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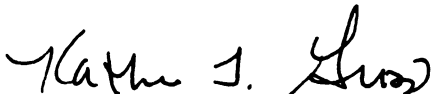
AGROECOSYSTEM DIVERSITY: IMPACTS ON WEED
COMMUNITIES AND CROP YIELD

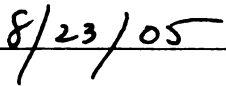
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**AGROECOSYSTEM DIVERSITY: IMPACTS ON WEED COMMUNITIES AND
CROP YIELD**

By

Richard Garner Smith

A DISSERTATION

**Submitted to
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ABSTRACT

AGROECOSYSTEM DIVERSITY: IMPACTS ON WEED COMMUNITIES AND CROP YIELD

By

Richard Garner Smith

Ecological theory regarding the role of species diversity in the functioning of terrestrial ecosystems may have important implications for the design and management of agricultural systems that are less reliant on inputs of synthetic chemical fertilizers and pesticides for fertility and pest control. However, much of the evidence supporting the importance of diversity in ecosystem function comes from grassland systems where biotic conditions and disturbance regimes differ from those in most managed systems. Furthermore, agricultural studies that purport to demonstrate the impacts of crop diversity on crop yields and pest regulation are often confounded with applications of chemical fertilizers and pesticides. My research aims to understand how ecological theory regarding the role of diversity in ecosystem function can be used to predict weed and crop yield response to increasing crop diversity.

I examined the relationships between row-crop diversity and ecosystem functions related to weed population regulation and crop productivity in two long-term experimental agroecosystems. The first system compared corn grown in continuous monoculture and in rotation with soybean and winter wheat under two input management systems: conventional and organic-based. The second system was an experimental manipulation of crop diversity with no external chemical inputs of fertilizer or herbicides. Crop diversity was manipulated by growing corn, soybean, and

winter wheat continuously and in two and three-crop rotations and with either no, one, or two cover crops annually.

Weed communities and crop yield both varied in response to these treatments. In the first system, weed communities were most variable from year to year in the organic rotation, while corn yield variability was highest in the least diverse cropping system (conventional monoculture). In the diversity experiment, crop diversity had relatively little effect on the abundance or composition of weeds. Cover crops in wheat had strong suppressive effects on weeds in both continuous wheat grown in monocultures and in rotation with corn and soybean, while cover crops had little effect on weed abundance or species composition in corn and soybean.

In contrast to the effect on weed communities, crop diversity had large effects on crop productivity. Corn yields varied across the diversity treatments and in the most diverse treatments were comparable to those in conventionally managed systems in the region. The positive effect of crop diversity on yields in corn was driven by increased soil N that was related to the number of legume species in the rotation (red clover and soybean). Soybean yields were also higher in rotations with higher crop diversity, while winter wheat yields were unaffected by the number of crops in the rotation.

These results suggest that increasing crop diversity can have significant impacts on crop yields, particularly in corn, and may decrease the need for intensive chemical management by suppressing weeds during phases of the rotation that are conducive to high cover crop growth (i.e. winter wheat) and by increasing soil nitrogen and the competitive advantage of crops over weeds.

Dedicated to my late grandparents, George L. Smith and Irene E. Smith

ACKNOWLEDGMENTS

This work could not have been accomplished without the help of many people. Foremost, I would like to thank my major advisor, Dr. Katherine Gross, for her patience, thoughtful advice, ecological insight, and friendship throughout my graduate career. My professional and personal life has been greatly enriched by our interactions. I would also like to thank the past and present members of my graduate committee: Dr. Richard Harwood, Dr. Doug Landis, Dr. Carolyn Malmström, Dr. Gary Mittelbach, and Dr. Doug Buhler, for guidance over the past six and a half years.

My field work was made much easier, and infinitely more enjoyable, by the assistance and dedication of Laura Bell, Joey Dembs, Ryan Disney, Matt Gorentz, Cinnamon Hayes, Jonathan Hernandez, Stephanie Januchowski, Beth Jasiak, Chelsea Leroy, Mark Mittelbach, John Mittelbach, Jenny Morrison, Pam Moseley, Nate Rathbun, Justin Rensch, Kendra Sales, Chris Start, Lee Sutkowi, C.J. Wyckoff, Pete Wyckoff, and Margaret Yancey. I would especially like to acknowledge the assistance of Brandon Young, whose life enriched the lives of all who knew him, and who will be greatly missed.

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CHAPTER 1

INTRODUCTION

There is growing evidence that diversity plays an important role in the functioning of terrestrial ecosystems (Chapin et al. 2000, Diaz and Cabido 2001, Hooper et al. 2005, Spehn et al. 2005). Community and ecosystem-level processes such as productivity (Hector et al. 1999, Tilman et al. 2001, Lambers et al. 2004), community stability (Cottingham et al. 2001) invasibility (Levine and D'Antonio 1999, Naeem et al. 2000, Fargione and Tilman 2005) and nutrient cycling (Hooper and Vitousek 1998) have all been shown to vary with species or functional diversity. While the exact mechanisms by which diversity impacts these functions are often debated (Naeem et al. 2000, Huston 1997, Wardle 1999, Loreau and Hector 2001) there is little argument that the conservation and maintenance of diversity has important implications for ecosystem services required for human survival (Hooper et al. 2005).

The relationship between diversity and ecosystem function may also have important implications for the functioning of agricultural systems. The reduction in cropping-system diversity associated with the intensification of agriculture and the concomitant increase in the need for chemical inputs for fertility and pest control (Tilman et al. 2002, Robertson and Swinton 2005) suggest that ecosystem processes related to production agriculture may also be regulated by diversity (Altieri 1999, Minns et al. 2001). Support for the importance of diversity in agricultural systems come from a number of recent studies showing that more diverse cropping-systems often out-perform less diverse systems in functions such as weed population regulation (Liebman and Dyck 1993, Teasdale et al. 2004, Westerman et al. 2005), yield quantity

and quality (Vandermeer 1989, Reganold et al. 2001), nutrient cycling (Drinkwater et al. 1998), and disease resistance (Zhu et al. 2000). Increasing cropping-system diversity has been advocated as an important tool for the management of weeds and for reducing reliance on chemical inputs (Dekker 1997, Liebman and Gallandt 1997, Kegode et al. 1999, Liebman and Staver 2001, Westerman et al. 2005).

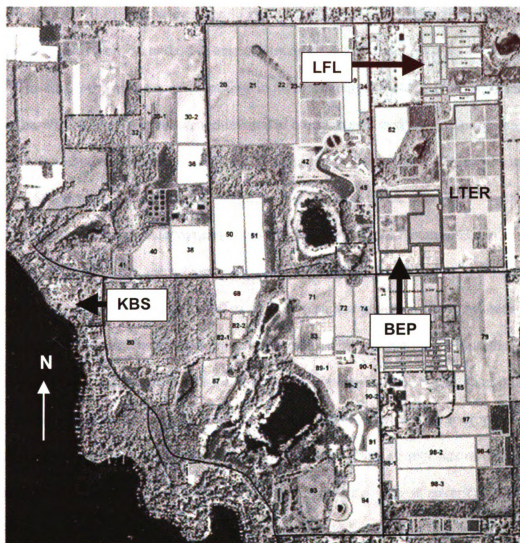
However, much of the theory and experimental evidence supporting the direct link between diversity and ecosystem function has been developed in experimental grassland systems (Hooper et al. 2005), where biotic conditions and disturbance regimes are very different from those in most agricultural systems (Schläpfer and Schmid 1999). In addition, a large component of diversity in most agricultural systems is temporal (crop rotation) (Liebman and Dyck 1993, Liebman and Staver 2001), meaning that many of the interactions among crop species are indirect, in contrast to grassland systems where many species interact directly (Tilman 1999). Furthermore, many agricultural studies supporting the importance of diversity are performed in the presence of external chemical inputs such as fertilizer and herbicide that can vary with each crop and may confound the effects of crop diversity on weed abundance and yields (Liebman and Dyck 1993, Doucet et al. 1999). It is therefore unclear whether and to what extent the observed relationships between community diversity and ecosystem function reported in grassland studies can be applied to weed communities and crops in agroecosystems. The goal of this dissertation was to investigate these relationships in annually tilled row-crop agricultural systems.

Study sites

The general question I was interested in was: Can ecological theory regarding the role of diversity in ecosystem function be used to predict weed and crop yield response to increasing row-crop diversity? Components of this general question were examined in two long-term cropping-system experiments, the Living Field Laboratory (LFL) and the Biodiversity Experiment Plots (BEP), located at the W. K. Kellogg Biological Station (KBS) Long Term Ecological Research (LTER) project in agroecology at Michigan State University in Hickory Corners, MI (Figure 1.1). The KBS LTER also includes a larger (42 ha) cropping-system manipulation (main site, 7 treatments); however, the purpose of the treatments in the main site study is not to manipulate crop diversity, but rather chemical inputs and tillage. Therefore the main site treatments were not sufficient to examine questions related to effects of crop diversity.

Living Field Laboratory

The studies reported in Chapters 2 and 3 were done at the Living Field Laboratory (LFL; Sanchez et al. 2004). The LFL is located within a matrix of agricultural fields just northwest from the LTER main site (Figure 1.1). Soils at the site consist primarily of Kalamazoo silt loam (Typic Hapludalfs) and are 43% sand, 40 % silt, 17 % clay, have pH of 6.68, and contain 1.08% soil organic carbon (Robertson et al. 1997). The LFL was established in 1993 by Dr. Richard R. Harwood, then the Mott Chair in Sustainable Agriculture at MSU, and was designed to evaluate the effects of extended rotations and different input management systems on crop yield, weed and



<http://lter.kbs.msu.edu/Maps/Thematic/Figure3.htm>

Figure 1.1: Aerial photo of the KBS LTER main site and surrounding landscape. Arrows indicate study sites. Abbreviations are LFL, Living Field Laboratory; BEP, Biodiversity Experiment Plots; LTER, Long Term Ecological Research site; KBS, W. K. Kellogg Biological Station academic campus.

insect pressure, and soil health. The plots are maintained by the Farm Systems Center (FSC), which also manages the fields adjacent to these plots. A heavily grazed horse pasture borders the LFL on the west and likely is a seed source of perennial wind-dispersed weeds to the LFL and other annual row crops in this area.

The LFL experiment consists of four input management systems (conventional, organic-based, integrated fertilizer, and integrated compost) crossed with crop rotation treatments (continuous corn and each phase of a 4 yr corn-corn-soybean-winter wheat rotation). The design is a split-plot in a randomized complete block with four replications. Input management system is the whole plot factor and rotation is the subplot factor. In addition, the rotation subplots under organic-based management are split by a second factor; the western half of each plot is planted with cover crops each year. However, because the cover crop treatment is not applied randomly within the rotation subplots, and because there is no cover crop treatment in the conventional input system, observations in the organic subplots are restricted to either the cover-cropped or non cover cropped portions of each subplot. Therefore the effective plot size of the rotation subplots in the organic-based input management systems (with cover crops or without cover crops) is half that of the conventional input management subplots. All plots are chisel plowed and field cultivated prior to planting. Details regarding the conventional and organic-based input systems are described below.

The conventional input system receives full inputs of fertilizer, herbicides and pesticides at rates recommend for the region (Sanchez et al. 2001). Starter fertilizer is applied to corn at planting and after a pre side-dress nitrate test in June. No fertilizer is applied to soybeans. Fertilizer was applied to winter wheat in fall at planting through

1994. Since 1995, application has occurred in early spring. Lime was applied to all plots in September 1992 at a rate of 2T/a. Herbicides (broadcast applications) and pesticides are applied in spring prior to planting and as needed any time thereafter. Details regarding herbicide and pesticide applications can be found on the KBS LTER website at (http://lter.kbs.msu.edu/Data/LTER_Metadata.jsp?Table=KBS042-010).

The only external nutrient source in the organic-based plots is composted dairy manure that is obtained from various sources, including the KBS Dairy. Compost is applied on a dry weight basis based on estimated nitrogen, phosphorus and potassium requirements and the rate of application takes into account moisture and nitrogen content of the compost. Since 1995 the application rate is determined after correction for sand content. Row cultivation and rotary hoeing is performed as necessary early in the growing season to manage weeds in corn and soybean crops in the organic treatments. In addition, the western half of each organic sub-plot is planted with cover crops each year. Cover crops vary depending on the crop and include: annual ryegrass (*Lolium multiflorum* Lam.), hairy vetch (*Vicia villosa* Roth), red clover – Michigan mammoth (*Trifolium pratense* L.), and crimson clover (*Trifolium incarnatum* L.). Additional details regarding the cover crops planted in the LFL can be found at (http://lter.kbs.msu.edu/Data/LTER_Metadata.jsp?Table=KBS042-007).

Biodiversity Experiment Plots

Data reported in Chapters 4 and 5 (and part of Chapter 2) were collected from the Biodiversity Experiment Plots (BEP) at the KBS LTER. The BEP was established in the spring (corn and soybean) and fall (winter wheat) of 2000 in an area that had previously been used for tillage trials for the LTER experiment. The plots are located to

the west of the main LTER experiment (Figure 1.1) and are bordered by B-Avenue to the south and 40th Street to the west.

The BEP was designed to determine the impacts of manipulations of row-crop diversity on ecosystem functions related to production agriculture. The treatments include corn, soybean, and winter wheat grown at six levels of crop diversity, ranging from continuous monocultures to two- and three-crop rotations with zero, one, and two cover crop species annually (Table 1.1). In total, there are 21 treatments: 18 cropping sequences (3 main crops x 6 crop-diversity treatments), two fallow treatments (spring vs. fall) and a bare-soil (continuously plowed) treatment. Diversity treatments were randomly applied to plots in three linear blocks; in the fourth block, treatments were arranged in sequence in a 4 x 5 block to facilitate demonstration of treatment effects. The four replicate blocks are separated by 8m grass buffers. Individual plots were 9.1m x 27.4m with no buffer strips between plots (Figure 1.2).

In treatment one each crop is planted in continuous monoculture; corn was planted in late April-early May, soybean in early May and winter wheat in October. Following crop harvest (October and November for soybean and corn, respectively, and July for wheat) plots were left fallow until the next season, at which time they were tilled (chisel plowed) and the same crop planted again (Figure 1.3). Treatment two is similar to treatment one except that a cover crop is planted each year (Figure 1.4). In the corn and wheat monocultures red clover (*Trifolium pratense* L.) is sown into the plots in July and March, respectively. Cereal rye (*Secale cereale* L.) is sown into soybean stubble following harvest in October. Treatment three is a two-crop rotation without cover crops (Figure 1.5). In one sequence soybean follows corn and in another

Table 1.1. Crop diversity treatments at the KBS LTER Biodiversity Experiment Plots (BEP). Treatments were established in 2000 and include monocultures and two- and three-crop rotations of corn (C), soybean (S) and wheat (W), with and without grass or legume cover crops. NA, not applicable.

Treatment Group	Sequence #	Rotation/ description	No. Crop species					
			Annually			Sum over rotation		
			Crops	Cover crops	Total	Crops	Cover crops	Total
BS	B21	Bare-soil	NA	NA	NA	NA	NA	NA
1	B20	W	1	0	1	1	0	1
1	B19	S	1	0	1	1	0	1
1	B18	C	1	0	1	1	0	1
2	B17	W	1	1	2	1	1	2
2	B16	S	1	1	2	1	1	2
2	B15	C	1	1	2	1	1	2
3	B14	W-S	1	0	1	2	0	2
3	B13	S-C	1	0	1	2	0	2
3	B12	C-S	1	0	1	2	0	2
4	B11	W-C-S	1	0	1	3	0	3
4	B10	S-W-C	1	0	1	3	0	3
4	B9	C-S-W	1	0	1	3	0	3
5	B8	W-C-S	1	1	2	3	2	5
5	B7	S-W-C	1	1	2	3	2	5
5	B6	C-S-W	1	1	2	3	2	5
6	B5	W-C-S	1	2	3	3	3	6
6	B4	S-W-C	1	2	3	3	3	6
6	B3	C-S-W	1	2	3	3	3	6
FS	B2	Fallow _{spring}	NA	NA	NA	NA	NA	NA
FF	B1	Fallow _{fall}	NA	NA	NA	NA	NA	NA

Biodiversity Experiment Plots

Plot size: 9.1 m x 24.4 m

420 B20	419 B19	418 B18	417 B17	416 B16
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411 B11	412 B12	413 B13	414 B14	415 B15
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410 B10	409 B9	408 B8	407 B7	406 B6
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401 B1	402 B2	403 B2	404 B4	405 B5
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301 B15	302 B17	303 B1	304 B14	305 B7	306 B3	307 B4	308 B16	309 B11	310 B8	311 B18	312 B5	313 B12	314 B9	315 B19	316 B2	317 B6	318 B20	319 B13	320 B10
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201 B1	202 B12	203 B3	204 B14	205 B9	206 B2	207 B6	208 B18	209 B10	210 B16	211 B17	212 B13	213 B15	214 B8	215 B20	216 B11	217 B5	218 B19	219 B7	220 B4
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101 B16	102 B2	103 B19	104 B4	105 B7	106 B1	107 B6	108 B18	109 B12	110 B11	111 B3	112 B15	113 B13	114 B5	115 B14	116 B17	117 B10	118 B8	119 B9	120 B20
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Figure 1.2: Plot map showing locations of 20 of 21 treatments in four replicate blocks at the Biodiversity Experiment Plots at the Kellogg Biological Station Long Term Ecological Research site. See Table 1.1 for treatment codes. Treatment B21 is located on the western edge of blocks 1-3 and on the western edge of plot 420 in block 4.

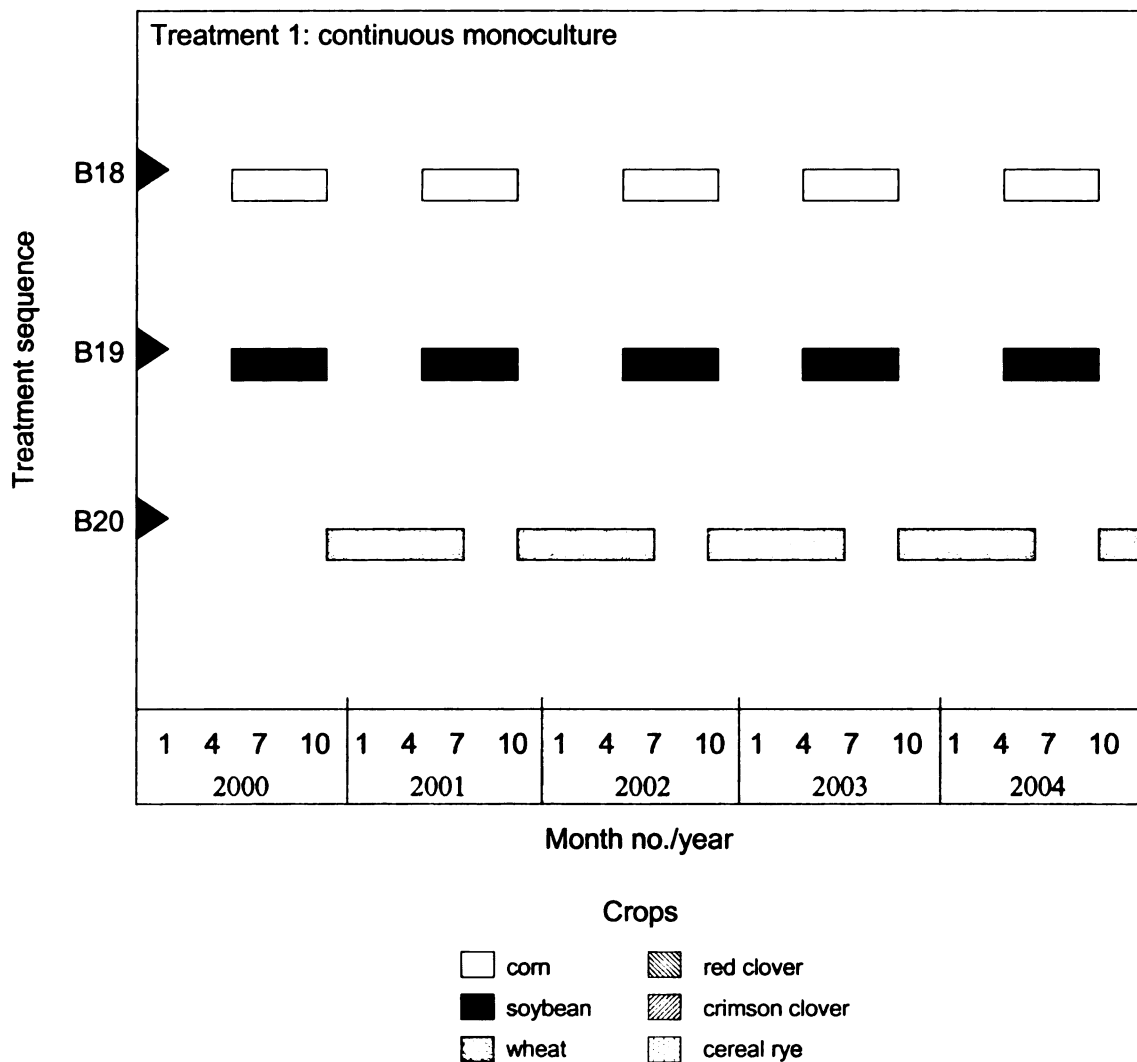


Figure 1.3: Schematic representation of Treatment Group1 (continuous monocultures of each crop species) in the BEP over the study period. Colored bars indicate length of time, from crop sowing to harvest, that each species is present in each of the three treatment sequences. Months are 1, January; 4, April; 7, July; 10, October.

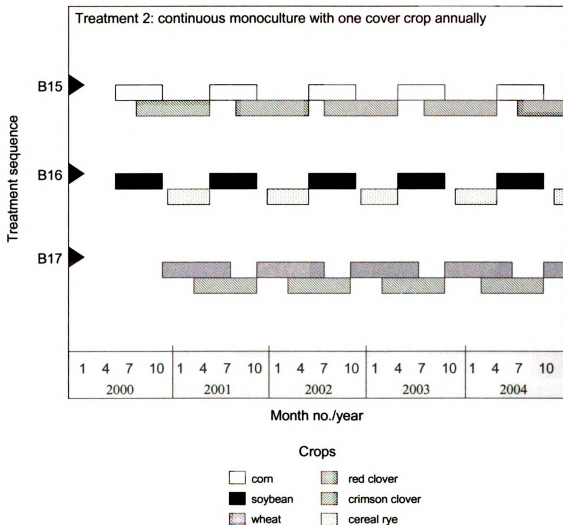


Figure 1.4: Schematic representation of Treatment Group 2 (continuous monocultures with a cover crop) in the BEP over the study period. Colored bars indicate length of time, from crop sowing to harvest, that each species is present in each of the three treatment sequences. Months are 1, January; 4, April; 7, July; 10, October.

