed in both years in the conventional and no-till systems did not translate in overall seedbank constancy. The Euclidean distance analysis showed higher constancy in species composition for samples from the organic system than from the conventional and no-till systems.

Integration of weed aboveground and seedbank studies and implications for weed management

Three patterns emerged from our analysis of the aboveground and germinable seedbank weed communities of annual row crops. First, agricultural management systems have a strong influence on weed community composition. Second, the disturbance regime of agroecosystems influences the diversity of the weed community. Third, despite the higher values of weed abundance, species density, and diversity observed in the low-input and organic systems, weed community composition was more constant over time in these systems than in conventional and no-till systems.

Management systems and weed community composition.—Although interactions between local biotic and abiotic conditions make it difficult to generalize on the impact of individual crop management practices on weed abundance and composition (Buhler et al. 1994, Buhler 1995, Swanton et al. 1999), our study demonstrated that management systems play a major role in determining weed community composition and dynamics in row crop agriculture. The relative abundance of two summer annual grasses, *D. sanguinalis* and *P. dichotomiflorum,* and one annual dicot, *C. album,* differed across the four studied systems and were important determinants of the observed differences in weed community composition. Three possible mechanisms may account for these observed results. First, differential responses may occur among grasses and broadleaf species to herbicides and tillage practices. Second, incorporation of legume residue into soil may influence soil structure, soil microbial activity, and soil micro- and mesofauna (Abawi and Widmer 2000, Grunwald et al. 2000) and consequently affect weed species. Finally, because the rate of N release differs between synthetic fertilizer and legume residue, N source (synthetic fertilizer in the conventional and no-till systems, legume residue in the low-input and organic systems) might have played an important role in differentiating weed communities (Ladd et al. 1983, Dyck et al. 1995). Future studies in weed community dynamics should test the relative importance of herbicides, tillage, and N source, as well as the existence of synergistic interactions among these management practices.

Disturbances and weed species diversity.—The ''intermediate disturbance hypothesis'' (sensu Connell 1978, Huston 1979, Menge and Sutherland 1987) suggests that in repeatedly and highly disturbed habitats, plant community diversity should be low. On the other hand, species diversity is expected to increase when disturbance is reduced, reaching its maximum at intermediate disturbance intensities. Whereas conventionally managed agroecosystems can be characterized by a series of frequent and intensive disturbances such as tillage, cultivation, and pesticide and herbicide application (Landis and Menalled 1998), a primary focus in the development of alternative farming systems is to reduce such management practices and generate less disturbed systems (Rasmussen and Ascard 1993). In accordance with the ''intermediate disturbance hypothesis,'' we observed lower values of weed aboveground and seedbank diversity in the conventional and no-till systems than in low-input and organic ones. Previous studies (Rasmussen and Ascard 1993, Clementes et al. 1994, Van Elsen 2000) have also detected an increase in weed species abundance and diversity in less disturbed agroecosystems.

This study showed that adoption of alternative management systems affects the composition of the weed community. This raises the question: is decreasing weed diversity a desirable goal of weed management? One outcome of agriculture intensification is the establishment of extensive monocultures with low species diversity (Hall 1995). Weed suppression has been a major focus of conventional agriculture and weed species generally have been studied as an unrelated set of targets for control rather than as ecological communities. Consequently, there is relatively little information on the importance of weed diversity per se on the success of weed management (Clements et al. 1994). Because of the observed increase in weed species diversity in reduced disturbance systems, the development of organic management programs should incorporate weed community parameters and containment strategies for potential shifts in weed species dominance. An effective weed community management strategy should also incorporate a threshold for cultural, biological, and chemical control practices based on the entire community rather than on a subset of species.

If a systems approach is adopted in the design of agroecosystems, it is necessary to consider the importance of weed density on processes that go beyond reducing weed interference on crops. It has been proposed that, when weed abundance is maintained below an accepted economic threshold level, it can translate into several beneficial effects. First, exudates of weed roots can have considerable effect on soil microbial activity, soil biochemistry, availability of nutrient cations, and soil physical properties (El Titi 1995). Second, the existence of noncrop plants might improve pest management through an increase in the effectiveness of natural enemies and a reduction in herbivore survivorship (Price et al. 1980, Andow 1991, Altieri 1994, Tonhasca and Byrne 1994, Wratten and Van Emden 1995, Letourneau 1997). This increase in natural enemy abundance may help decrease the need for pesticide treatments, reducing production costs and pollution. Third, increasing weed diversity may provide a buffer against the development of herbicide resistance (Clements et al. 1994). Finally, the presence of weeds can help reduce erosion and water run-off from agricultural fields into ditches, streams, ponds, or lakes (Zimdahl 1999).

Weed community constancy.—Forecasting the impact of crop–weed interactions on yield loss is essential to integrate weed management programs into the design of cropping systems that promote adequate profits while reducing human health and environmental problems associated with the use of off-farm chemical inputs (Liebman and Gallandt 1997). However, agricultural weed communities are generally unstable, and a proactive weed management program should be aimed at increasing weed community predictability (Clements et al. 1994). Our results show that weed communities associated with the low-input and organic systems were more productive, diverse, and constant over time than those associated with the same crops in conventional or no-till systems. Thus, the selection of a particular weed management program should be done after evaluating the costs and benefits of two conflicting goals:

first, to reduce weed biomass production with an associated increase in uncertainties regarding weed species composition; and second, to increase constancy of weed community composition at the expense of a rise in weed productivity. This process should also take into account environmental and yield cost/benefit relationships of the selected management strategy.

In conclusion, the design of weed management programs aimed at reducing reliance on off-farm inputs should go beyond assessing the relationship between specific management practices and focal species. Strategies to reduce weed interference must incorporate weed community parameters and be developed as a part of an integrated farming system. This study showed that different agricultural management systems can have both immediate and long-term effects on both the aboveground and seedbank weed communities. Systems with a high dependence on off-farm chemical inputs (conventional and no-till) increased the abundance of annual weeds and decreased weed diversity, richness, and constancy in composition across crops and years. In contrast, the low-input and organic systems were dominated by annual and perennial dicot species and, although they had higher species diversity and overall weed biomass, community composition was more similar over years. These differences in species and life-history composition of the weed communities create challenges for the development of weed management practices. Understanding how environmental and economic factors affect the adoption of a given set of management practices is an essential step towards the design of alternative weed management strategies.

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APPENDIX

A table presenting the main agronomic practices applied between 1993 and 1997 at the W. K. Kellogg Biological Station Long Term Ecological Research site in Michigan, USA, is available in ESA's Electronic Data Archive: *Ecological Archives* A011-018.