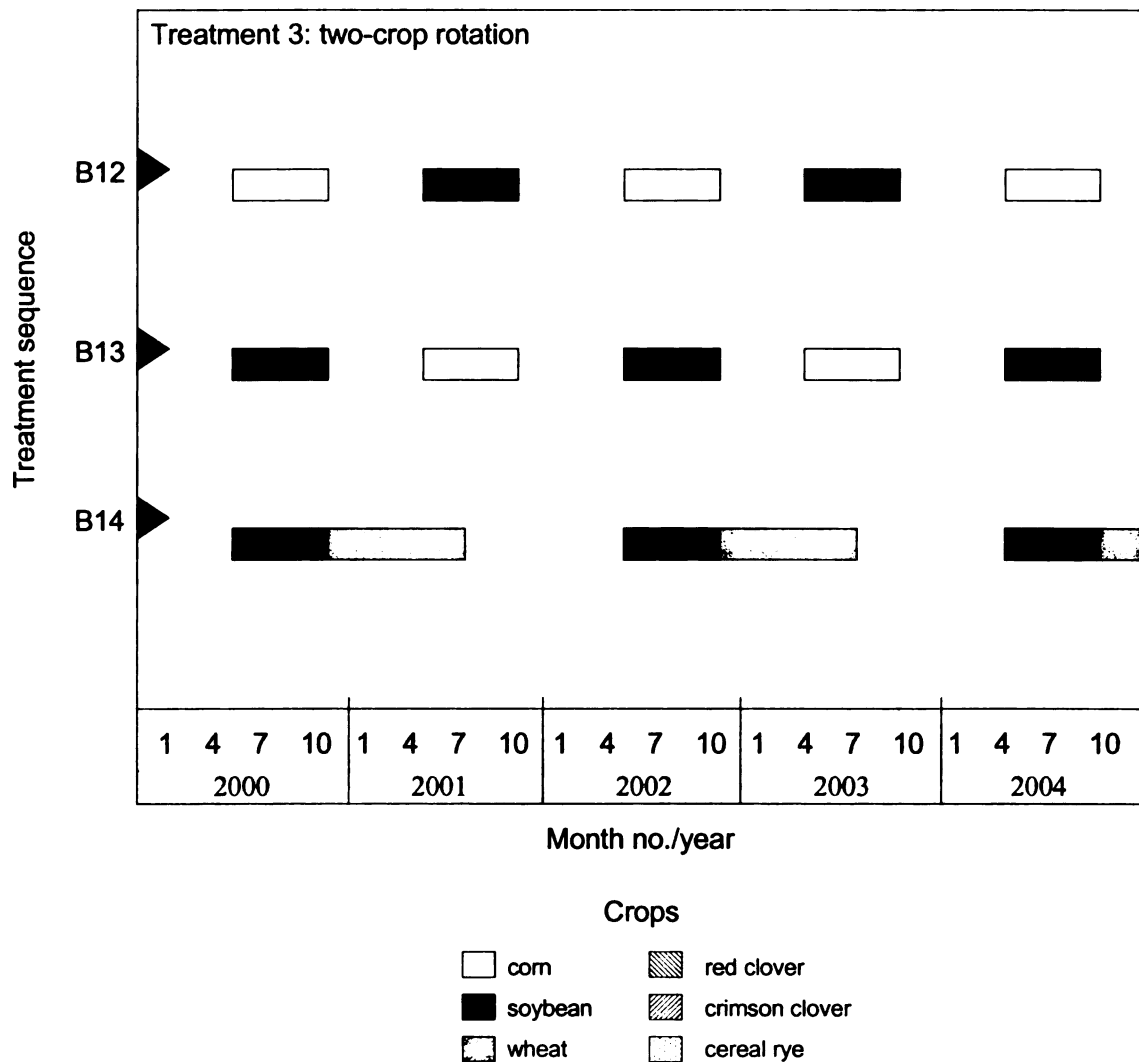


Figure 1.5: Schematic representation of Treatment Group 3 (two-crop rotation) in the BEP over the study period. Colored bars indicate length of time, from crop sowing to harvest, that each species is present in each of the three treatment sequences. Months are 1, January; 4, April; 7, July; 10, October.

corn follows soybean. In the third sequence wheat follows soybean. There is no corn-wheat sequence; therefore wheat is not present in this treatment one out of every two years. Treatment four is a three-crop rotation (Figure 1.6). The order of crops in the three-crop rotation is always corn-soybean-wheat; however each entry point of the rotation is present each year (i.e. three sequences: corn-soybean-wheat, soybean-wheat-corn, and wheat-corn-soybean). Treatment five is similar to treatment four except that one cover crop is planted each year (Figure 1.7). In July, red clover and crimson clover (*Trifolium incarnatum* L.) are planted during the corn and soybean phases, respectively. Red clover is frost seeded into wheat in March. Treatment six is similar to treatment five except that an additional cover crop, cereal rye, is planted in corn and wheat stubble in October or November (Figure 1.8). Cereal rye is not planted in the soybean phase of the rotation. Tillage and planting times are the same for all crops across all treatments. Data on weed abundance and composition and soil resource levels were also collected in the spring and fall fallow treatments and are presented in the appendix to Chapter 4. No data was collected in the bare soil treatment.

Protocols for crop management in the BEP are identical to those in the LTER main site Treatment 4 (T4). All plots are chisel plowed and soil finished prior to planting main crops (corn, soybean and wheat). Weeds are managed with inter-row cultivation and rotary hoeing in corn and soybean early in the growing season. No additional weed management is performed in wheat. Importantly for the questions I was interested in addressing, there are no additions of chemicals to these plots, and except for the prescribed differences in cover crops or crop rotations, the plots were

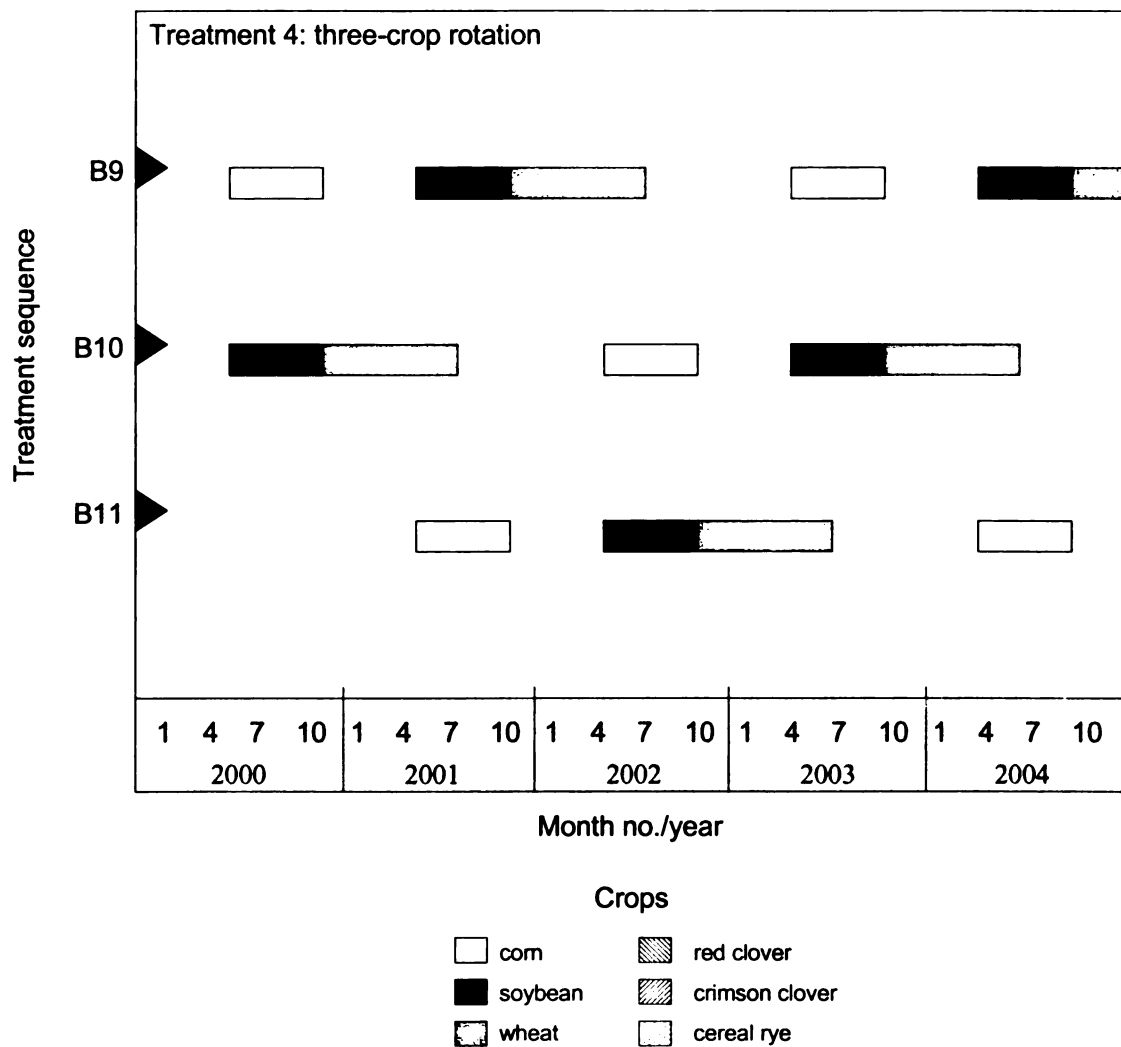


Figure 1.6: Schematic representation of Treatment Group 4 (three-crop rotation) in the BEP over the study period. Colored bars indicate length of time, from crop sowing to harvest, that each species is present in each of the three treatment sequences. Months are 1, January; 4, April; 7, July; 10, October.

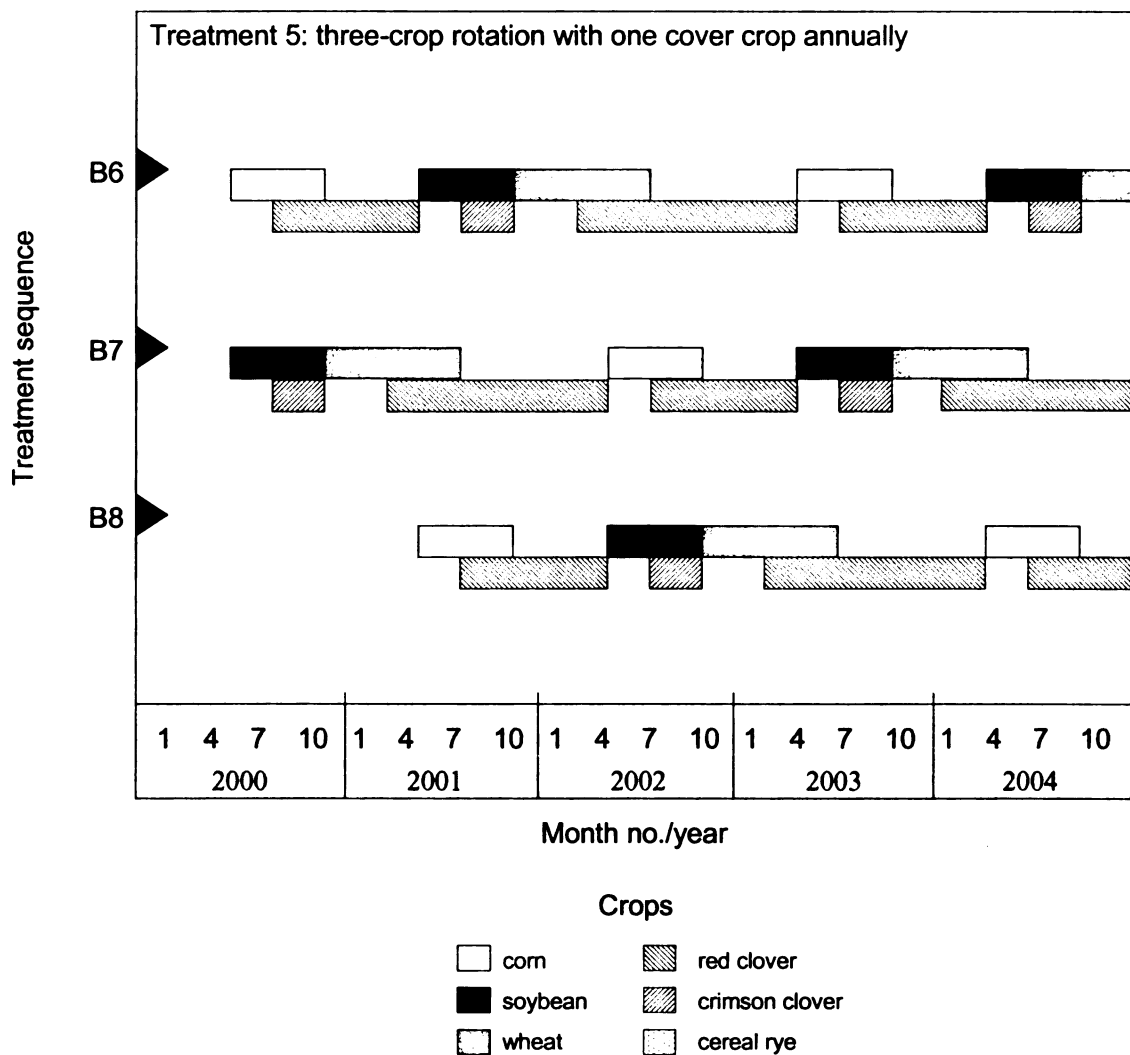


Figure 1.7: Schematic representation of Treatment Group 5 (three-crop rotation with one cover crop annually) in the BEP over the study period. Colored bars indicate length of time, from crop sowing to harvest, that each species is present in each of the three treatment sequences. Months are 1, January; 4, April; 7, July; 10, October.

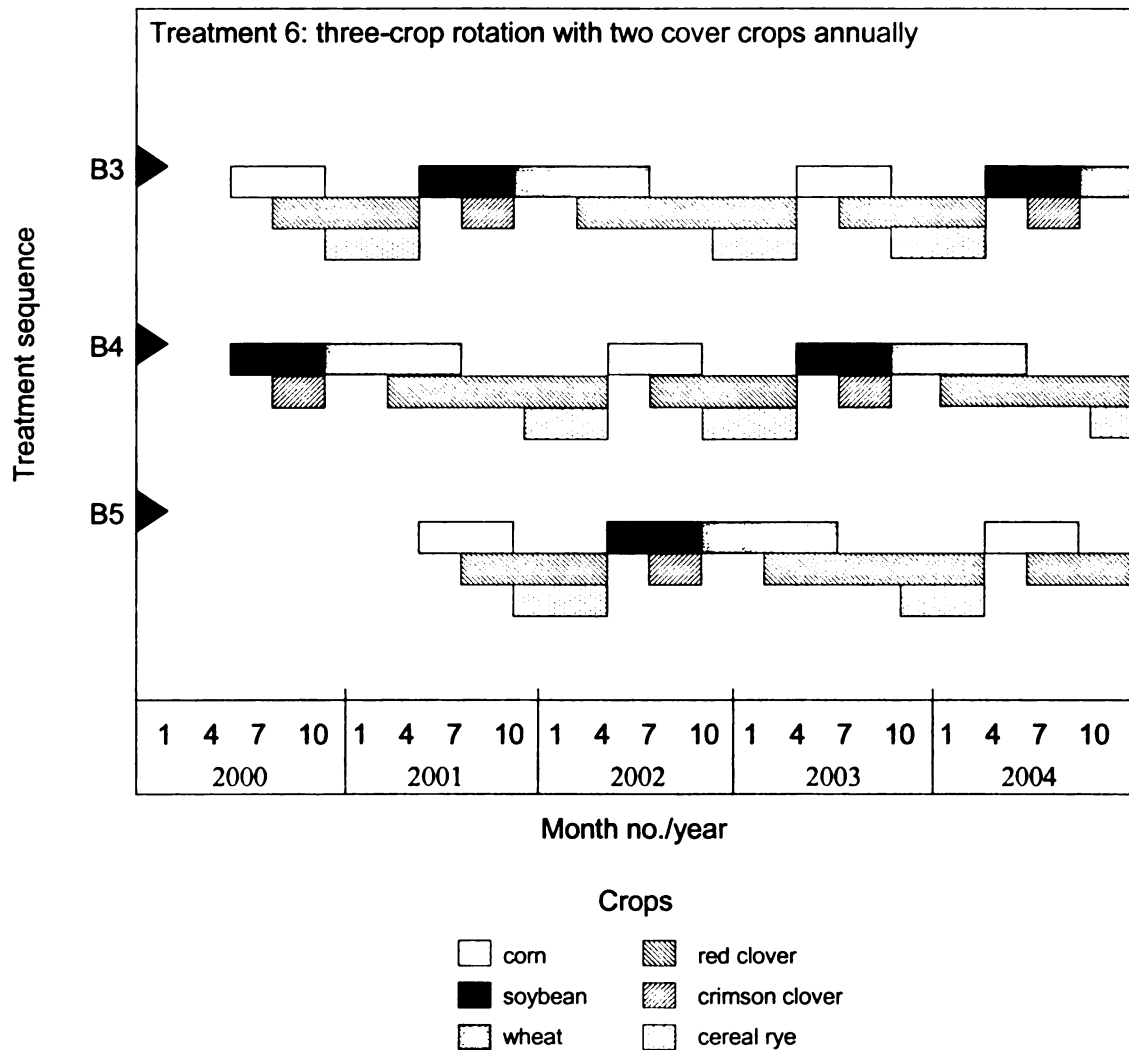


Figure 1.8: Schematic representation of Treatment Group 6 (three-crop rotation with two cover crops annually) in the BEP over the study period. Colored bars indicate length of time, from crop sowing to harvest, that each species is present in each of the three treatment sequences. Months are 1, January; 4, April; 7, July; 10, October.

managed identically. More detailed descriptions of the treatments can be found at http://lter.kbs.msu.edu/Agronomic_Protocols/2004AgronomicProtocol%20.pdf.

The original treatment plan for the BEP called for no applications of fertilizer, herbicide or pesticide. However, agronomic log records indicate that in 2001 fertilizer (28% UNA solution) was applied to corn (31 May) and herbicide was applied to wheat stubble (29 August). This was apparently an accidental application. No additional inputs have been applied to the treatments from 2002 to the present.

Questions of interest

The general question I was interested in was: Can ecological theory regarding the role of diversity in ecosystem function be used to predict weed and crop yield response to increasing row-crop diversity? One prediction of ecological theory is that diverse plant communities should be more stable, in terms of community biomass, productivity, and nutrient cycling, than simple plant communities (Cottingham et al. 2001). One way in which this can occur is when increased species richness leads to larger differences in species' responses to environmental variability, such that species that respond positively compensate for those that respond negatively. However, there is little theory to suggest how plant species should respond when a large component of diversity is temporal (i.e. crop rotation) or how the diversity of crop species in a rotation should impact the stability or diversity of weed species in a particular crop and if this will differ under organic and conventional inputs. The treatments in the LFL allowed us to examine these questions within the context of annually tilled row-crop agricultural systems in which the number of crop species in a rotation and management inputs varied (Chapter 3). Treatments included the extreme ends of the crop diversity

gradient; simple (continuous corn, conventional management) and diverse cropping-systems (corn-corn-soybean-wheat rotation, organic management). Because these treatments had been in place since 1993 the diverse cropping-systems had completed two cycles of the four-year rotation by the time weed communities and crop yields were sampled in the summer of 2001.

The BEP provided an excellent system within which to test predictions related to diversity-ecosystem function across a broad gradient in row-crop diversity. For many ecosystem properties and processes the shape of the relationship between diversity and ecosystem function has been shown to be positive, but saturating at higher levels of diversity (Hooper et al. 2005). This suggests that at the levels of diversity most amenable to manipulation in most agricultural systems (i.e. at the low end of the diversity gradient) small increases in crop diversity should have relatively large effects on agroecosystem function. Again however, there is little theory to suggest how biomass, productivity, and nutrient cycling should respond to increasing crop diversity when a large component of diversity is temporal. I examined the response of the weed community, crop yields, and resource availability across six levels of crop diversity ranging from one crop species grown continuously, to two- and three-crop rotations with zero, one, and two cover crop species annually and up to six crop species over a three year rotation cycle. Because there were no external inputs applied to any of the treatments in the BEP, the impacts of crop diversity on weeds, crop yields, and soil resource levels could be analyzed without the possible confounding effects of variation in fertilizer and herbicide inputs.

Organization of dissertation

The dissertation includes four empirical chapters formatted as manuscripts for journal submission. In Chapter 2, I report the results of a study investigating the response of the soil seed bank to manipulations of row-crop diversity (crop rotation) in two different weed and input management systems (conventional vs. organic-based). I also discuss the results in terms of the implications of using weed seed bank data to infer the long-term weed suppressive potential of certain management practices. In Chapter 3, I report the results of a study investigating how row-crop diversity and input management affect the inter-annual variability (stability) of the emergent weed community and crop yield. Data in these chapters were taken from treatments in the LFL. In Chapters 4 and 5, I report results from the first three years (2002-2004) of the BEP, a unique long-term row-crop diversity study that includes a broad range of crop diversity through rotation (1-5 species over the rotation) and is conducted in the absence of chemical inputs, which are often confounding in many other agronomic studies. In Chapter 4, I report how increasing cropping-system diversity through manipulations of rotations and cover crops impacts the abundance, composition and dynamics of the emergent weed community in three crops: corn, soybean, and winter wheat. I further examine how changes in the weed community are related to changes in soil resource levels and light across the diversity treatments. In Chapter 5, I report how crop yields vary across this same diversity gradient and evaluate whether these yield responses are correlated with changes in the weed community and soil resource levels.

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CHAPTER 2

EVIDENCE OF RAPID SEED BANK DYNAMICS IN ROW CROPS

ABSTRACT

The dynamics of soil seed banks in crop rotations of maize, soybean, and winter wheat were investigated to determine whether weed seed inputs associated with earlier phases of the rotation persist in subsequent phases. In one study we compared seed banks in maize grown continuously and in a long-term rotation that included winter wheat. A second study followed seed bank composition and abundance over three years in plots that were planted to maize and soybean in successive years following planting to winter wheat in 2001. Seed banks were measured by direct germination in a heated glasshouse. Seed banks in continuous maize and the maize phase of the rotation did not differ in species composition or abundance despite significant differences in the winter wheat phase of the rotation. Seed bank abundance and composition in plots planted to winter wheat in 2001 quickly changed following planting of maize and soybean in 2002 and 2003, respectively. Data from the two experiments suggest that seed banks in annual row crops are highly dynamic and are strongly influenced by the most recent crop. This may limit our ability to infer longer-term effects of weed management practices from studies of soil seed banks.

INTRODUCTION

Seed banks in annual row-crops are assumed to contain seeds that have been shed over multiple growing seasons, reflecting the sum effects of past and present weed management on weed survival and reproduction (Cavers and Benoit 1989, Clements et al. 1996, Dorado et al. 1999). The assumption that seed banks are a memory of past

management is a long-standing paradigm in weed ecology (Cavers and Benoit 1989, Swanton and Booth 2004) and has often been invoked as justification for using the seed bank to measure the long-term weed suppression potential of a given management system (Cardina et al. 2002, Moonen and Barberi 2004, Swanton and Booth 2004). However, this assumption may not be valid if weed seed banks do not persist for more than a few growing seasons or are highly dynamic.

The ability of seeds to persist in the soil depends on a number of physiological, environmental, and evolutionary factors. In desert systems, for instance, annual plant species have evolved dormancy as a bet-hedging strategy to maintain populations in environments that are temporally variable, and a large percentage of the seed bank remains dormant even when conditions are conducive to germination (Philippi 1993, Pake and Venable 1996). In contrast, most agricultural weeds have evolved to maximize growth and reproduction during favorable conditions (Grime 1977) and therefore germinate when the appropriate micro-environmental cues are detected. Although there are a few well-known examples of seeds of some arable weed species persisting for relatively long periods of time and under controlled conditions (Cavers and Benoit 1989, Telewski and Zeevaart 2002), the majority of studies in cultivated systems suggest that most seeds germinate or die in the first few years after entering the soil seed bank (Cavers and Benoit 1989, Lutman et al. 2002, Teasdale et al. 2004). The discrepancy between such studies and assumptions of long-term seed bank persistence indicates that the dynamics of seed bank communities in annual row crop systems are still not well understood.

Crop rotations provide useful systems for evaluating the persistence and dynamics of weed seed banks because weed management, and therefore seed inputs to the soil, varies with each crop in rotation (Liebman and Dyck 1993). Because certain crops are often associated with distinct weed communities (Cavers and Benoit 1989, Squire et al. 2000), inputs of seed during that phase of the rotation can leave a unique signature within the seed bank. The persistence of this seed input signature can be measured in successive crop phases to determine how long seed inputs remain in the seed bank.

The aim of this study was to examine weed seed bank dynamics and determine the relative persistence of seed inputs to the soil in annually tilled row crops. Specifically, we were interested in whether weed seed inputs associated with the winter wheat (*Triticum aestivum* L.) phase of a rotation were apparent in the seed bank in successive phases of a maize (*Zea mays* L.)-soybean (*Glycine max* L.)-winter wheat rotation. Fall-sown crops such as winter wheat have been shown to be associated with a weed flora that is distinct from spring-sown crops (Squire et al. 2000, Crawley 2004) such as maize and soybean. Data from two studies were examined to investigate seed bank dynamics and persistence. The first study compared weed seed banks in maize grown continuously and in a long-term crop rotation with soybean and winter wheat under conventional and organic-based input management. The two input management systems were compared to determine whether the method of weed control and nutrient inputs affected seed bank persistence. The second study followed seed bank abundance and composition in replicate plots that were planted to winter wheat in 2001, maize in 2002 and soybean in 2003 in a rotation experiment managed without external chemical

inputs. Seed banks were sampled each year in spring and the composition and abundance of seeds in the soil assessed by direct germination in a heated glasshouse.

MATERIALS AND METHODS

Study Sites

Two studies were carried out in experimental plots located at the W. K. Kellogg Biological Station Long Term Ecological Research (KBS LTER) site in SW Michigan, USA. Soils at both study sites were a mixture of Kalamazoo (fine-loamy, mixed, mesic Typic Hapludalfs) and Oshtemo (coarse-loamy, mixed, mesic Typic Hapludalfs) sandy loams (Sanchez et al. 2001). Annual precipitation is 90 cm; about half as snow, and mean annual temperature is 9.7° C. Detailed site and soil and management descriptions of the site are available at <http://lter.kbs.msu.edu>.

The first study was conducted in 2001 at the Living Field Lab experimental plots (hereafter LFL). The LFL was established in 1993 to examine the effects of extended rotations and different input management systems on nutrient cycling and agroecosystem function. The site was planted to lucerne (*Medicago sativa* L.) in 1992 and rotation treatments consisting of continuous maize and each phase of a four-year maize - maize -soybean-winter wheat rotation were initiated in 1993. Rotation treatments were randomly assigned to plots within blocks that received one of four input management treatments in a split-plot design. All phases of the rotation were present each year. For this study we focused only on continuous maize (CM) and the second year maize (rotation maize, RM) and winter wheat (rotation wheat, RW) phases of the rotation in two management systems; a conventional system that received full inputs of fertilizer, herbicides (broadcast applications) and pesticides, at rates

recommended for the region (Sanchez et al. 2004), and an organic-based system which received composted dairy manure, but no chemical inputs. Weed management in the organic input system was via periodic (2-4 times/yr) inter-row cultivation (row cultivation and rotary hoeing). Each phase represented different times since the last appearance of winter wheat in the rotation. Plots planted to continuous maize (CM) had never been planted to winter wheat; second-year maize plots (RM) had been planted to maize the previous year and to winter wheat three and seven years prior to sampling; and winter wheat plots (RW) had been planted to wheat the previous season and five years prior. Plots in both input systems were chisel plowed and soil finished each year prior to planting. All treatments (management system x rotation) were replicated four times. Plot sizes differed between the two input treatments and measured 15 x 9 m (conventional) and 15 x 4.5 m (organic).

The second study was conducted from 2002-2004 at the Biodiversity Experiment Plots (hereafter BEP) approximately one km south of the LFL site. The BEP was established in 2000 to investigate the effects of manipulating row-crop diversity on ecosystem functioning. Treatments in the BEP include continuous monocultures and two and three-crop rotations of maize, soybean, and winter wheat grown with and without cover crops. The BEP was managed without external chemical inputs and plots were chisel plowed and soil finished each year prior to planting. All phases of the rotation treatments were present each year. Plots were 9 x 27 m and treatments were arranged in a randomized complete block with four replications. For this study we followed seed bank abundance and composition in four replicate plots that

were planted to winter wheat in 2001, maize in 2002, and soybean in 2003 and compared these to the seed banks of continuous monocultures of the same crops.

Seed bank sampling

Soil seed banks were sampled in a similar manner in both the LFL and BEP studies. In 2001 (LFL study) and 2002-2004 (BEP study) soil seed banks were sampled by taking ten soil cores (2 cm diameter) to a depth of 5 cm from a 25 x 25 cm area in three central locations in each plot. Sampling occurred in mid-May after the plots had been tilled and crops planted, but prior to crop emergence. Sampling in the spring has been shown to provide reliable estimates of the viable seed bank (Forcella 1992) because it allows natural dormancy-breaking mechanisms to operate over the winter. Sampling immediately after tillage and planting also ensured that seed banks were thoroughly mixed. Each ten-core soil sample was composited and spread on sterile growing medium (Sunshine Germinating Mix #3, Sun Gro Horticulture, Bellevue, Washington, USA) in 25 x 25 cm half-flats in a glasshouse. Flats were watered daily from above with a mist sprayer to keep the soil surface moist. Flats were monitored for germination approximately twice a week from May to October. Seedlings that emerged from the flats were identified and removed. Seedlings that could not be identified immediately were transplanted and grown in separate pots until identification was possible.

Statistical analyses

For each soil sample collected from the LFL, we calculated the density (total seedlings emerged) and species richness (number of species). Data were averaged for the three samples taken from each plot, and plot means used as the unit of replication.

The effects of management system and rotation on seed bank density and species richness were analyzed using a split-plot design with management system (conventional, organic) as the whole plot factor and rotation phase (continuous maize, rotation maize, rotation wheat) as the subplot factor. Analyses of variance were performed using the MIXED procedure in SAS (SAS Version 8.02; SAS Institute, Cary, NC, USA). Treatment means were separated with errors appropriate for a split-plot design using the Tukey-Kramer Test at the $P = 0.05$ level. Seedling density and species richness data were square root transformed prior to analysis to satisfy the assumptions of ANOVA. Seedling density data are expressed as number of emerged weed seedlings per m^2 (assuming 25 cm^2 per sample). Data were back transformed for presentation in tables and figures.

To visualize plot-level patterns in species abundance and composition among the rotation and management system treatments, we performed non-metric multidimensional scaling, (NMDS: Mather 1976, McCune and Grace 2002) using the PC-ORD package (version 4.25, McCune and Mefford 1999). NMDS is an ordination method that maximizes rank order correlation between distances derived from the original dataset and those in ordination space, and is often the most appropriate ordination method for community datasets (McCune and Grace 2002). Prior to ordination, seedling abundance values were $\log(x + 1)$ transformed and a distance matrix was calculated using the Bray-Curtis distance metric. Forty runs of the ordination (at random starting configurations and with a maximum of 400 iterations per run) were performed using an instability criterion of 0.00001. These runs were

compared to 50 randomized runs to assess the significance of the reduction in stress from six to one dimensions (Monte-Carlo Test).

In addition to the ordination, we used non-parametric distance-based multivariate analysis (DISTLM v.5, Anderson 2001, 2004) to test for significant differences in seed bank community composition and abundance among the treatments. Main effects of inputs, rotation phase, and their interaction on species composition and abundance were tested by permutation (9999 permutations) using error terms appropriate for a split plot design. The test statistic (pseudo F) is analogous to Fisher's F-ratio and was calculated from a distance matrix of Bray-Curtis dissimilarity coefficients. Species abundance values were $\log(x + 1)$ transformed prior to analysis.

Seed bank data from the BEP were analyzed using NMDS ordination to determine how seed bank composition and abundance changed when plots planted to winter wheat in 2001 were subsequently planted to maize in 2002 and soybean in 2003. NMDS was performed on the species abundance values measured for the four replicate plots of the rotation treatment each year from 2002-2004 and the four replicates of the continuous monoculture that corresponded to the crop planted in the rotation replicates (i.e. continuous monoculture of winter wheat in 2001, maize in 2002, and soybean in 2003). Seedling abundance data were $\log(x + 1)$ transformed prior to calculating Bray-Curtis distances and performing ordination.

RESULTS

LFL Seed bank density and species richness

In the LFL plots, there was no effect of input management system (organic vs. conventional) on seed bank density or species richness (density: $P = 0.76$; richness: $P =$

0.14); however, there was a significant effect of rotation phase (density: $F_{2,12} = 4.89$, $P = 0.03$; richness: $F_{2,12} =$, $P = 0.007$). In both input systems, seed bank density and species richness were significantly greater in the winter wheat phase (RW, last planted to winter wheat in 2000) than the rotation maize phase (RM, last planted to winter wheat in 1998) or continuous maize monoculture (CM) (Figure 2.1). Seed bank density and richness did not differ between the two maize treatments (RM and CM); and there was no interaction between input management system and rotation phase on seed bank density or richness (density: $P = 0.99$; richness: $P = 0.26$).

LFL Community abundance and composition

Thirty-seven species were identified from the soil samples collected in the LFL (Table 2.1). Of these, six were unique to the wheat phase of the rotation (RW). These tended to be monocots that were present at relatively low relative densities within the seed bank ($\sim < 1\%$).

The NMDS ordination reduced the dimensionality of the LFL seed bank dataset to three main axes (minimum stress = 9.86, $P = 0.02$), which accounted for 58.2, 19.7, and 14.0 % (cumulative $r^2 = 91.9\%$) of the information in the analytical data set, respectively. Ordination showed a clear distinction in seed bank abundance and composition between the winter wheat phase of the rotation and the continuous and rotation maize (Figure 2.2). The non-parametric multivariate analysis confirmed that differences among seed banks were due to the effect of rotation phase (rotation phase: pseudo $F_{2,12} = 8.82$, $P = 0.0001$) and that effects of input management and their interaction were not significant (inputs: $P = 0.055$; interaction: $P = 0.084$).

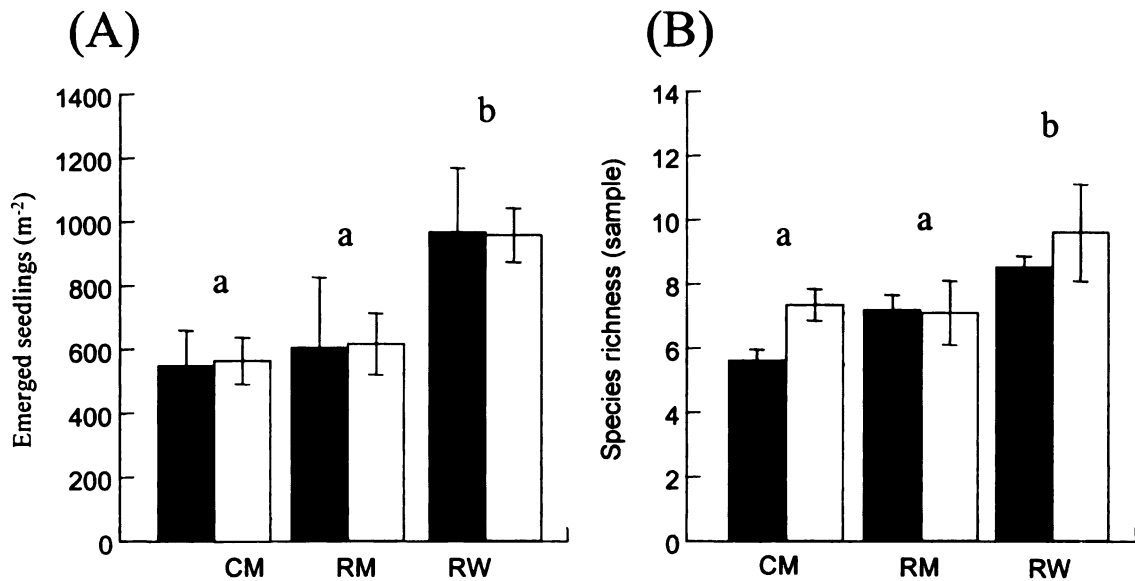


Figure 2.1: Density (A) and species richness (B) in May 2001 of seedlings emerged from the soil seed bank in continuous maize (CM, never planted to winter wheat) and the rotation phase of maize (RM, planted to winter wheat in 1998) and winter wheat (RW, planted to winter wheat in 2000) of a four year maize-maize-soybean-winter wheat rotation under conventional (black bars) and organic-based (white bars) nutrient and weed management. Bars are means ± 1 S.E. There was no effect of input system (organic vs. conventional) so bars sharing the same lower case letter indicate no significant difference among rotation phases at $P = 0.05$ (Tukey-Kramer Test).

Table 2.1: Relative density (%) of weed species that emerged from the soil seed bank samples collected in May 2001 in continuous maize (CM, never planted to winter wheat) and the rotational phase of maize (RM, last planted to wheat in 1998) and winter wheat (RW, last planted to wheat in 2000) phases of the rotation.

Weed species	Rotation phase		
	CM	RM	RW
<i>Amaranthus retroflexus</i> L.	0.00	0.59	1.03
<i>Ambrosia artemisiifolia</i> L.	0.00	0.24	1.03
<i>Arabidopsis thaliana</i> (L.) Heynh.	9.97	8.83	3.59
<i>Aster</i> sp.	0.00	0.12	0.00
<i>Capsella bursa-pastoris</i> (L.) Medicus	0.00	1.18	0.00
<i>Cardamine hirsuta</i> L.	0.26	0.00	0.00
<i>Chenopodium album</i> L.	7.93	11.43	1.76
<i>Conyza canadensis</i> (L.) Cronq.	0.00	0.12	0.59
<i>Digitaria ischaemum</i> (Schreb. ex Schweig.) Schreb	0.13	0.71	1.54
<i>Digitaria sanguinalis</i> (L.) Scop.	0.90	0.47	3.45
<i>Echinochloa crus-galli</i> (L.) Beauv.	0.26	0.00	0.00
<i>Eleusine indica</i> (L.) Gaertn.	0.38	0.12	0.00
<i>Epilobium</i> sp.	0.00	0.00	0.07
<i>Eragrostis cilianensis</i> (All.) E.Mosher	0.00	0.00	0.07
<i>Erigeron strigosus</i> Muhl. ex Willd.	0.64	0.00	0.07
<i>Juncus tenuis</i> Willd.	0.13	0.00	0.07
<i>Lepidium virginicum</i> L.	0.13	0.12	0.00
<i>Mollugo verticillata</i> L.	0.26	14.72	0.07
<i>Oxalis stricta</i> L.	1.15	2.36	4.91
<i>Panicum capillare</i> L.	0.00	0.00	0.07
<i>Panicum dichotomiflorum</i> Michx.	0.00	0.24	5.94
<i>Panicum</i> sp.	0.00	0.00	0.15
<i>Plantago major</i> L.	0.00	0.35	3.96
<i>Poa</i> sp.	11.89	3.06	0.51
<i>Polygonum aviculare</i> L.	0.00	0.00	0.29
<i>Polygonum convolvulus</i> L.	0.26	0.24	0.00
<i>Polygonum persicaria</i> L.	0.13	1.53	1.91
<i>Portulaca oleracea</i> L.	0.64	1.18	0.51
<i>Setaria faberi</i> Herrm.	0.00	0.00	0.07
<i>Setaria glauca</i> (L.) Beauv.	0.00	0.12	0.07
<i>Setaria viridis</i> (L.) Beauv.	0.00	0.12	0.07
<i>Solanum ptycanthum</i> Dun.	0.00	0.12	0.15
<i>Stellaria media</i> (L.) Vill.	22.63	23.79	2.49
<i>Taraxacum officinale</i> Weber in Wiggers	11.51	5.18	54.62
<i>Trifolium repens</i> L.	0.13	0.00	0.07
<i>Veronica peregrina</i> L.	29.80	22.03	10.56
<i>Veronica persica</i> Poir.	0.90	1.06	0.29

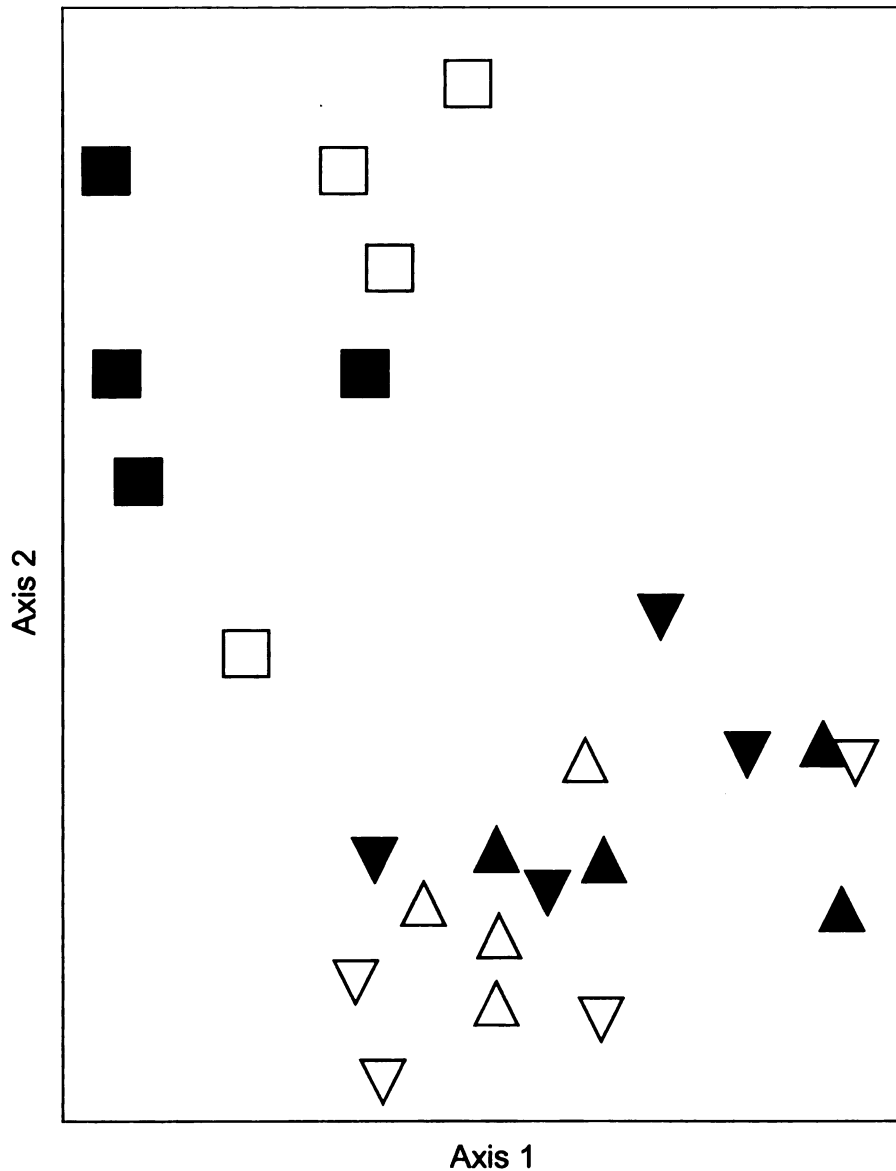


Figure 2.2: NMDS ordination of weed seed banks from soils collected in May 2001 in continuous maize (never planted to winter wheat) (triangles) and the rotation phase of maize (last planted to winter wheat in 1998) (inverted triangles) and winter wheat (last planted to winter wheat in 2000) (squares) of a four year maize-maize-soybean-winter wheat rotation under conventional (filled symbols) and organic-based (open symbols) nutrient and weed management. Values plotted are replicate scores. Only the two most explanatory axes ($r^2 = 0.779$) are displayed.

BEP Seed bank dynamics

In the BEP plots the seed bank was measured each year in four replicate rotation plots, and the corresponding continuous monocultures. Eight weed species were unique to both the continuous wheat and rotation plots planted to wheat in 2001 (Table 2.2). After two years, following planting to maize (2002) and soybean (2003), only three of these species were still detectable in the seed bank of the rotation replicates in 2004. The species still present in 2004 tended also to be associated with maize (Table 2.1).

The NMDS ordination performed on the BEP species abundance data reduced dimensionality to three main axes (minimum stress = 11.30, $P = 0.020$), which explained 49.6, 28.3, and 8.7% (cumulative $r^2 = 86.6\%$) of the information in the analytical dataset. The ordination showed that seed banks in the continuous monocultures of wheat, maize, and soybean were distinct from one another, and that there were dramatic changes in seed bank abundance and composition from year to year in the crop rotation replicates (Figure 2.3). Following planting to wheat in 2001, seed bank abundance and composition in three of the four rotation replicates was similar to that of continuous wheat in 2002. In 2003, after a year of maize, seed bank abundance and composition had shifted towards that of continuous maize. In 2004, the abundance and composition of the seed bank had again shifted, this time in the direction of continuous soybean. The seed bank in the fourth replicate was less similar to that of continuous wheat in 2002, but still showed a similar pattern of change following planting to maize and soybean.

Table 2.2: Relative densities (%) in the soil seed bank of the eight weed species common to both the continuous winter wheat monoculture and the wheat rotation in 2001 and following planting of maize (2002) and soybean (2003).

Weed species	2001 Wheat	2002 Maize	2003 Soybean
<i>Chenopodium album</i> L.	4.8	37.1	25.5
<i>Digitaria ischaemum</i> (Schreb. ex Schweig.) Schreb	1.6	0	0
<i>Digitaria sanguinalis</i> (L.) Scop.	8.0	2.9	0
<i>Erigeron spp.</i>	1.6	0	0
<i>Mollugo verticillata</i> L.	34.9	2.9	9.6
<i>Panicum dichotomiflorum</i> Michx.	3.2	0	0
<i>Potentilla norvegica</i> L.	3.2	0	0
<i>Stellaria media</i> (L.) Vill.	25.4	51.4	46.8

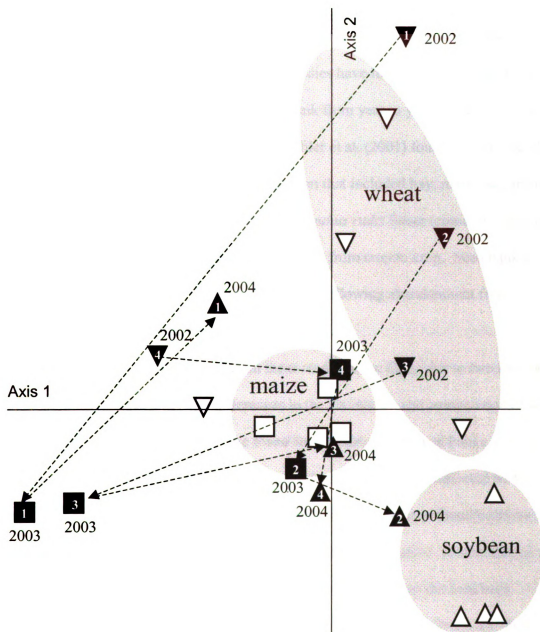


Figure 2.3: NMDS ordination of weed seed banks in four replicate plots (filled symbols) in 2001, 2002, and 2003 following planting to winter wheat (inverted triangles), maize (squares), and soybean (triangle), respectively, and the corresponding continuous monoculture in that year. Replicate plots are labeled 1-4 and dashed arrows indicate each plot's trajectory through time. Ellipses around monocultures (open symbols) are for illustrative purposes and do not imply confidence intervals. Only the two most explanatory axes ($r^2 = 0.780$) are displayed.

DISCUSSION

Results of both the LFL and BEP studies showed that weed seed banks in the crop rotations were highly dynamic. Other studies have found similar rapid changes in the abundance and composition of the seed bank from year to year (Leck and Leck 1998, Teasdale et al. 2004). For example, Buhler et al. (2001) found that the seed bank changed with each crop over a five-year rotation that included hay, maize, soyabean, and oat; and that abundances of seeds of *Amaranthus rudis* Sauer (common waterhemp) and *Setaria* species (foxtail) changed 2 to 33-fold from crop to crop. Seed bank density in an oldfield increased 14-fold in just two years following abandonment from agriculture (Leck and Leck 1998).

The rapid dynamics observed in these studies were likely due to two factors: low seed bank persistence and large differences in the abundance and composition of seed inputs associated with each crop. We found little evidence that seed banks were highly persistent in either the LFL or BEP studies, or that persistence was affected by the system of nutrient and weed management. Other researchers have found a similar lack of long-term persistence of seed banks in agricultural field studies. A summary of crop management studies found that most viable seeds were lost from the seed bank following one to four years of reduced or eliminated seed inputs (Cavers and Benoit 1989). Buhler (1999) found that *Setaria faberi* Herrm. (giant foxtail) seed densities in the soil decreased rapidly when seed inputs were eliminated. In a controlled field study, Lutman et al. (2002) reported annual seed loss rates from 20 to 58% for sixteen weed species.

The observation from the LFL study that a few species were present in both the winter wheat and maize rotation phases, but not continuous maize (Table 2.1) suggests that there is limited short-term persistence in the seed bank. Studies reporting higher species diversity in crop rotations compared to continuous monocultures (Liebman and Dyck 1993, Dorado et al. 1999, Cardina et al. 2002) support the notion of limited short-term persistence in some species. The few seeds in the soil that do persist for more than one or two seasons are likely important for the maintenance of populations across rotation cycles (Liebman and Dyck 1993, Buhler and Hartzler 2001). However, because these persistent seeds are present at such low population levels, their detection within the seed bank may be difficult and may not provide useful information regarding past weed management. While external factors such as seed predators or other biotic agents (Brust and House 1988, Liebman and Dyck 1993) could have affected seed bank persistence, there is little *a priori* reason to expect long-term seed bank persistence in most arable systems, as most weed species have evolved in environments that are conducive to rapid growth and reproduction rather than prolonged dormancy (Grime 1977, Clements et al. 2004).

Annual inputs of seed to the soil are a consequence of “filters” operating within the context of the cropping system (Cavers and Benoit 1989, Booth and Swanton 2002). These filters exclude some species and allow others to establish and reproduce, and can include the crop and timing of crop sowing (Hald 1999, Hallgren et al. 1999, Menalled et al. 2001, Booth and Swanton, 2002, Crawley 2004). For example, a comparison of the emergent weed communities under three different 6-yr crop rotations in southern Alberta found the species of crop was a much more important factor influencing the

weed flora than crop rotation (Andersson and Milberg 1998). Similarly, Doucet et al. (1999) found that when continuous monocultures and 3-crop rotations containing maize, soybean, and winter wheat that had been in place for nine years were planted to maize in the tenth year there were few residual effects of the rotation on the emergent weed community. In our study, the strong filtering effects of different crops, coupled with the lack of long-term seed bank persistence, likely contributed to the observed similarities in seed banks between crops in rotation and monocultures of the same crop.

The relatively rapid seed bank dynamics and low degree of seed bank persistence observed in the present study are not likely specific to crop rotations. Crop rotations only make these phenomena more apparent. Given the rapid dynamics and short persistence times of arable weed seeds in the soil, we suggest caution be exercised when using the seed bank to infer past trends in weed control or weed seed production, or evaluate the weed management efficacy of a given cropping system. Seed banks at any given point in time should likely be viewed more as a reflection of the weed management success or failures that occurred the previous season rather than the cumulative effects of management occurring over longer-time scales. Therefore, it may be unwise to use the seed bank to infer the long-term weed suppression potential of a given management system or to relate the size and composition of the seed bank to weed management practices occurring over time scales longer than one or two cropping seasons.

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CHAPTER 3

WEED COMMUNITY AND CROP YIELD VARIABILITY IN DIVERSE CORN AGROECOSYSTEMS

ABSTRACT

The effects of crop rotation and input management on inter-annual variability in weed communities and crop yields were assessed in a four-year study in corn in SW Michigan, USA. Variability of the weed community and corn yields was assessed using the coefficient of variation (CV) and a multivariate dissimilarity index (Bray-Curtis) that accounted for changes in both weed species abundance and composition. The treatments included two rotations: continuous corn and a corn-corn-soybean-wheat rotation, and two input management systems: conventional (CONV) and organic-based (ORG). Weed biomass was significantly higher in the ORG input system; however, there was no effect of crop rotation on weed biomass or number of weed species in a treatment (species richness). Inter-annual variability in weed community composition and structure was affected by both crop rotation and input management system and was highest in the ORG rotation. In contrast to the weed community, variability in corn yield was highest in the least diverse cropping system (CONV monoculture), despite that system having a more constant weed community. Corn yield in the ORG rotation was not significantly different from that in the CONV monoculture. Results of this study suggest that management aimed at increasing cropping system diversity may have additional effects on weed communities and crop yields beyond those commonly reported, and these may have important implications for the development of more efficient and sustainable weed and crop management practices.

INTRODUCTION

The relationship between taxonomic diversity and ecosystem functions (e.g., productivity, stability) has long been a topic of interest in ecology (MacArthur 1955, Elton 1958, Cottingham et al. 2001) and may have important implications for the management of agricultural systems (Altieri 1999). Ecological theory and experimental evidence from a variety of ecosystems suggest that communities made up of many interacting species should be less temporally variable (i.e. more stable) than simple communities made up of few interacting species. This theory also predicts that while variability at the community level should decrease with diversity, variability at the population level should increase (Tilman 1996, Lehman and Tilman 2000, Cottingham et al. 2001) – that is, abundances of individual species may vary over time, but overall community biomass should remain relatively stable. It is thought that population-level variability helps maintain aggregate community stability because differential responses among species to environmental fluctuations compensate for the loss of other species, thus stabilizing aggregate ecological properties, such as community productivity across time (Tilman 1996, Micheli et al. 1999, Cottingham et al. 2001, Tracy and Sanderson 2004). As more growers adopt agronomic practices that increase cropping system diversity and reduce their reliance on chemical inputs, determining the degree to which these practices affect the temporal variability of weeds and crop yields may have important implications for the development of more efficient and sustainable weed and crop management practices (Helmets et al. 2001, Menalled et al. 2001, Davis et al. 2005).

Predicting weed abundance and its effects on crop yield is an important component of integrated weed management (Lutman et al. 1996). Weed communities that are less variable may require fewer proactive control measures, such as the use of broadcast herbicide applications (Maxwell and Luschei 2005). However weed community variability may also impact other ecosystem processes, such as resource use efficiency (Tracy and Sanderson 2004) and maintenance of natural enemies (Showler and Greenberg 2003) and these too may impact weeds and crop yields (Altieri 1999). For example, Thorbek and Bilde (2004) found that highly variable weed communities did not provide reliable habitat for the maintenance of generalist natural enemy populations.

While the degree of inter-annual variability in weed communities may have important implications for the management of weeds and crop yields in agricultural ecosystems, much of the ecological theory concerning diversity and ecosystem function has been developed within the context of spatial diversity and in less heavily managed systems (Schläpfer and Schmid 1999, Cottingham et al. 2001). In many agricultural systems, however, diversity is both spatial and temporal and little is known about how the temporal component of diversity (number of different crops or cover crops included in a rotation) or different agricultural management systems, have on the variability of weed communities or crop yields.

Here we report results of a study comparing how corn grown in continuous monoculture and in a 4-yr corn-corn-soybean-wheat rotation under two input management systems (conventional and organic-based with cover crops) affects inter-annual variability in weed communities and crop yields. We tested the hypothesis that

aggregate properties of the weed community (total biomass, community structure), as well as crop yields, should be less variable in more diverse cropping systems that have a greater number of potential ecological interactions (organic input management systems and crop rotations) compared to simpler cropping systems with fewer potential ecological interactions (conventional input systems and continuous monocultures). In accordance with ecological theory, we also expected that inter-annual variability at the weed population-level (species richness, species abundance) would be higher in more diverse cropping systems (Tilman 1996). Variability was assessed at both the community and population-level using the coefficient of variation (weed community and population-level and crop yield) and a multivariate dissimilarity index (weed community-level only). The relationship between inter-annual variability in weed and crop yield was also assessed.

MATERIALS AND METHODS

Study Site

The study was conducted at the Living Field Lab experimental plots (hereafter LFL) at the W. K. Kellogg Biological Station Long Term Ecological Research (LTER) site of Michigan State University in SW Michigan, USA. The LFL was established in 1993. Soils at the LFL site are a mixture of Kalamazoo (fine-loamy, mixed, mesic Typic Hapludalfs) and Oshtemo (coarse-loamy, mixed, mesic Typic Hapludalfs) sandy loams (Sanchez et al. 2001). In 1992 the site was planted to alfalfa. In 1993 rotation treatments were randomly assigned to plots within blocks that were managed with different input systems. The rotation treatments were continuous corn and each phase of a four-year corn-corn-soybean-winter wheat rotation. Only continuous corn and the

first-year corn phase of the rotation are compared in this study. The input management systems examined in this study included a conventional system (hereafter CONV) that received full inputs of fertilizer and herbicides (broadcast applications), at rates recommended for the region (Sanchez et al., 2004) and an organic-based input system (hereafter ORG) which received composted dairy manure, but no synthetic chemical inputs. Each year in the ORG system, crimson clover (*Trifolium incarnatum* L.) was sown into standing corn in the continuous corn and the first corn phase of the rotation in late June; Italian ryegrass (*Lolium multiflorum* Lam.) was sown into the standing corn in the second corn phase; and red clover (*Trifolium pretense* L.) was frost seeded into standing winter wheat in late March. No cover crops were sown in the soybean phase of the rotation.

Weed management in the ORG input system was via periodic (2-4 times/yr) inter-row cultivation (row cultivation and rotary hoeing). Plots in both input systems were chisel plowed and soil finished each year prior to planting. All treatments (input x rotation) were replicated four times. Blocks were separated by 8 m grass buffers. Subplots (rotation treatments) measured 15 x 9 m (CONV) and 15 x 4.5 m (ORG) and were not separated by buffers. Additional descriptions of the site and management can be found at: http://lter.kbs.msu.edu/Data/LTER_Metadata.jsp/Dataset/KBS042.

Sampling

Each year from 2001 to 2004 weeds were harvested at peak biomass (early September) from a 0.25 x 1.0 m quadrat placed in each CONV and ORG replicate plot. Because of the difference in size between the CONV and ORG subplots, two locations in each CONV and one location in each ORG replicate plot were sampled each year.

Within each plot, the quadrat was placed perpendicular to the crop row to ensure equal sampling of row and inter-row areas. The position of the quadrat within the plot was varied each year to avoid harvesting in the same location in successive seasons. All weeds rooted within the quadrat were clipped at ground level, sorted to species, and dried to constant biomass at 60° C. Dried biomass of each species was weighed to the nearest 0.01g. Corn was harvested in October or November each year and yields were calculated assuming moisture content of 15.5%.

Calculation of Variability

The coefficient of variation (CV) was used to assess inter-annual variability in weed community and crop yield parameters (Tracy and Sanderson 2004). To assess aggregate community stability total weed biomass was calculated for each treatment replicate over the sampling period from 2001-2004. The CV was calculated as the standard deviation of weed biomass (2001-2004) / average weed biomass (2001-2004). The CV for quadrat-level species richness (number of weed species occurring in each quadrat) and corn yield was determined in the same manner. We assessed variability in species abundances (population-level variability) by calculating the CV for each species in each treatment replicate. The species CV's were then averaged for each replicate (by summing and dividing by the overall number of species present in that replicate).

In addition to variation in total weed biomass and species richness, we were also interested in a measure of community variability that would reflect overall community structure (the composition and abundance of species in the weed community). To obtain a multivariate measure of community variability we calculated a matrix of Bray-

Curtis dissimilarity coefficients (McCune and Grace 2002) using a data set containing species biomass in each treatment replicate for each of the four years. Prior to calculating the dissimilarity matrix data were $\log(x + 0.01)$ transformed and species occurring in less than 5% of the plot-years were deleted to reduce the influence of outliers and rare species. For each treatment replicate we calculated dissimilarity in community abundance and composition from one year to the next from 2001-2004. The average annual dissimilarity over the four-year period for each replicate was used as our measure of community-level variability.

Statistical Analysis

Analysis of variance was used to examine treatment effects on weed community and crop yield parameters. The model was a split-plot, randomized complete block with three factors (block, system, and rotation) and the system by rotation interaction. The block factor was considered random. Tests of main effects were performed with error terms appropriate for a RCB, split-plot design with input system as the whole plot factor and rotation as the subplot factor. Treatment means were compared with Tukey's HSD test at the 5% level of confidence when main effects were significant. All analyses were performed with SAS (SAS Version 8.02; SAS Institute, Cary, NC, USA) using the MIXED procedure (Little et al. 1996). Treatment effects on weed biomass and species richness were also analyzed, and these data were log and square root transformed, respectively, prior to analysis to improve homoscedasticity.

RESULTS AND DISCUSSION

The effects of the input management system and crop rotation on overall weed community biomass, richness, and community composition are presented and discussed

first, followed by presentation and discussion of the treatment effects on weed community and population-level variability. The third section deals with treatment effects on crop yields and crop yield variability and their relationship to weed community variability. Potential explanations for the observed results and their implications for weed management are discussed in the final section.

Weed community biomass and richness

There was substantial variation in precipitation and temperature over the course of the study (Figure 3.1) and this no doubt contributed to significant yearly variation in the weed community. Weed community biomass and richness varied from year to year in some treatments by as much as 500 and 300%, respectively (Table 3.1). Averaged across years, total community biomass was over ten times higher in the ORG compared to the CONV input system (ANOVA, system: $F_{1,3} = 186.10$, $P < 0.001$) (Figure 3.2a). Total weed biomass was unaffected by crop rotation or the interaction between inputs and rotation (ANOVA, rotation: $F_{1,6} = 0.04$, $P = 0.84$; interaction: $F_{1,6} = 0.42$, $P = 0.54$).

There were only marginally significant effects of input system and crop rotation on weed species richness (ANOVA, system: $F_{1,3} = 8.59$, $P = 0.06$; rotation: $F_{1,6} = 4.59$, $P = 0.076$; interaction: $F_{1,6} = 1.35$, $P = 0.2894$) (Figure 3.3a). However, the identity of dominant weed species differed among the treatments (Table 3.2). Abundant weed species (species making up more than 10% of total weed biomass over the four years) in the CONV input system included *Digitaria ischaemum* (Schreb.) Schreb. ex Muhl. (DIGIS), *Solanum carolinense* L. (SOLCA), *Stellaria media* (L.) Vill. (STEME), and *Taraxacum officinale* G.H. Weber ex Wiggers (TAROF). In contrast, two annual dicots, *Ambrosia artemisiifolia* L. (AMBEL) and *Chenopodium album* L. (CHEAL),

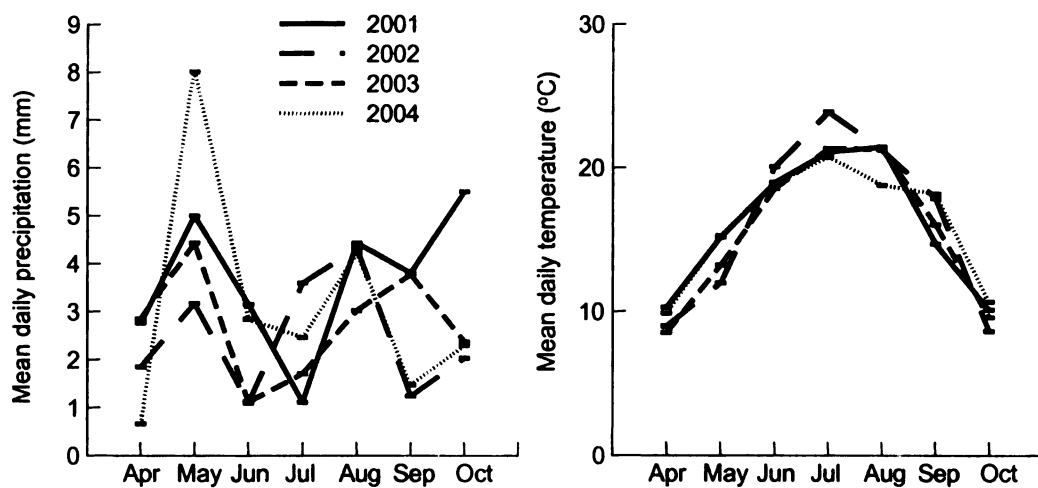


Figure 3.1: Mean daily precipitation and air temperature at the KBS LTER for each month from April-October over the four-year study.

Table 3.1: Weed biomass, species richness, and crop yields (mean \pm SE; n = 4) in corn (2001-2004) in conventional (CONV) and organic (ORG) input systems in the KBS LFL. Rotations are continuous (CC) and rotated (R) corn (see text).

Inputs	Rotation	Year	Weed biomass (g m ⁻²)	SE	Species richness (0.25 m ⁻²)	SE	Corn yield (bu A ⁻¹)	SE
CONV	CC	2001	49.0	16.3	5.0	0.8	54.9	4.9
		2002	3.4	2.4	3.9	0.4	95.1	1.3
		2003	16.5	11.2	4.5	0.8	77.2	6.5
		2004	4.9	2.7	5.0	0.6	138.4	5.3
	R	2001	41.7	8.6	7.9	0.8	87.4	6.1
		2002	2.6	0.8	7.3	1.8	122.2	2.1
		2003	12.2	3.8	4.8	0.4	112.0	2.3
		2004	23.5	14.2	4.1	0.9	159.7	7.0
ORG	CC	2001	126.5	70.6	6.3	0.6	65.1	4.7
		2002	168.1	90.5	5.5	1.0	80.1	13.4
		2003	180.7	112.6	5.8	0.5	73.0	4.8
		2004	347.8	76.6	10.3	0.8	48.6	6.4
	R	2001	32.1	5.4	6.3	0.3	77.9	10.4
		2002	178.5	46.3	10.8	1.5	96.6	10.7
		2003	1.0	0.5	3.3	0.5	112.5	3.7
		2004	554.2	185.0	9.5	0.7	65.7	11.6

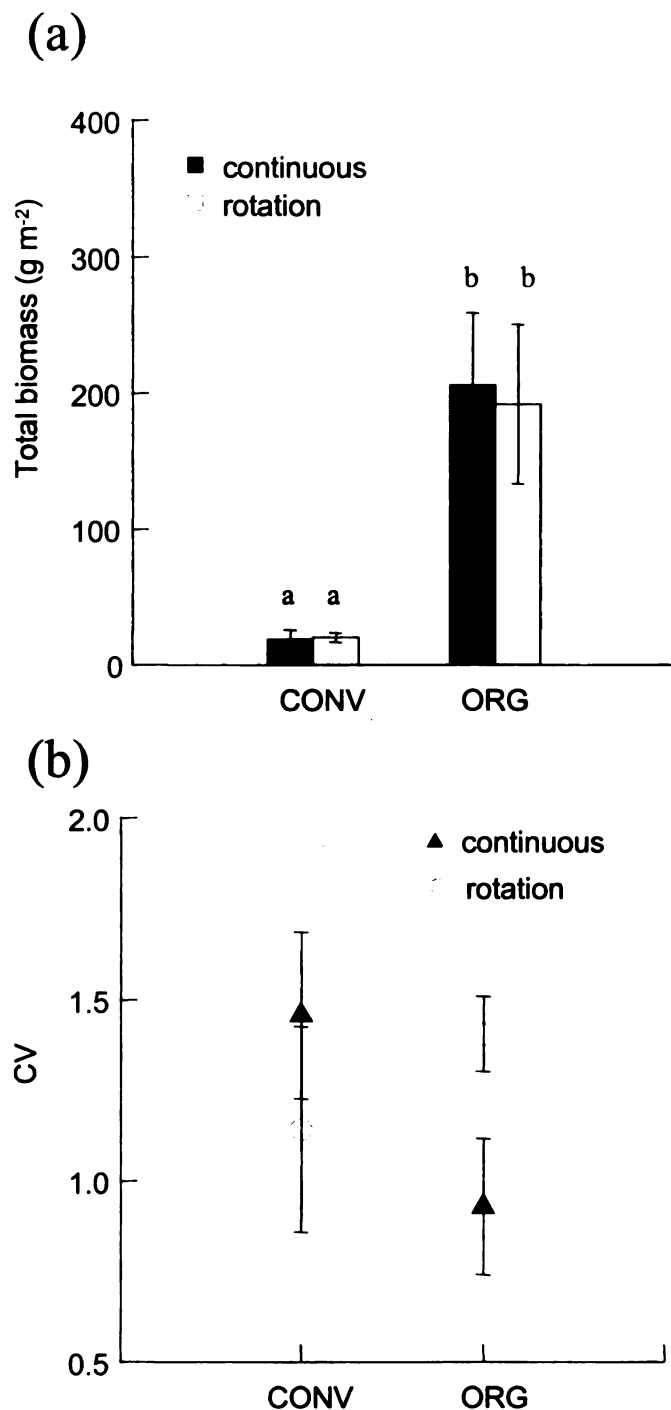


Figure 3.2: Effects of conventional (CONV) and organic (ORG) inputs and crop rotation on a) weed community biomass from 2001-2004 and b) inter-annual variability as measured by the coefficient of variation, CV. Error bars are ± 1 SE; total biomass, $n = 16$; CV of biomass, $n = 4$. Bars sharing the same letter are not significantly different at the $P = 0.05$ level (Tukey-Kramer Test).

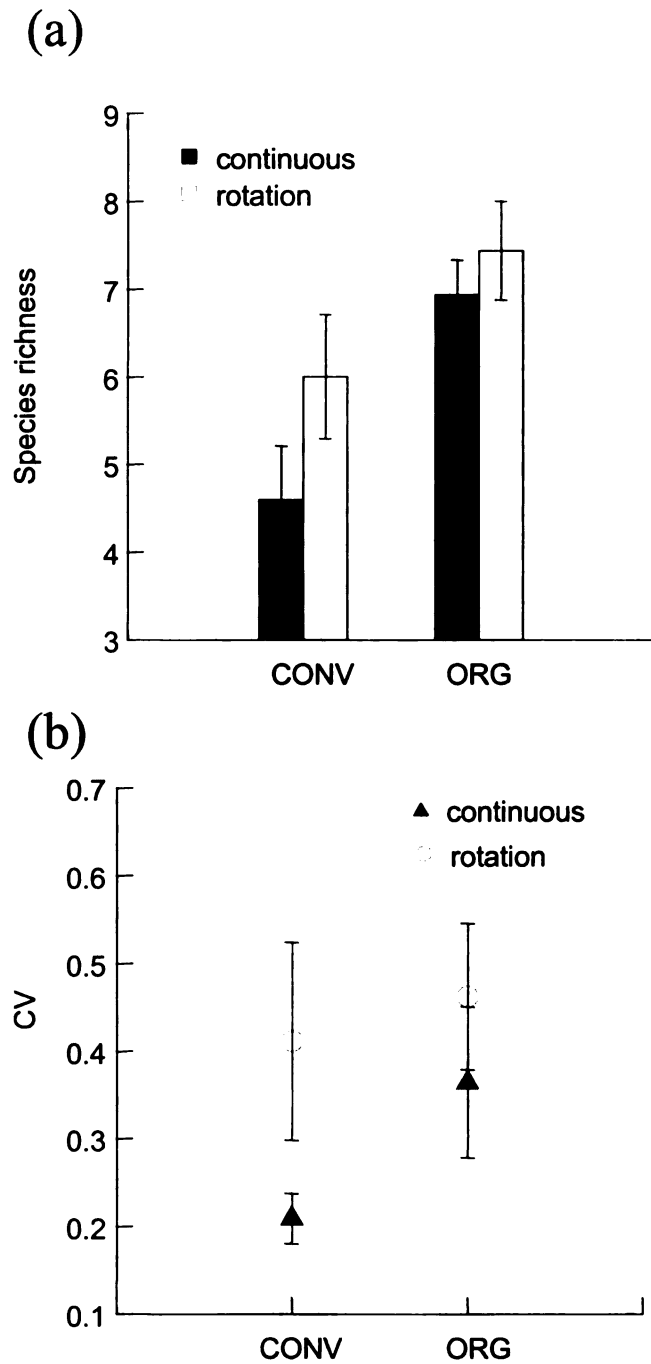


Figure 3.3: Effects of conventional (CONV) and organic (ORG) inputs and crop rotation on a) weed community species richness from 2001-2004 and b) inter-annual variability as measured by the coefficient of variation. Error bars are ± 1 SE; richness, $n = 16$; CV of richness, $n = 4$. Bars sharing the same letter are not significantly different at the $P = 0.05$ level (Tukey-Kramer Test).

Table 3.2: Weed species abundance in conventional (CONV) and organic (ORG) input systems under continuous (CC) and rotation (R) production. Values are mean % of total weed biomass and CV averaged across years (2001-2004).

Species	CONV			ORG		
	Biomass (%)	CV		Biomass (%)	CV	
		CC	R		CC	R
<i>Abutilon theophrasti</i>				0.08	0.50	0.43
<i>Amaranthus retroflexus</i>	0.04		0.45	7.97	0.48	0.50
<i>Ambrosia artemisiifolia</i>				30.40		0.43
<i>Arabidopsis thaliana</i>	0.60	0.35	0.40	0.05	0.43	0.40
<i>Cardamine</i> sp.	0.01	0.50				
<i>Chenopodium album</i>	0.65	0.30	0.26	35.06	0.37	0.46
<i>Conyza canadensis</i>	0.00		0.50			
<i>Daucus carota</i>	0.05		0.50			
<i>Digitaria ischaemum</i>	14.98		0.50	0.17		0.46
<i>Digitaria sanguinalis</i>	1.20	0.37	0.34	0.03	0.45	0.43
<i>Echinochloa crus-galli</i>				0.81	0.37	0.50
<i>Elymus repens</i>	2.29	0.50	0.50	6.55	.40	0.47
<i>Eragrostis cilianensis</i>	0.00		0.50	0.00		0.50
<i>Erigeron</i> sp.				0.16	0.50	
<i>Lamium</i> sp.	0.08	0.36	0.50	0.03	0.36	0.43
<i>Mollugo verticillata</i>	0.01		0.50			
<i>Oxalis stricta</i>	0.08		0.46	0.04	0.50	
<i>Panicum dichotomiflorum</i>	0.87		0.45	0.00		0.50
<i>Plantago major</i>	0.03		0.50	0.25	0.50	
<i>Poa</i> sp.	0.68	0.26	0.30	0.01	0.33	0.50
<i>Polygonum aviculare</i>				0.09	0.50	0.50
<i>Polygonum convolvulus</i>				1.12	0.36	0.50
<i>Polygonum persicaria</i>				2.35	0.44	0.50
<i>Portulaca oleracea</i>	0.03	0.50	0.40	0.00	0.50	
<i>Rumex obtusifolius</i>	1.58	0.50	0.38	0.01		0.50
<i>Setaria faberi</i>	0.02		0.50	2.68		0.50
<i>Setaria pumila</i>	0.01		0.50	1.61	0.50	0.50
<i>Setaria viridis</i>	0.08		0.50	3.15	0.50	0.46
<i>Solanum carolinense</i>	17.39	0.47	0.41	1.15	0.49	0.50
<i>Solanum ptychanthum</i>	0.00		0.50	0.05	0.50	0.48
<i>Sonchus oleraceus</i>	0.07	0.50				
<i>Stellaria media</i>	19.13	0.43	0.45	2.31	0.44	0.48
<i>Taraxacum officinale</i>	37.83	0.38	0.39	1.11	0.24	0.42
<i>Veronica persica</i>	0.05		0.50	0.06	0.50	0.40
<i>Veronica peregrina</i>	0.41	0.49	0.50	0.03	0.50	0.47

were the most abundant in the ORG input system, making up 30 and 35%, respectively, of the total biomass.

We had expected that these input systems would vary in total weed biomass because mechanical control measures are often less effective than chemicals at controlling weeds, particularly later in the growing season when crop canopy architecture precludes mechanical cultivation (Pleasant et al. 1994). Given the number of studies that have reported significant rotation effects on weed abundance and diversity (Liebman and Dyck 1993), the absence of a rotation effect in our study is somewhat surprising; though not unique. Doucet et al. (1999) found few residual effects after nine years of a corn-soybean-wheat rotation on the composition and abundance of weeds following planting of corn in the 10th year. Similarly, in an earlier study in the LFL, the previous crop, rather than the number of different crops in the rotation was found to have the greatest impact on the abundance and composition of seeds in the soil (Smith and Gross, in review).

Weed community variability

We used a number of different metrics to characterize the level of inter-annual variability in the weed community in response to the input management system and rotation treatments and although we detected differences among the treatments, they were not consistent with the predictions we had developed based on diversity-stability theory (Schläpfer and Schmid 1999, Cottingham et al. 2001). For example, based on ecological theory we predicted that the more diverse rotation (ORG rotation) would be less prone to fluctuations in weed biomass. However, we found that community-level variability was higher in the ORG rotation compared to the ORG monoculture

(ANOVA, interaction: $F_{1,6} = 26.09$, $P = 0.002$, Tukey-Kramer, $P = 0.0188$) (Figure 3.2b). Similar results were observed when we analyzed weed community variability using a dissimilarity metric that combined data on both species abundance and composition (Bray-Curtis distance). The analysis indicated that weed communities were significantly more dissimilar in abundance and composition from year to year in the ORG rotation than the ORG or CONV monoculture or CONV rotation (system: $F_{1,3} = 20.97$, $P = 0.02$; rotation: $F_{1,6} = 13.28$, $P = 0.011$; interaction: $F_{1,6} = 5.56$, $P = 0.056$) (Figure 3.4a). Taken together these results suggest that both input management and crop rotation can affect weed community variability but that crop rotation may be a more important driver of variability. Our results are rather similar to those of Davis et al. (2005) who reported little difference in the constancy of weed communities in conventional and organic rotations. This is in contrast, however, to a similar study conducted by Menalled et al. (2001) that reported weed communities in organic systems were more diverse and more constant compared to conventional-input systems, suggesting that it may be difficult to make general predictions about how input management will affect temporal variability in weed communities (Davis et al. 2005).

Diversity-stability theory predicts that as the number of species in a community increases, variability in the abundance of individual species should also increase (Tilman 1996). We found this to be true; weed population-level variability (average CV for individual species) was highest in the most diverse cropping system (ORG rotation) and lowest in the least diverse cropping system (CONV monoculture) (system: $F_{1,3} = 10.18$, $P < 0.05$; rotation: $F_{1,6} = 8.01$, $P = 0.03$, interaction: $F_{1,6} = 0.13$ $P = 0.73$) (Table 3.2 and Figure 3.4b). However, weed population and community level variability did

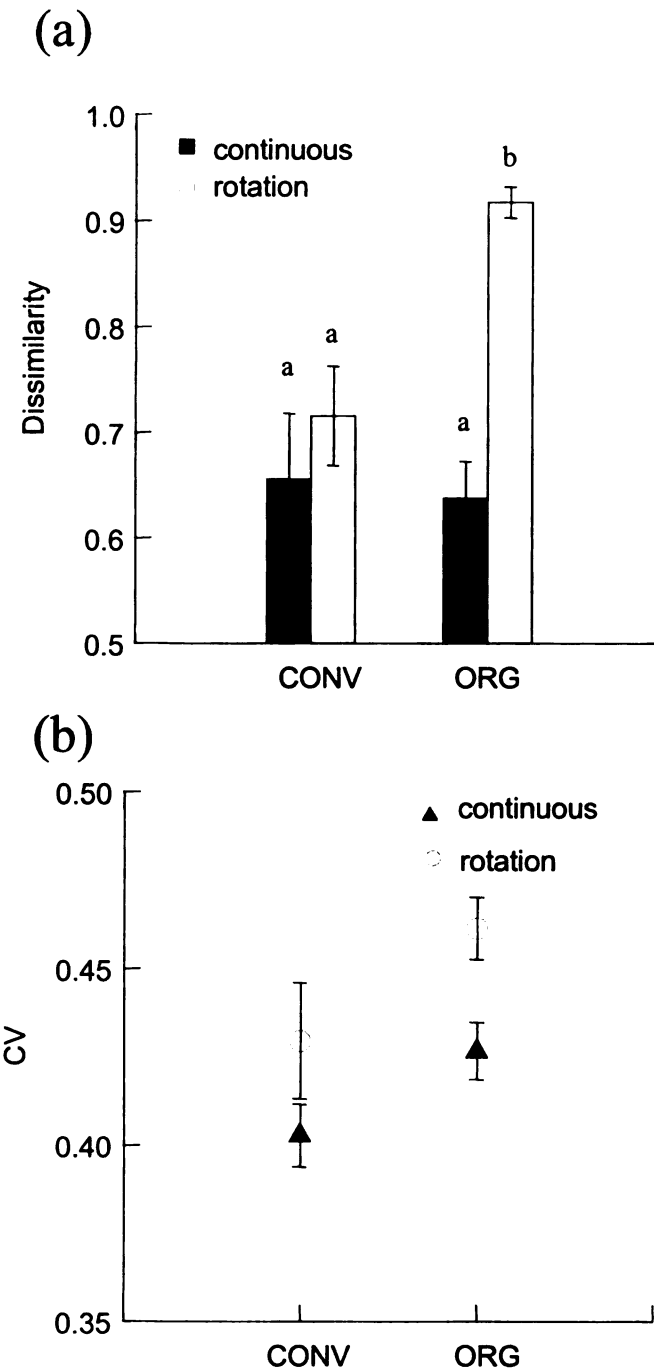


Figure 3.4: Effects of conventional (CONV) and organic (ORG) inputs and crop rotation on a) weed community dissimilarity and b) population-level inter-annual variability as measured by the coefficient of variation. Error bars are ± 1 SE; $n = 4$. Bars sharing the same letter are not significantly different at the $P = 0.05$ level (Tukey-Kramer Test).

not appear linked in the manner predicted by diversity-stability theory, as community level-variability was also higher in the ORG rotation (Figs. 3.2b and 3.4a). This suggests that the link between weed population and community-level stability may be weak in systems that are highly disturbed, such as agricultural fields that are annually tilled (Chesson and Huntly 1997).

Variability in community richness (CV richness) was not affected by either of the treatments (only a marginally significant effect of rotation: $F_{1,6} = 4.91$, $P = 0.07$) (Figure 3.3b).

Corn yields and variability

Corn yields also varied among years (Table 3.1). Averaged across the four years, corn yields were highest in the CONV rotation, intermediate in the CONV monoculture and ORG rotation, and lowest in the ORG monoculture (system: $F_{1,3} = 19.81$, $P = 0.02$; rotation: $F_{1,6} = 168.5$ $P < 0.0001$, interaction: $F_{1,6} = 3.08$, $P = 0.13$) (Figure 3.5a). As predicted from diversity-stability theory, we found that inter-annual variability in corn yield was highest (highest CV) in the simpler cropping system (CONV) (system: $F_{1,3} = 12.44$, $P = 0.04$; rotation: $F_{1,6} = 0.54$, $P = 0.49$, interaction: $F_{1,6} = 2.10$, $P = 0.20$) (Figure 3.5b). This result is in contrast to that of Tracy and Sanderson (2004) who found no relationship between the diversity of forage species and inter-annual yield variability.

We found no relationship between variability in corn yields and variability in the weed community using any of the weed community variability indices as independent variables in a linear regression (data not shown).

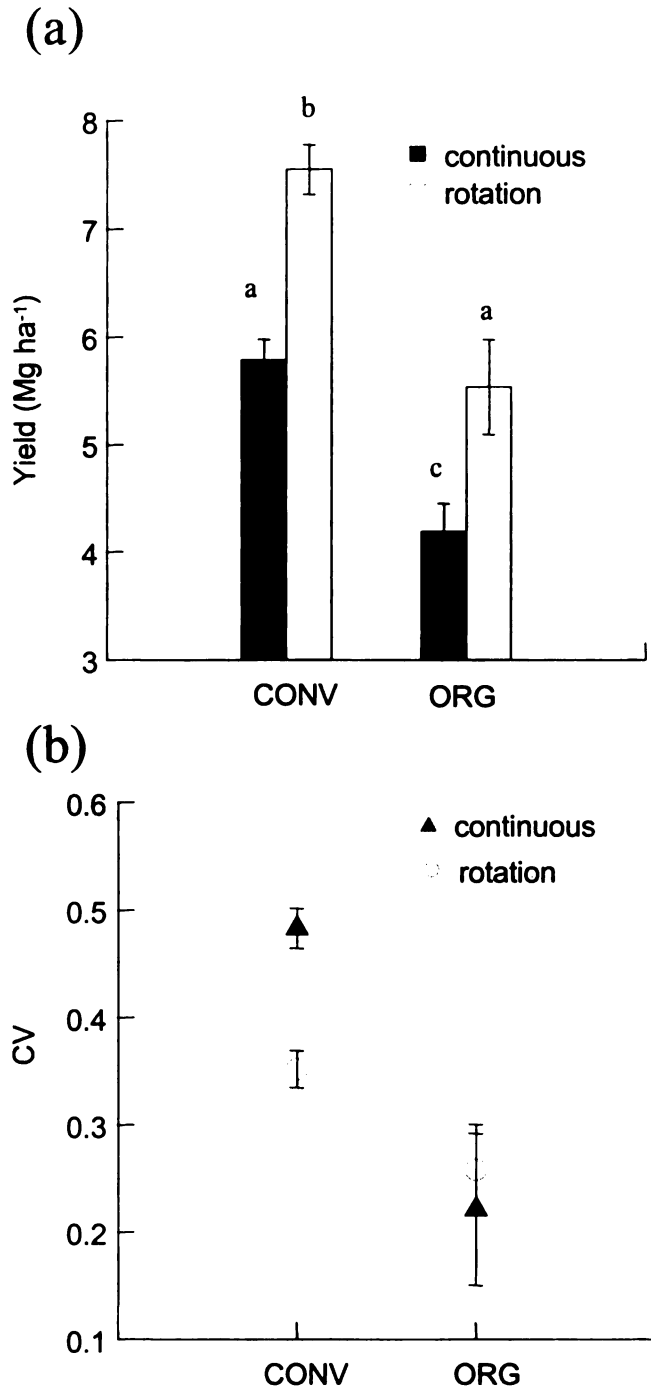


Figure 3.5: Effects of conventional (CONV) and organic (ORG) inputs and crop rotation on corn a) yields from 2001-2004 and b) inter-annual variability as measured by the coefficient of variation. Error bars are ± 1 SE; yield, $n = 16$; CV, $n = 4$. Bars sharing the same letter are not significantly different at the $P = 0.05$ level (Tukey-Kramer Test).

Potential explanations and implications

One potential explanation for the lower inter-annual variability in weed communities in the continuous corn compared to the rotation could be the fact that within a block, continuous corn is planted in the same location each year. This is in contrast to rotated corn, which, because each phase of the rotation is present each year, occurs in a different location within the block each of the four years. If spatial differences in weed species abundance between continuous corn and rotated corn were responsible for the observed differences in inter-annual variation then one would expect that within years, differences among replicates would be greater in the rotated corn treatments compared to continuous corn. To test this, we compared mean intra-year dissimilarity among replicate plots for each treatment using Bray-Curtis dissimilarity coefficients. We found that annual dissimilarity between replicates did not differ among the treatments (ANOVA, system: $F_{1,3} = 0.12$, $P = 0.75$; rotation: $F_{1,6} = 3.21$ $P = 0.123$; interaction: $F_{1,6} = 0.36$, $P = 0.571$), indicating that temporal autocorrelation was likely not responsible for the observed effects of rotation on community variability.

Another potential explanation may be that effects of diversity at the scale of the crop are independent of those at the scale of the weed community. This may be especially true when crop diversity is temporal (as in our crop rotations) and punctuated by high rates of annual disturbance. High rates of annual disturbance can lead to weak interactions among species (Chesson and Huntly 1997), and this may affect the compensatory responses among weed species necessary for generating stability (Cottingham et al. 2001).

If cropping system diversity *per se* has little direct effect on weed community variability, how can the differences in variability among the rotation treatments be explained? One possible answer may be the soil seed bank. Seeds in the seed bank contribute to most of the weeds emerging in a field in any given year and the age of seeds in the seed bank can vary (Cavers and Benoit 1989). Seed age has been shown to affect germinability (Lindgren and Schaaf 2004), and can affect recruitment in some species (Rice and Dyer 2001). In our study, many of the weeds that emerged each year in the corn phase of the rotation likely germinated from seeds that were shed the last time corn appeared in the rotation (i.e. > 2 years earlier). This is in contrast to continuous corn, in which the majority of weeds likely emerged from seeds shed the previous year (Cavers and Benoit 1989). The seed bank in rotated corn also likely contained an abundance of species associated with winter wheat (Smith and Gross, in review), which might also have contributed to compositional variation.

Our results suggest that in addition to the environmental costs often associated with conventional agricultural management (Robertson and Swinton 2005) crop yields in conventionally managed systems may be more prone to inter-annual variability (Helmers et al. 2001). This is in contrast to the organic rotation, in which yields were significantly less variable, and were just as high as those in the conventional monoculture, despite this system having greater weed abundance and weed community variability. This suggests that either the interactions among crops and weeds are lower in diversified organic input systems (Stevenson et al. 1998) or that some other property of the weed community, which we did not measure, contributes to increased crop yield

stability. A better understanding of the factors contributing to temporal yield variation in row-crops will help answer this question.

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CHAPTER 4

WEED COMMUNITY RESPONSE TO INCREASING CROP DIVERSITY

ABSTRACT

Increasing diversity in cropping systems may have important implications for agroecosystem functions related to the regulation of weed populations. However, the impacts of cropping system diversity *per se* on weed communities have not been formally evaluated in a study comparable to those performed in grassland systems, where much of the evidence regarding diversity-ecosystem function has been reported. Here we report results from three yrs of a long-term study designed to examine the effects of crop diversity on the abundance, diversity, and composition of the weed community. Crop diversity was manipulated through rotations of corn (*Zea mays* L.), soybean (*Glycine max* (L.) Merr.), winter wheat (*Triticum aestivum*) and cover crops. Weed community abundance and composition was measured at peak biomass (August-September) for three years from 2002-2004; soil resources and light levels were measured in 2004. Weed abundance and diversity were both affected by crop diversity; however, effects were stronger in winter wheat than corn and soybean. In winter wheat weed abundance and diversity (species richness, H' and D) were lowest in the two highest diversity treatments. The effects of crop diversity in wheat were due mainly to the presence of cover crops in the higher diversity treatments and likely reflected the impacts of cover crops on soil resource and light levels. The effects on weed community structure of crop diversity *per se* were slight compared to the effects of crop identity. Crop rotation had little persistent effect on weed abundance and composition despite large differences among crops. This study suggests that increasing crop

diversity may decrease the need for weed management, not because of its effects on weed abundance and composition, but because of its effects on resource availability and crop competitiveness.

INTRODUCTION

Increasing cropping-system diversity may have important implications for the functioning of agricultural ecosystems (Altieri 1999, Minns et al. 2001) and has been advocated as a potential means of decreasing the need for intensive chemical inputs for weed control (Dekker 1997, Kegode et al. 1999, Westerman et al. 2005, Liebman and Gallandt 1997, Liebman and Staver 2001). However, ecological context can affect diversity-ecosystem function relationships (Schläpfer and Schmid 1999) and much of the experimental evidence regarding diversity and ecosystem function has been reported from studies conducted in relatively undisturbed natural and synthetic grassland systems where biotic conditions and disturbance regimes vary from those in most managed systems (Lambers et al. 2004, Hooper et al. 2005, Loreau et al. 2001, Tilman et al. 2001, Levine and D'Antonio 1999, Cottingham et al. 2001). It is therefore unclear whether and to what extent the relationships between community diversity and ecosystem function commonly reported in experimental grasslands can be applied to managed systems, such as row-crop agroecosystems.

Studies conducted in grasslands differ from those in annual row-crop agroecosystems in several ways that might impact the generality of diversity-ecosystem function relationships and their application to weed management. In synthetic grassland communities, manipulations of diversity include a relatively large number of species and potential species combinations (Schläpfer and Schmid 1999; Hooper et al. 2005).

Diversity manipulations in these systems also tend to span relatively large diversity gradients (Tilman et al. 1997, Hooper and Vitousek 1998, Hector et al. 1999), with treatment levels in some experiments ranging from one to as many as 32 species (Hector et al. 1999). In addition to having many levels of diversity, the densities of individuals in grassland manipulations tend to be high. High densities coupled with low disturbance rates following initial community establishment allow the potential for strong interactions among species (Cousens 1985). Inter and intra-specific interactions are hypothesized to drive many of the observed relationships between diversity and ecosystem function and underlie many of the mechanistic predictions regarding diversity's effect on community productivity and the establishment of new species (Tilman et al. 1997, Schlöpfer and Schmid 1999, Lambers et al. 2004, Hooper et al. 2005).

In contrast to grassland systems, studies of diversity in most agricultural systems typically include a limited number of crop species and potential species combinations. Because of the low numbers of crops and realistic cropping combinations, the gradients of diversity manipulated in many agricultural studies tend to be narrow and often only include a few levels of crop diversity (Jolliffe 1997, Schlöpfer and Schmid 1999). Row spacing and planting densities are controlled in most agricultural systems, resulting in relatively low densities of individuals compared to grassland systems. Most agricultural systems are also highly disturbed by management practices such as cultivation, and the applications of fertilizer and herbicides; and these can also affect the density of individuals and the strength of species interactions (Huston 1979, Wiener et al. 2001, Cardinale and Palmer 2002). In addition, a large component of diversity in

most agricultural systems is temporal (crop rotation) (Liebman and Dyck 1993, Liebman and Staver 2001), meaning that many of the interactions among crop species are indirect, in contrast to grassland systems where many species interact directly (Tilman 1999).

There have been many studies comparing weed communities in relatively simple and complex cropping systems (Liebman and Dyck 1993, Barberi and Lo Cascio 2001, Legere and Stevensen 2002, Cardina et al. 2002, Moonen and Barberi 2004, Teasdale et al. 2004, Westerman et al. 2005). However, there have been no large-scale manipulations of diversity in agricultural systems that are comparable to those performed in grassland systems. Additionally, there have been no studies of diversity in agricultural systems that span a relatively broad range of crop diversity and that do not include management practices such as fertilizer inputs and herbicide applications (Liebman and Dyck 1993, Schläpfer and Schmid 1999), which can potentially confound or obscure the effects of diversity *per se* (Doucet et al. 1999).

Here we report data from the first three years (2002-2004) of a long-term cropping-system diversity study established in 2000 to examine the effects of crop diversity on ecosystem functions and processes related to row crop agriculture. For this paper we focus on how crop diversity influences the abundance, diversity, and composition of the emergent weed community over a three-year period from 2002 to 2004. Crop diversity was manipulated through rotations of corn, soybean, winter wheat (main crops) and cover crops. After 2001 the experiment was conducted in the absence of external chemical inputs (chemical fertilizer, herbicides, and pesticides), so that diversity effects could be separated from those of specific management practices that

can vary with each crop. In this study we examined five main questions: (1) Does increasing crop diversity affect the overall abundance of weeds?, (2) Does crop diversity affect the diversity, composition, and structure of weed communities ?, (3) Do the effects of crop diversity on the weed community differ depending on the identity of the main crop?, (4) What is the relative importance of cover crops versus crop rotation on crop diversity-ecosystem function relationships, and (5) Are the effects of crop diversity on weed communities related to changes in soil resource levels and/or the light environment?

MATERIALS AND METHODS

Study site

The study was conducted at the Biodiversity Experiment Plots (hereafter BEP) at the W. K. Kellogg Biological Station (KBS) Long Term Ecological Research (LTER) project in agricultural ecology in Hickory Corners, Michigan, USA. Soils at the study site are dominated by Kalamazoo silt loam (Typic Hapludalfs), and are made up of 43% sand, 40 % silt, and 17 % clay (Robertson et al. 1997). Mean annual temperature at the LTER site is 9.7°C. Annual precipitation is 890 mm¹, with about half in the form of snow (<http://lter.kbs.msu.edu/siteDescription.html>).

Diversity treatments

The BEP was established in 2000 to examine the effects of realistic manipulations of row crop diversity on ecosystem functions related to row crop agriculture. Treatment systems consist of three row-crops, corn (*Zea mays* L.), soybean (*Glycine max* (L.) Merr.), and winter wheat (*Triticum aestivum* L.) grown in continuous monoculture and in two- and three-year annual rotations with and without cover crops

(zero, one, or two legume/small grain species). The six crop diversity treatments range in diversity from one to three crop species annually and one to six species over a three-year period (Table 4.1) and include: (1) continuous monoculture (1 spp), (2) continuous monoculture with one cover crop annually (2 spp), (3) two-crop rotation (2 spp), (4) three-crop rotation (3 spp), (5) three-crop rotation with one cover crop annually (2 spp annually; 4 spp over 3 yr rotation), and (6) three-crop rotation with two cover crop species annually (3 spp annually; 6 spp over 3 yr rotation). In the two-crop rotation (treatment 3), only three of the possible sequences were included in the design: corn-soybean, soybean-corn, and soybean-wheat. The three-crop rotations (treatments 4-6) are all planted in the same sequence: corn-soybean-wheat. Each phase of the two and three-crop rotations is present every year allowing comparisons to be made among the six diversity treatments for each of the three main crop species.

Cover crops used in the experiment vary depending on the main crop and include red clover (*Trifolium pratense* L.), crimson clover (*Trifolium incarnatum* L.) and cereal rye (*Secale cereale* L.). In treatments receiving a single cover crop (treatments 2 and 5), *T. pratense* is sown into corn in July and wheat in March, and *S. cereale* is sown in soybean (treatment 2 only) in October. For the highest diversity treatment (treatment 6) each crop is grown with two cover crops: *T. pratense* is planted into corn and wheat as above, and *T. incarnatum* is planted into soybean in July. *Secale cereale* is sown into corn and wheat stubble in October.

Diversity treatments were randomly applied to plots in three linear blocks; in the fourth block, treatments were arranged in sequence in a 4 x 5 block to facilitate

Table 4.1: Crop diversity treatments at the KBS LTER Biodiversity Experiment Plots (BEP). Treatments were established in 2000 and include monocultures and two- and three-crop rotations of corn, soybeans and wheat, with and without grass and legume cover crops.

Treatment Group #	Description	No. crop species					
		Annual			Sum over rotation		
		Crops	Cover crops	Total	Crops	Cover crops	Total
1	Continuous monoculture	1	0	1	1	0	1
2	Continuous monoculture, one cover crop annually	1	1	2	1	1	2
3	Two-crop rotation	1	0	1	2	0	2
4	Three-crop rotation	1	0	1	3	0	3
5	Three-crop rotation, one cover crop annually	1	1	2	3	2	5
6	Three-crop rotation, two cover crops annually	1	2	3	3	3	6

demonstration of treatment effects. Replicate blocks were separated by 8m grass buffers. Individual plots measure 9.1m x 27.4 m with no buffer strips between plots. All plots are chisel plowed and soil finished prior to planting the main crop. The exact timing of planting each year is dependent on weather conditions. Corn and soybean are planted in late April or May, respectively, and winter wheat is planted in late September or early October. No external inputs (herbicides, pesticides, or fertilizer) were applied to any of the treatments after 2001; however, periodic inter-row cultivations (cultivation/rotary hoeing) were performed in corn and soybean each year early in the growing season.

Vegetation sampling

Aboveground weed and cover crop biomass was harvested at peak biomass (August-September) from two 0.25 x 1 m quadrats placed in two central locations in each plot. Weed species composition was determined from a 0.5 x 2 m quadrat that included the area harvested. The sampling location was changed each year to minimize edge effects and avoid harvesting weeds from areas that had been harvested the previous season. Harvested weed biomass was separated to species, dried at 65° C for 48 hrs and weighed to the nearest 0.01g.

Soil Resources and light

To determine the relationship between crop diversity, weed communities and soil resource levels, we measured inorganic soil nitrogen (NO_3^- and NH_4^+) at the end of the growing season (November) in 2002 and at three times: 28 June (mid-season), 23 August (late-season), and 16 November (post-season) in 2004. Soils were sampled to a depth of 25 cm (four-2 cm diameter cores) within the central 3 x 9 m of each plot from

both the rows and inter-rows. Aggregated samples were sieved through a 4 mm screen to remove stones and large pieces of organic material. Following sieving, a portion of each aggregated sample (20-30 g) was processed for gravimetric soil moisture analysis. The remaining sample was subdivided; 20 g was processed for N extraction with 100 ml of 1M KCL (20 g) and the rest air-dried and archived. Nitrogen (NO_3^- and NH_4^+) was analyzed with an AlpKem 3550 continuous-flow colorimetric analyzer (OI Analytical, College Station, TX, USA). Soils were stored at 4 ° C and were processed within 48 hrs of collection. In addition, soils sampled in 2002 and on 16 November in 2004 were also analyzed for net-mineralizable N following incubation for 28 days at 25 ° C.

To determine how the manipulations of crop diversity affected the light environment throughout the growing season, the percentage of Photosynthetically Active Radiation (PAR) at the soil surface was measured with an AccuPar LP-80 Ceptometer (Decagon Devices, Inc., Pullman, WA, USA) on three dates in 2004: 23 July (mid-season), 22 August (late-season), and 19 September (post-season). PAR was measured at solar noon \pm 2 hrs by placing the ceptometer parallel to the crop row at two locations within the center 3 x 5 m of each plot. The two readings were averaged to represent overall plot-level PAR.

Statistical analyses

Analysis of variance was used to test for the effects of crop diversity, main crop identity, and year of sampling on weed biomass, species richness (number per m²), and several measures of community diversity. The initial model included four factors (block, diversity, crop, and year) and the factorial combinations of crop diversity, crop, and year. Data were analyzed as a repeated measures, randomized complete block

design using PROC MIXED (Little et al. 1996) in SAS (SAS Version 8.02; SAS Institute, Cary, NC, USA). Separate analyses were performed for each crop and for each crop x year when higher order interactions were significant. Treatment means were compared with Tukey's HSD test at the $P < 0.05$ level of probability when main effects were significant. In all analyses, the block effect was considered random.

We chose to investigate several different diversity measures because each emphasize different aspects of community structure (Magurran 1988) and the predicted effects of crop diversity on weed community structure are somewhat unclear (Liebman and Dyck 1993, Liebman and Staver 2001). The diversity measures were: Shannon diversity: $H' = -\sum p_i(\log p_i)$, where p_i is the proportion of biomass accounted for by species i per sample (Magurran, 1988), Evenness: $E = H'/\ln(\text{species richness})$ (Pielou, 1969, p. 233), and Simpson's index of diversity: $D = 1 - \sum p_i^2$ (McCune and Grace 2002). Weed biomass and species richness data were log and square root transformed, respectively, to improve homoscedasticity. Analysis of variance also was used to analyze treatment effects on soil resource levels and percent active radiation (PAR).

Several multivariate analyses were employed to examine treatment effects on the weed community and to visualize differences in community composition and structure among the six crop diversity treatments. Prior to performing analyses on species abundance and composition data, all values were $\log(x + 1)$ transformed. A dissimilarity matrix using Bray-Curtis coefficients was then calculated from the transformed species abundance values. Unknown and very rare species (those occurring in fewer than 5% of the plot-years) were deleted prior to analysis.

The first analysis investigated treatment effects on community abundance and composition in each crop using a distance-based multivariate analysis for a linear model (DISTLM v.5, Anderson 2001, 2004). The data set contained log-transformed weed species abundance data collected from 2002 through 2004. For the multivariate linear model, three factors (block, crop diversity, and year) and the interaction between crop diversity and year were analyzed using a randomized complete block design with repeated measures. Year was the repeated factor and block was treated as a random factor. Treatment effects were tested by permutation (9999 permutations) using error terms appropriate for a randomized complete block design. A Monte Carlo sampling procedure was then used to generate P –values from the asymptotic permutation distribution (Anderson 2004).

Forward multivariate multiple regression (McArdle and Anderson 2001, Anderson 2003) was performed to characterize species abundance and composition in 2004 in relation to resource levels (inorganic N, soil moisture, and %PAR) measured during the 2004 growing season. Species abundance data were $\log(x + 1)$ transformed prior to calculating Bray-Curtis dissimilarity coefficients. For each crop, marginal tests were performed on all predictor variables first, followed by forward selection of variables with conditional tests. Significance was assessed by permutation (9999 permutations) (Anderson 2003).

To help visualize treatment effects on community structure, we performed non-metric multidimensional scaling ordination (NMDS) (McCune and Grace 2002) on $\log(x + 0.1)$ transformed species composition and abundance data from 2004. Ordination was performed for each crop separately so that differences among treatments would be

more easily detected. Pearson correlation coefficients and r^2 between the NMDS ordination axes scores and soil resource and light levels were also calculated to examine the strength of the relationship between community structure on soil resources and light using the PC-ORD software package (McCune and Mefford 1999).

For each main crop, species-level responses to the diversity treatments were analyzed with indicator species analysis (ISA; Dufrene and Legendre 1997) using diversity system as the grouping variable. Indicator values (IV) were calculated by multiplying the relative abundance and relative frequency of each species in each diversity treatment in 2004. For each species, the significance of the highest indicator value (corresponding to the diversity system with which it was most associated) was tested with a Monty Carlo procedure (1000 permutations) at a the $P < 0.05$ level of probability. ISA was also performed on presence/absence data across diversity treatments, using crop identity as the grouping variable, to determine the strength of species associations for each main crop.

RESULTS

Weed biomass

Weed biomass was affected by crop diversity, crop identity, year of sampling, and the interaction between all three factors (3-way interaction: $F_{29,109} = 4.36$, $P < 0.000$; Figure 4.1). Subsequent repeated measures analyses for each main crop showed that most of the effects across crops were driven by a significant crop diversity-by-year interaction in wheat ($F_{9,33} = 13.15$, $P < 0.0001$). In all three years, wheat grown in treatments that did not include cover crops (i.e. treatments 1, 3, and 4) had higher weed biomass than wheat grown in treatments that included cover crops (treatments 2, 5, and

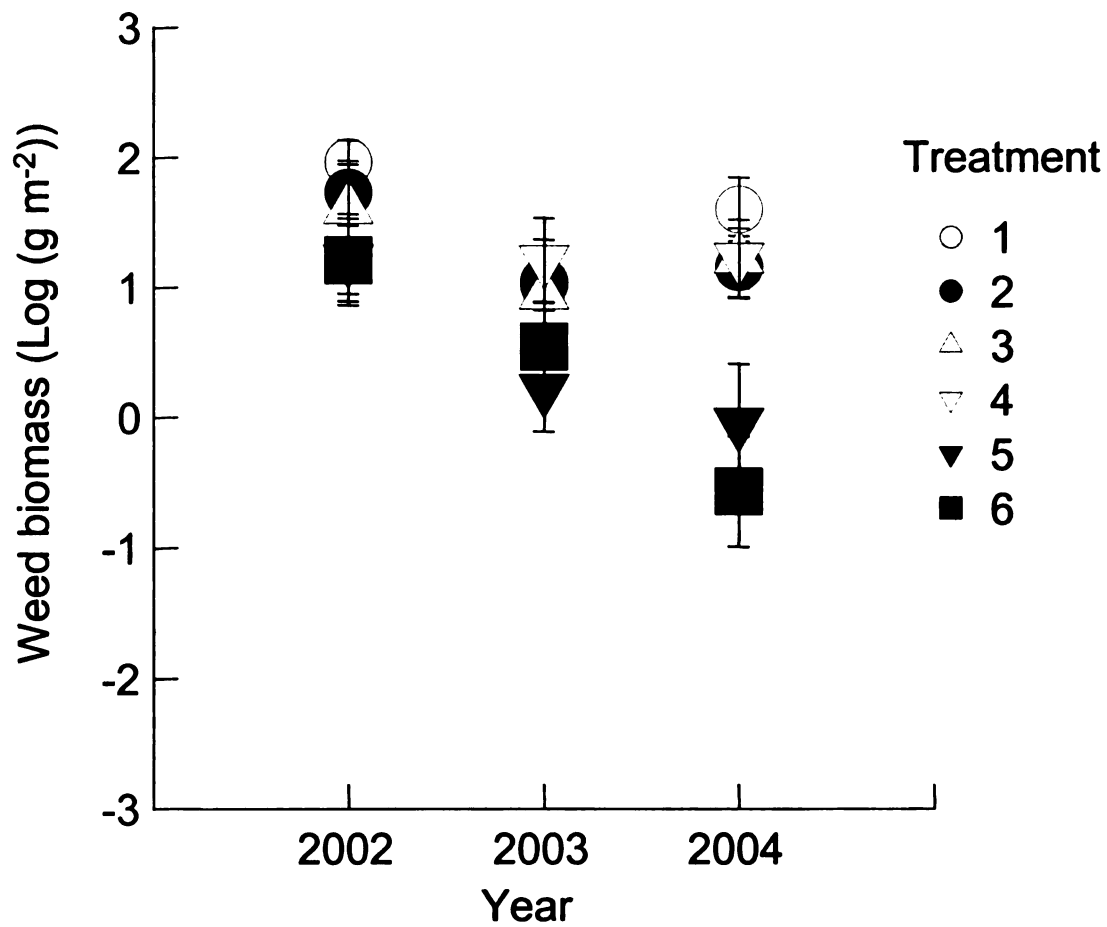


Figure 4.1: Weed biomass in relation to crop diversity over time in the KBS Biodiversity Experiment Plots. Symbols refer to crop diversity treatments (see Table 4.1). Symbols that are shaded indicate treatments with cover crops. Values are means (\pm SE; $n = 12$) averaged across the three crops.

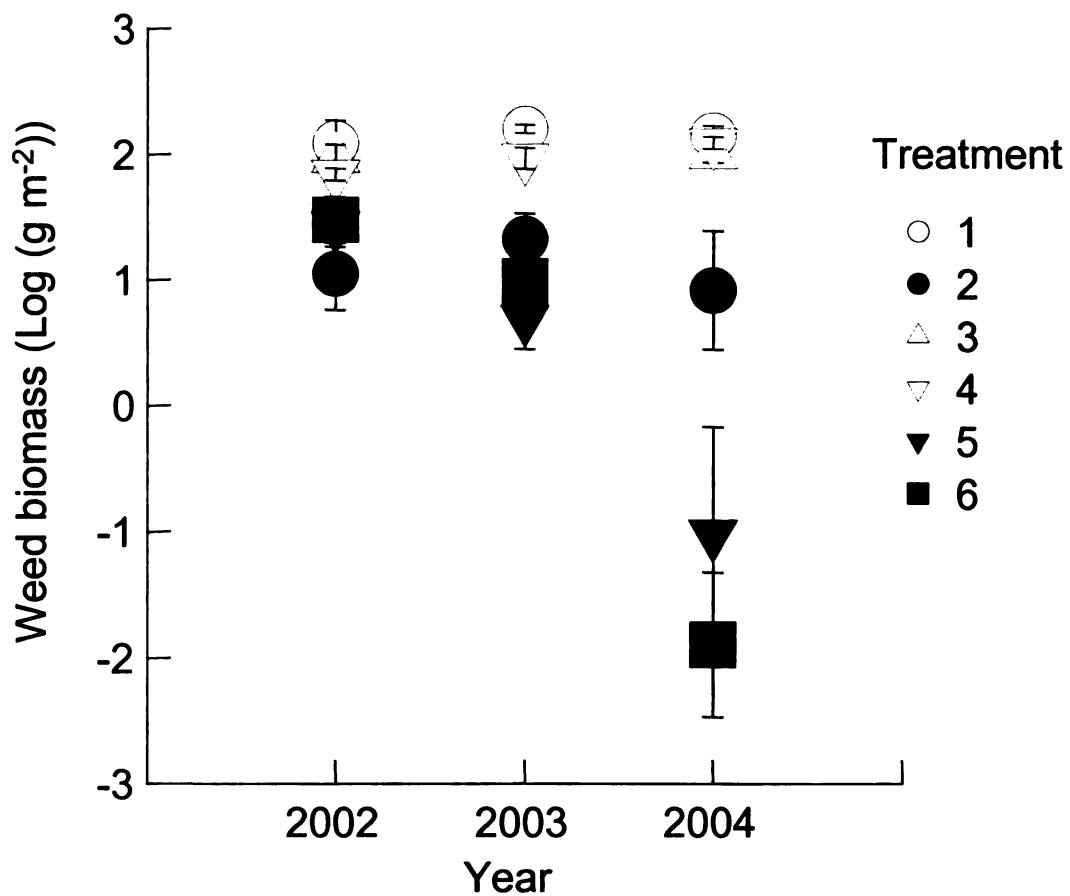


Figure 4.2: Weed biomass in winter wheat planted under different crop diversity treatments (2002-2004). Symbols refer to crop diversity treatments (see Table 4.1). Symbols that are shaded indicate treatments with cover crops. Values are means (\pm SE; $n = 4$).

6; Tukey test $P > 0.05$; Figure 4.2). While there was a significant effect of year on weed biomass in both corn and soybean (corn: $P = 0.02$; soybean; $P < 0.001$), there was no significant crop diversity or crop diversity-by-year interaction for either crop (data not shown).

Species richness and diversity

Weed species richness was affected by the interaction of crop identity, crop diversity, and year (3-way interaction: $F_{29,109} = 4.36$, $P < 0.0001$) and overall was lower in the lowest diversity treatments (Figure 4.3). Subsequent repeated measures analysis revealed significant crop diversity-by-year interactions in all three main crops (2-way interaction, corn: $F_{10,36} = 2.99$, $P = 0.008$; soybean: $F_{10,40} = 4.96$, $P = 0.0001$; wheat: $F_{9,33} = 8.82$, $P < 0.0001$). In corn, differences among treatments were significant in 2003 ($P = 0.0168$) and 2004 ($P = 0.0378$); however, an adjusted multiple-comparison test indicated that in 2003 only diversity treatments 2 and 4 (continuous monoculture with cover crop and the three-crop rotation, respectively) were significantly different from the others; none of the diversity treatments were different in 2004 (Tukey HSD test, $P < 0.05$). In soybean, differences among diversity treatments were significant only in 2003; treatments 5 and 6 (three-crop rotation with one and two cover crop species, respectively) differed from treatment 3 (two-crop rotation), Tukey HSD test, $P < 0.05$). In contrast, there were large differences in weed species richness among treatments planted to wheat in all years, and the differences among diversity treatments increased over time (Figure 4.4). In general, wheat grown in treatments that included cover crops (treatments 2, 5, and 6) had lower weed species richness compared to treatments without cover crops. Species richness did not differ between treatments 1, 3

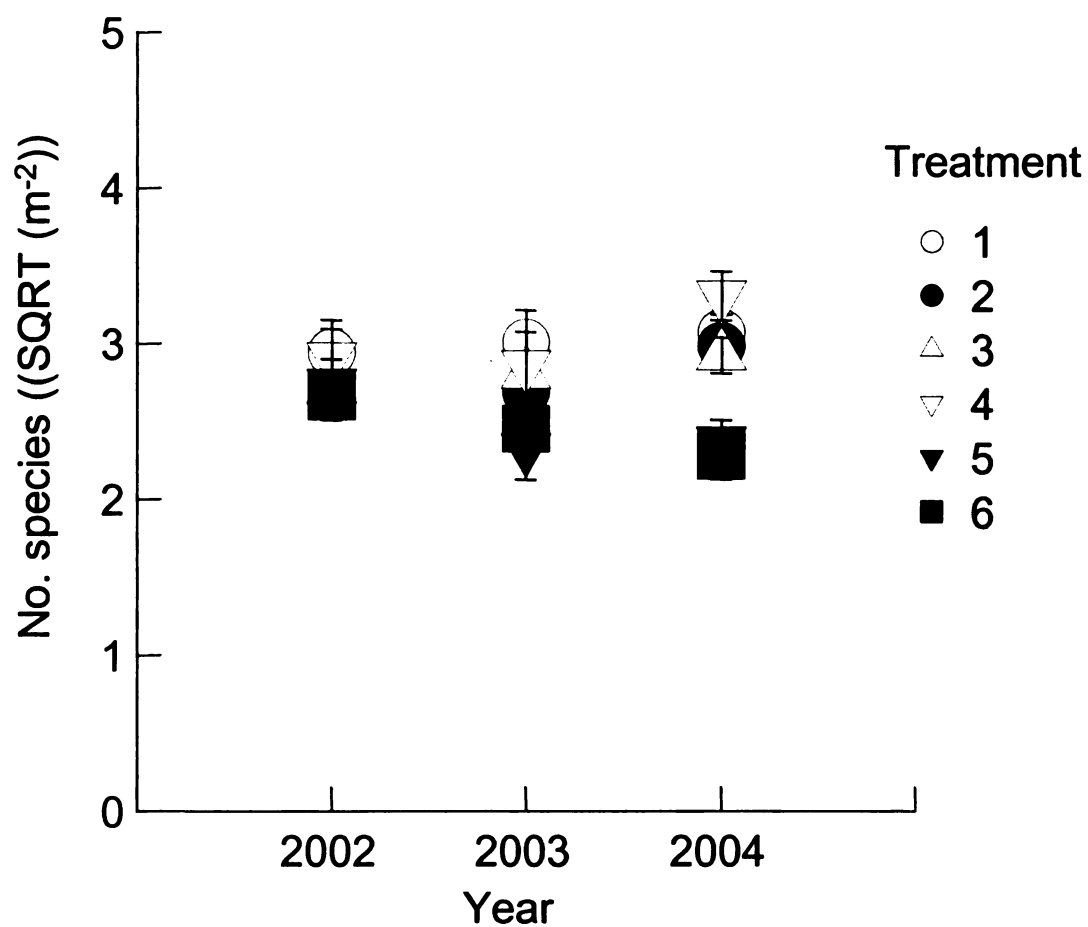


Figure 4.3: Number of weed species from 2002 through 2004 in crop diversity treatments at the KBS Biodiversity Experiment Plots. Symbols refer to crop diversity treatments (see Table 4.1). Symbols that are shaded indicate treatments with cover crops. Values are means (\pm SE; $n=12$) averaged across the three main crops.

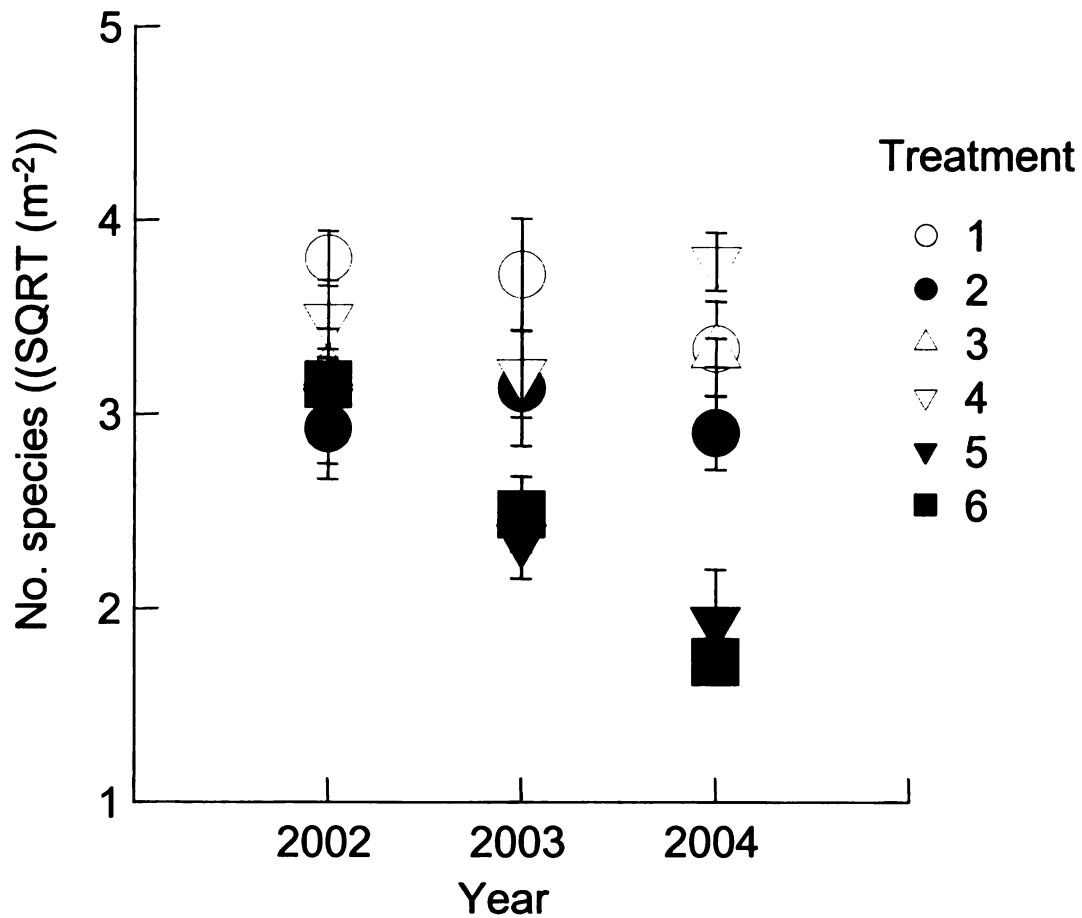


Figure 4.4: Number of weed species from 2002 through 2004 in cropping-system diversity treatments planted to winter wheat. Symbols refer to crop diversity treatments (see Table 4.1). Symbols that are shaded indicate treatments with cover crops. Values are means (\pm SE; $n = 4$).

and 4 suggesting that presence of a cover crop, rather than crop rotation, was the important determinant of weed species richness in wheat.

The impact of crop diversity on weed diversity varied, depending on what metric of weed diversity was analyzed. Species evenness was affected by crop identity and year of sampling (crop effect: $F_{2,51} = 17.18$, $P < 0.0001$; year effect: $F_{2,109} = 4.92$, $P = 0.009$), but not crop diversity, and was lower in soybean compared to corn and wheat. In contrast, analysis of the Shannon and Simpson's diversity indices revealed a three-way interaction between crop diversity, crop identity, and year of sampling (interaction, S: $F_{29,109} = 2.0$, $P = 0.006$; D: $F_{29,109} = 1.86$, $P = 0.012$). Separate repeated measures analyses for each crop revealed that diversity treatment effects on both diversity measures were significant only in wheat and only in 2004 (interaction, H: $F_{9,33} = 6.9$, $P < 0.001$; D: $F_{9,33} = 5.88$, $P < 0.0001$). In general, weed diversity in wheat was lower in the three-crop rotations with cover crops than the three-crop rotation without cover crops (Tukey HSD Test; Figure 4.5).

Community composition and structure

A total of 54 different weed species were observed over the three years of this experiment; of these 34 were observed in corn, 31 in soybean, and 47 in wheat. The importance of the identity of the main crop on weed species composition was apparent in the NMDS ordination of presence/absence data, which showed that weed communities in wheat were distinct from those observed in corn and soybean (Figure 4.6). ISA indicated that species that were significantly associated with winter wheat included broadleaf and grass species such as prostrate knotweed (*Polygonum aviculare*

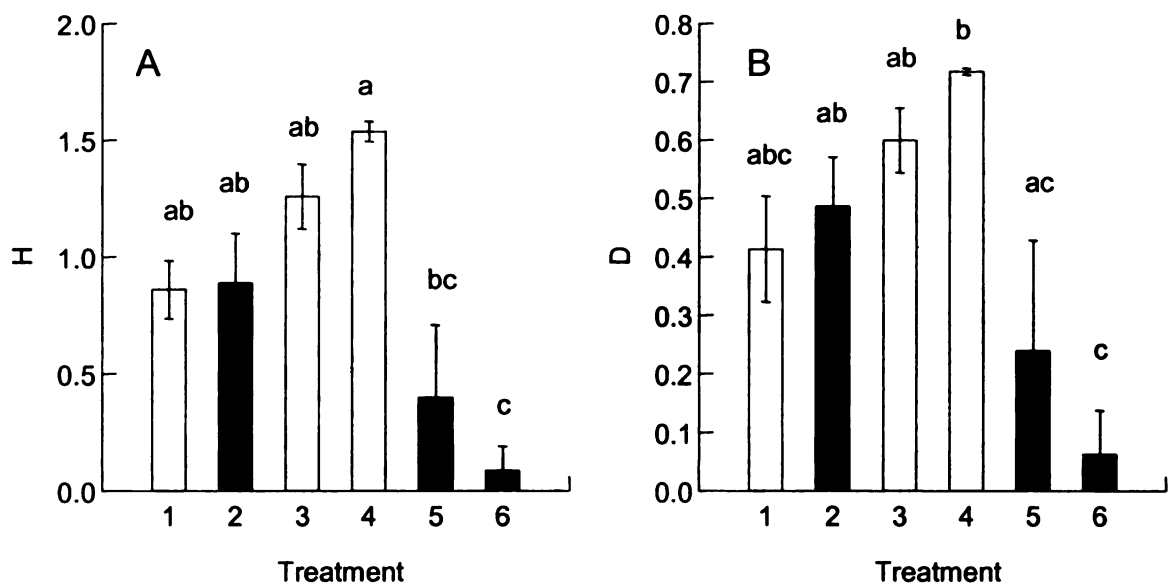


Figure 4.5: Shannon diversity (A) and Simpson's index of species diversity (B) of the weed community in winter wheat in 2004 in six cropping-system diversity treatments at the Biodiversity Experiment Plots. Means (\pm SE; $n = 4$) followed by the same letter are not significantly different at the $P < 0.05$ level of probability (Tukey HSD test). See Table 4.1 for treatment codes.

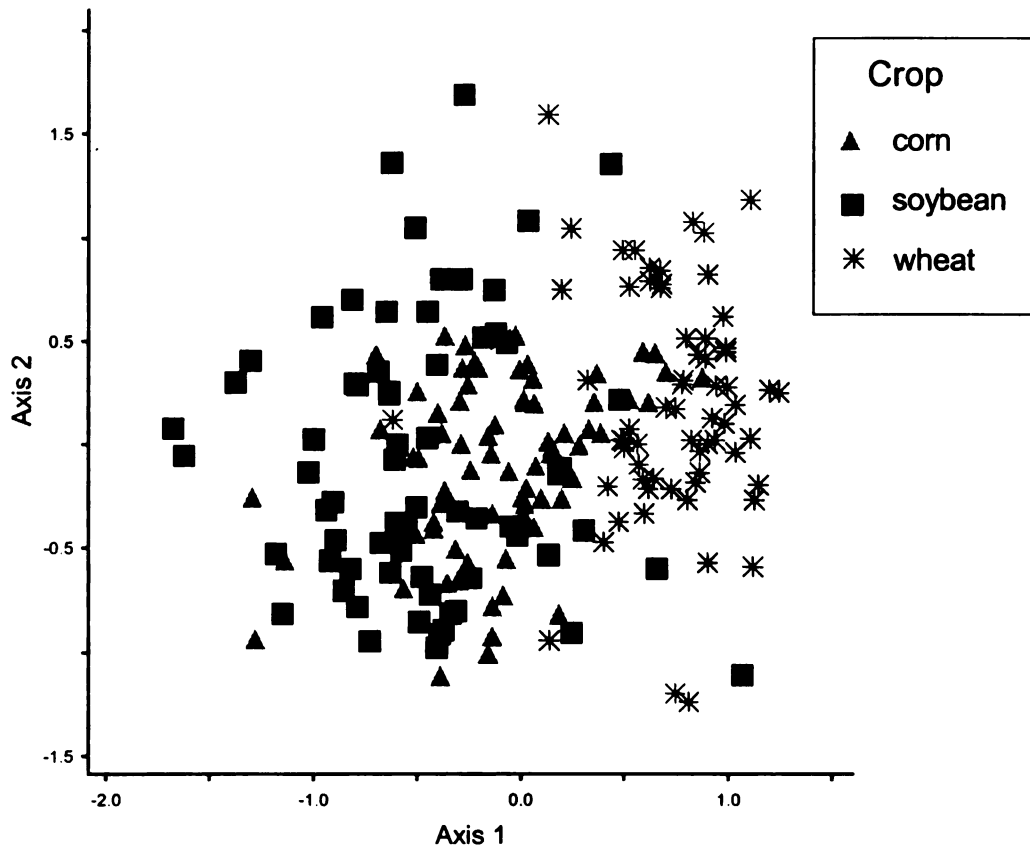


Figure 4.6: Plot scores for the first two most explanatory axes of non-metric multidimensional scaling analysis of weed composition (presence/absence) from 2002 through 2004 in six cropping-system diversity treatments (Table 4.1) at the Biodiversity Experiment Plots at the Long Term Ecological Research site at W. K. Kellogg Biological Station in Hickory Corners, MI. NMDS: stress = 17.992, $P < 0.05$, cumulative r^2 for axes 1 and 2 = 0.638.

L.) and fall panicum (*Panicum dichotomiflorum* Michx.). Species associated with corn and soybean included broadleaf species such as common chickweed (*Stellaria media* (L.) Vill.) and common lambsquarters (*Chenopodium album* L.). Overall, more weed species were associated with winter wheat than corn or soybean (ISA, Table 4.2).

In addition to the strong effects of crop type on weed communities, we were also able to detect significant crop diversity effects on weed community composition and abundance. The distance-based multivariate analysis indicated that for each crop, weed species composition and abundance was affected by crop diversity, year of sampling, and their interaction (Table 4.3). NMDS ordination of the species abundance data from 2004 showed that within each main crop, treatment replicates with higher crop diversity tended to ordinate separately from replicates with lower crop diversity (Figure 4.7). This was particularly evident in wheat; treatments without cover crops clustered together and were distinct from those with cover crops, which were fairly homogeneously dispersed in ordination space (Figure 4.7c).

Differences among treatments were reflected in the ISA analysis on data from each main crop in 2004. In corn the ISA analysis indicated that Canada bluegrass (*Poa compressa* L.), was most associated with treatment 3 (two-crop rotation; ISA: IV = 53.6, $P = 0.028$). For soybean, three species showed strong associations with particular diversity treatments. Dandelion (*Taraxacum officinale* G.H. Weber ex Wiggers) and large crabgrass (*Digitaria sanguinalis* (L.) Scop.) were both strongly associated with the soybean phase of the three-crop rotation without cover crops (treatment 4) (ISA, dandelion IV = 70.8, $P = 0.003$; crabgrass: IV = 53.3, $P = 0.042$) and giant foxtail (*Setaria faberi* Herrm.) was associated with soybean grown in continuous monoculture

Table 4.2: Results of indicator species analysis (ISA) on weed community composition (presence/absence) at the Biodiversity Experiment Plots. ISA Indicator Value (IV) calculated from annual biomass harvest averaged over three years (2002-2004). Bold type indicates significant associations with a crop species at the $P < 0.05$ level of probability.

Species	ISA		
	IV [†]	P-value	Crop [‡]
<i>Abutilon theophrasti</i> Medik.	22.8	0.002	corn
<i>Amaranthus retroflexus</i> L.	4.0	0.688	corn
<i>Ambrosia artemisiifolia</i> L.	39.2	0.001	wheat
<i>Arabidopsis thaliana</i> (L.) Heynh.	30.3	0.001	wheat
<i>Cardamine</i> spp.	13.7	0.008	soybean
<i>Chenopodium album</i> L.	36.1	0.002	corn
<i>Conyza canadensis</i> (L.) Cronq.	33.0	0.001	wheat
<i>Daucus carota</i> L.	5.5	0.109	corn
<i>Digitaria ischaemum</i> (Schreb.) Schreb. ex Muhl.	33.8	0.001	wheat
<i>Digitaria sanguinalis</i> (L.) Scop.	34.3	0.002	wheat
<i>Elymus repens</i> (L.) Gould	19.5	0.001	wheat
<i>Lamium</i> spp.	24.9	0.001	corn
<i>Mollugo verticillata</i> L.	12.9	0.049	corn
<i>Oxalis stricta</i> L.	45.5	0.001	wheat
<i>Panicum dichotomiflorum</i> Michx.	45.1	0.001	wheat
<i>Poa compressa</i> L.	14.9	0.358	soybean
<i>Polygonum aviculare</i> L.	53.7	0.001	wheat
<i>Polygonum convolvulus</i> L.	14.6	0.001	wheat
<i>Polygonum persicaria</i> L.	12.2	0.001	wheat
<i>Portulaca oleracea</i> L.	8.2	0.085	corn
<i>Rumex obtusifolius</i> L.	8.2	0.09	wheat
<i>Setaria faberi</i> Herrm.	18.5	0.006	wheat
<i>Setaria pumila</i> (Poir.) Roemer & J.A. Schultes	17.6	0.003	wheat
<i>Setaria viridis</i> (L.) Beauv.	13.7	0.002	wheat
<i>Solanum ptychanthum</i> Dunal	11.6	0.004	corn
<i>Sonchus oleraceus</i> L.	7.2	0.033	corn
<i>Stellaria media</i> (L.) Vill.	40.1	0.001	corn
<i>Taraxacum officinale</i> G.H. Weber ex Wiggers	21.2	0.085	corn
<i>Veronica peregrina</i> L.	6.8	0.04	wheat

[†] indicator value (% perfect indication).

[‡] crop in which species association was highest.

Table 4.3: Results of distance-based multivariate analysis of variance (Anderson 2001, McArdle and Anderson 2001) of the effects of blocking (B), crop diversity (D), and year (Y) on weed abundance and composition from 2002 through 2004 in the KBS Biodiversity Experiment Plots.

Crop	Factor	df	SS	MS	pseudo-F	P-value	
						Perm [†]	Monte Carlo [‡]
Corn	B	3	23971.37	7990.46	2.84	0.0004	0.0001
	D	5	20795.06	4159.01	1.48	0.0442	0.0516
	Error _M	15	42216.94	2814.46			
	Y	2	29699.24	14849.62	5.34	0.0001	0.0001
	D x Y	10	36023.64	3602.36	1.30	0.0553	0.0611
	Error _S	36	100021.56	2778.38			
	Total	71	252727.81				
Soybean	B	3	25079.54	8359.85	2.53	0.00010	0.00020
	D	5	26866.32	5373.26	1.63	0.00700	0.01000
	Error _M	15	49562.44	3304.16			
	Y	2	23630.92	11815.46	3.32	0.00010	0.00010
	D x Y	10	42695.66	4269.57	1.20	0.08350	0.10210
	Error _S	40	142508.75	3562.72			
	Total	75	310225.27				
Wheat	B	3	13986.91	4662.30	1.57	0.01890	0.03170
	D	5	48695.94	9739.19	3.28	0.00010	0.00010
	Error _M	15	44524.37	2968.29			
	Y	2	17731.92	8865.96	4.09	0.00010	0.00010
	D x Y	10	35796.18	3579.62	1.65	0.00010	0.00050
	Error _S	32	69423.52	2169.49			
	Total	67	225207.75				

[†] 9999 permutations.

[‡] P-value based on Monte Carlo samples from the asymptotic permutation distribution.

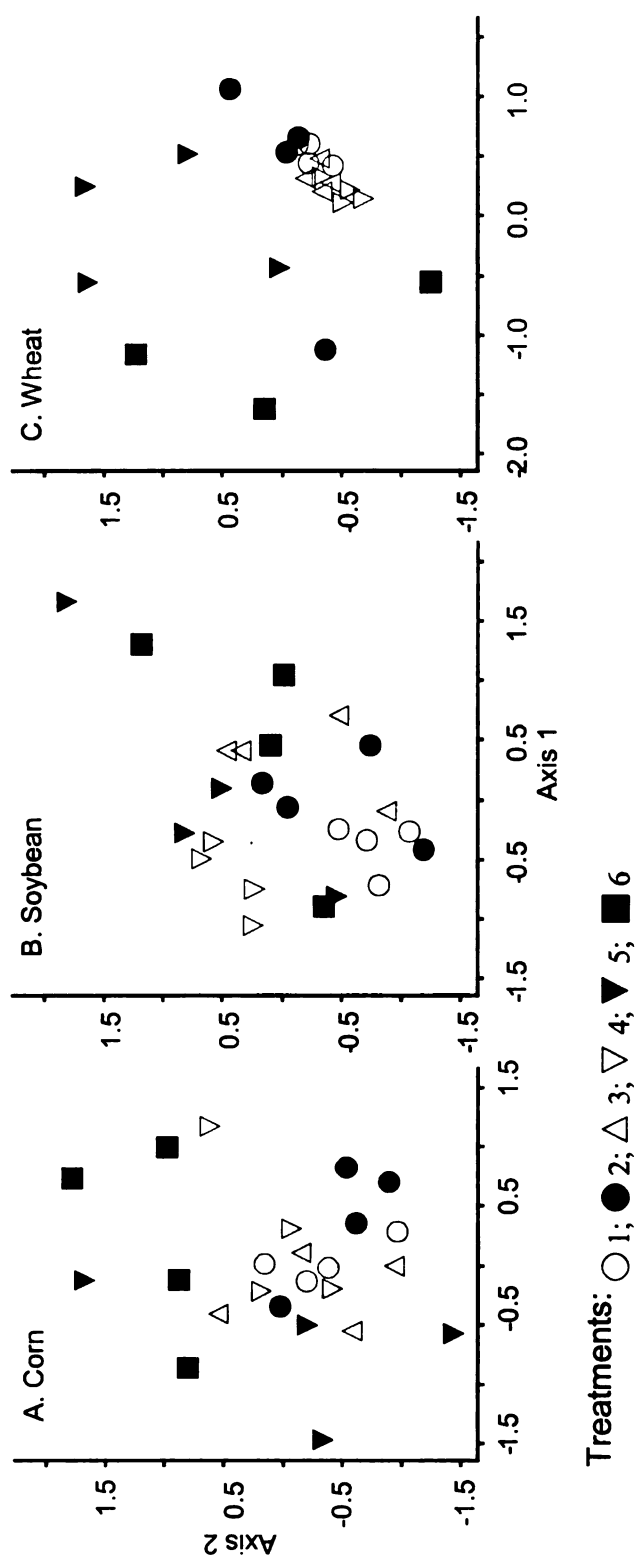


Figure 4.7: Plot scores for the first two most explanatory axes of non-metric multidimensional scaling analysis of weed abundance and composition in six diversity treatments (Table 4.1) in corn (A), soybean (B) and winter wheat (C) in 2004 at the Long Term Ecological Research site at W. K. Kellogg Biological Station in Hickory Corners, MI. NMDS, corn: stress = 18.74, $P < 0.05$, $r^2 = 0.704$; soybean: stress = 16.17, $P < 0.05$, $r^2 = 0.583$; wheat: stress = 18.95, $P < 0.05$, $r^2 = 0.711$.

(treatment 1; ISA: $IV = 47.7$, $P = 0.023$). Indicator species analysis identified five crop diversity treatment associations in wheat: common lambsquarters, yellow woodsorrel (*Oxalis stricta* L.), and dandelion were all associated with the wheat phase in treatment 4 (three-crop rotation without cover crops; ISP: lambsquarters: $IV = 84.0$, $P = 0.001$; woodsorrel: $IV = 70.3$, $P = 0.001$; dandelion: $IV = 49.0$, $P = 0.006$). Quackgrass (*Elymus repens* (L.) Gould) was associated with treatment 3 (two-crop rotation; $IV = 61.3$, $P = 0.029$) and smooth crabgrass *Digitaria ischaemum* (Schreb.) Schreb. ex Muhl., was associated with treatment 1 (continuous monoculture; $IV = 51.2$, $P = 0.001$).

Soil and light resources and relationships to the weed community

In 2002, two years after the treatments had been initiated, there were indications of treatment effects on soil resources among crops; however, these were variable and depended on the identity of the main crop (ANOVA, diversity-by-crop identity interaction: $F_{10,51} = 2.91$, $P = 0.006$). Across replicates that had been sown to winter wheat in fall 2001, soil N measured in November 2002 was significantly higher in treatment 2 (monoculture with cover crops) compared to treatments 3, 4, and 5 (Tukey HSD Test, $P < 0.05$). However, there were no differences in soil N among plots sown to corn and soybean in 2002. Treatment effects were also not apparent among plots that were sown to wheat in October 2002 (a month prior to sampling) ($P = 0.093$), or those plots that would be sown to corn in the spring of 2003 ($P = 0.61$). Plots that would be sown to soybean in the spring of 2003 did show treatment differences ($F_{5,19} = 3.87$, $P = 0.013$); soil N pools and net mineralization rates were highest in the continuous monoculture (treatment 1) compared to the other diversity systems (Tukey HSD test, $P < 0.05$).

Two years later (4 yrs after treatments were initiated), treatment effects were even more pronounced, but still variable among main crops. Soil N pools measured in June 2004 showed a significant effect of crop diversity in corn and wheat, but not in soybean (interaction: $F_{10,51} = 2.98$, $P = 0.005$) (Figure 4.8). In August, crop diversity treatment effects on soil N pools were still significant for corn and wheat crops. In corn, soil N levels were higher in treatment 5 than treatments 1, 3, and 4; in wheat, N levels were higher in treatment 2 than treatment 3 and 4 (Tukey HSD test $P < 0.05$). By November, soil N pools in plots that had been sown to soybean in 2004 and wheat in 2003 varied across diversity treatments (interaction: $F_{10,51} = 5.21$, $P < 0.0001$), likely reflecting the recent planting to wheat (in October) in some of these treatments. Similar to 2002, soil N levels in plots sown to wheat in 2003 were higher in treatment 2 than treatments 3, 4, 5, and 6. Net soil N-mineralization also varied among cropping-system diversity treatments that were sown to wheat in 2003, but not those sown to corn and soybean in 2004 (interaction: $F_{10,51} = 2.89$, $P = 0.0062$) (Figure 4.9). However, unlike in 2002, there were significant treatment differences on N mineralization among plots sown to wheat in October 2004 ($F_{5,15} = 5.91$, $P = 0.003$), with treatment 2 having higher N pools than treatments 3, 4, and 6 (Tukey HSD test, $P < 0.05$). This may reflect the relative importance of cover crops versus soybean as a source of N-fixation, since treatments 3, 4, and 6 would each have been planted to soybean previously (May 2004) and where cover crop biomass tended to be low compared to wheat (see discussion).

Soil moisture levels measured in late June 2004 were unaffected by crop diversity ($P = 0.0708$), but were affected by crop identity ($F_{2,51} = 23.58$, $P < 0.0001$) and were lowest in wheat. At late-season (late August), soil moisture levels differed among

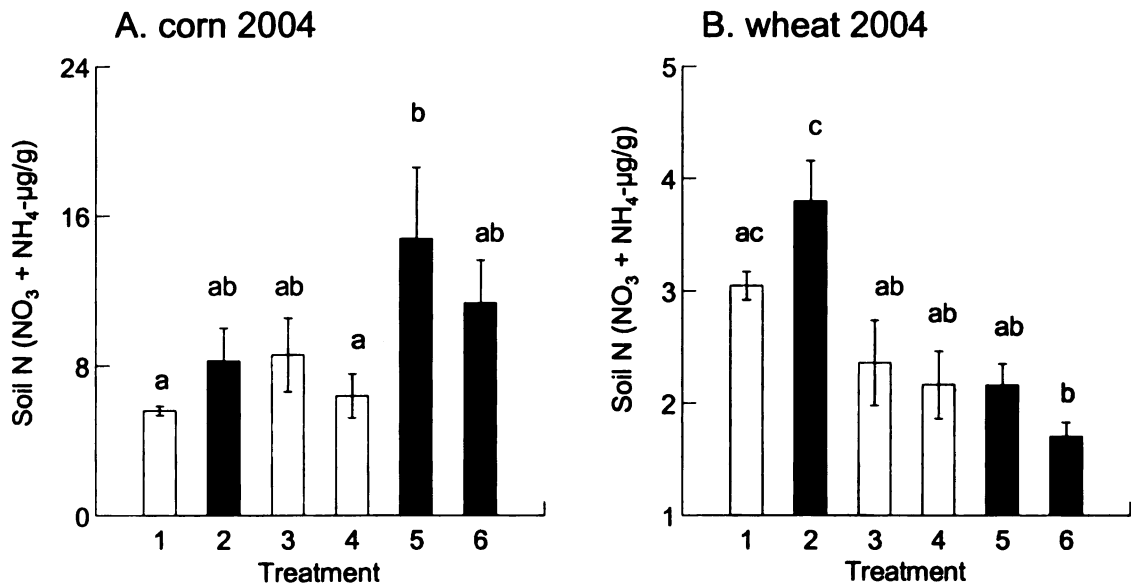


Figure 4.8: Soil inorganic N pools (NO₃-N + NH₄-N) in treatments planted to (A) corn and (B) winter wheat in six cropping-system diversity treatments (see Table 4.1) at the KBS Biodiversity Experiment Plots. Values are means (\pm SE; $n = 4$); bars with the same letter are not significantly different at the $P < 0.05$ level of probability (Tukey HSD test). Note different x-axis scales in panels A and B.

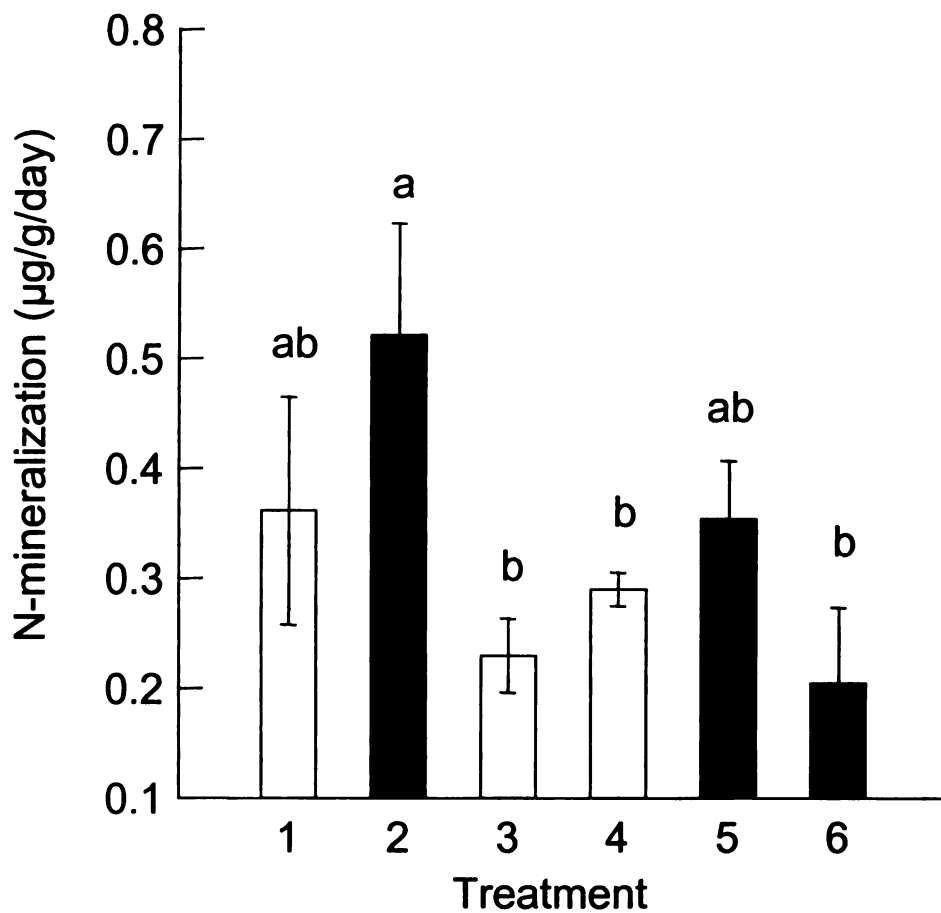


Figure 4.9: Net N-mineralization ($\mu\text{gN/g dry soil/day}$) in wheat in six cropping-system diversity treatments (Table 4.1) at the Biodiversity Experiment Plots. N-mineralization rate was measured following 28-day incubation (25°C) of soils collected on 16 November 2004. Values are means (\pm SE; $n = 4$); bars followed by the same letter are not significantly different at the $P < 0.05$ level of probability (Tukey HSD test).

crops ($F_{2,51} = 13.33$, $P < 0.0001$) and crop diversity treatments ($F_{5,51} = 6.66$, $P < 0.0001$) and were higher in corn compared to soybean and wheat (Tukey HSD test, $P < 0.05$). Overall soil moisture in August tended to be lower in the higher diversity treatments (Figure 4.10). By 16 November there were no significant differences in soil moisture related to crop type or crop diversity treatment (data not shown).

Light levels (% PAR) at ground level in late July differed among diversity treatments in wheat but not corn or soybean (interaction: $F_{10,42} = 2.14$, $P = 0.0426$) and were lowest in the highest diversity wheat treatments, particularly those with cover crops. At the end of the growing season (22 August) light levels differed among crop diversity treatments in corn and wheat but not in soybean (interaction: $F_{10,42} = 5.32$, $P < 0.0001$). In corn light levels were highest in treatment 1 (continuous monoculture). In wheat they were highest in the two- and three-crop rotation without cover crops. By 19 September light levels differed among diversity treatments in wheat, but not in corn and soybean (interaction: $F_{10,42} = 32.82$, $P < 0.0001$); wheat treatments with cover crops had significantly lower light levels compared to those without cover crops (Figure 4.11).

The relationship between resource levels and weed community structure in 2004 were investigated by examining correlations between resource variables measured in 2004 and the NMDS ordination axes scores. Data on cover crop biomass was also included in these analyses. There was little correlation between resource levels in 2004 and the NMDS ordination axes scores in soybean (highest $r^2 = 0.169$). In corn, only one variable, late-season soil moisture had an r^2 greater than 0.2 ($r^2 = 0.214$). In contrast, five variables showed relatively strong correlations ($r^2 > 0.2$) with the ordination axes

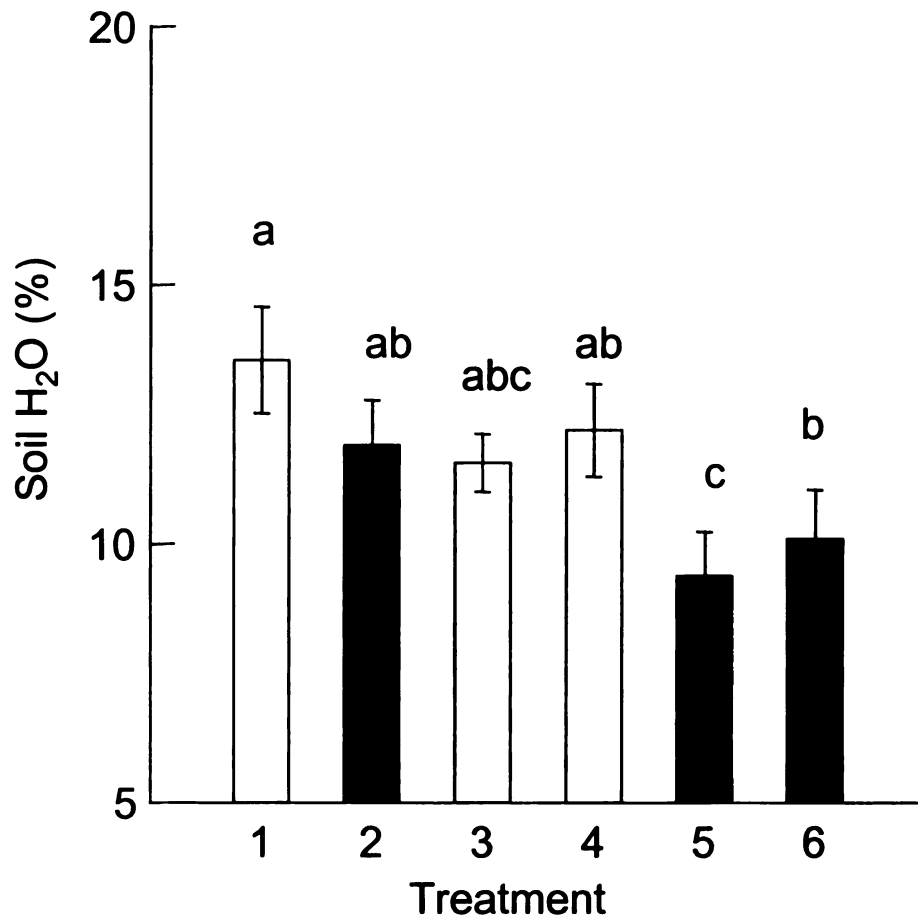


Figure 4.10: Soil moisture levels in relation to crop diversity treatments (see Table 4.1) at the KBS Biodiversity Experiment Plots. Soils were sampled at the end of the growing season 4 yrs after the treatments were initiated (August 2004). Bars are means (\pm SE; $n = 12$) are averaged across the three crops; bars with the same letter are not significantly different at the $P < 0.05$ level of probability (Tukey HSD test).

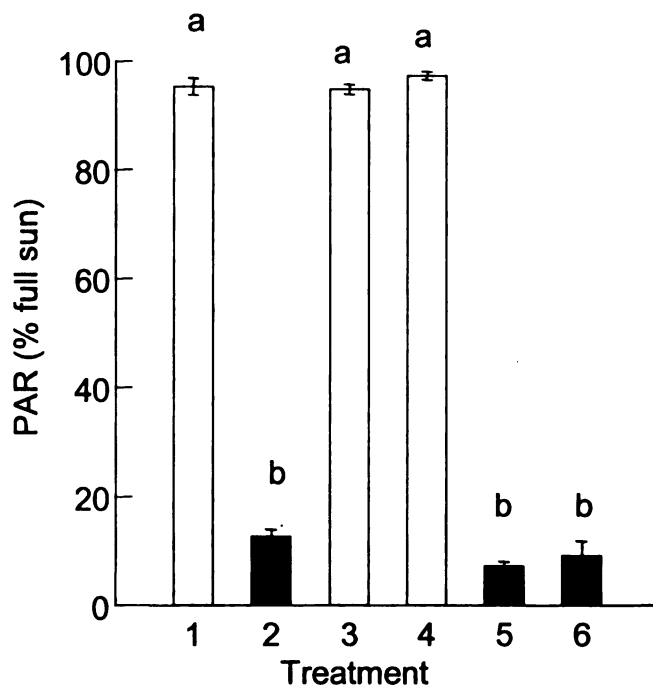


Figure 4.11: Light levels in winter wheat grown in different crop diversity treatments on 19 September 2004. Means (\pm SE; $n = 4$) followed by the same letter are not significantly different at the $P < 0.05$ level of probability (Tukey HSD test).

Table 4.4: Pearson correlation coefficients and r^2 between environmental and biological variables and axes scores from NMDS ordination analysis of weed abundance and composition 2004 in the KBS Biodiversity Experiment Plots.

Crop	Variable [†]	Axis 1		Axis 2	
		r	r^2	r	r^2
Corn	H ₂ O _M	0.462	0.214	-0.049	0.002
Soybean	-	-	-	-	-
Wheat	H ₂ O _M	0.491	0.241	-0.217	0.047
	H ₂ O _L	0.510	0.260	-0.407	0.166
	PAR _M	0.541	0.293	-0.561	0.315
	PAR _P	0.470	0.221	-0.534	0.285
	COVER _{BM}	-0.444	0.198	0.542	0.294

[†] Eight variables were analyzed, only those with $r^2 > 0.185$ for at least one axis are included in the table. Subscripts after variables are: M, mid-season; L, late-season; P, post-season; BM, biomass (m²).

scores in wheat, the strongest of which were those related to cover crop biomass and light availability (Table 4.4).

Relationships between the weed community and soil resources and light were also investigated using forward selection multivariate multiple regression. The analysis indicated that no resource variables explained any of the variation in community structure in corn (smallest P -value = 0.09) (data not shown). In soybean, light level (PAR) late in the season was identified as being a significant predictor of weed community structure ($r^2 = 0.08$, $P = 0.047$). When forward selection was applied, two factors, late season light, and mid-season soil moisture were identified as significant, and together explained 17 % of the variance in community structure in soybean (Table 4.5). Grouping of the resource variables did not improve the strength of the relationship (data not shown). In contrast to corn and soybean, soil moisture, light, and cover crop biomass were all significant predictors of weed community structure in wheat (data not shown). Forward selection of the variables indicated that post-season light levels and N mineralization rate together explained 24 % of the variation in weed community structure (Table 4.5). Grouping the factors improved the strength of the relationship, with each group (water, N, light, and cover crop) separately explaining over 12 % of the variance in community structure. However, forward selection of the model with the variables grouped indicated that only light resources were significant predictors of community structure, together explaining 24 % of the variation ($P = 0.0001$).

DISCUSSION

The results of this study suggest that the impacts of crop diversity on weed communities can be highly variable and depend on the identity of the main crop and the

Table 4.5: Results of distance-based multivariate multiple regression with forward selection (McArdle and Anderson 2001) on weed abundance and composition in 2004 in the KBS Biodiversity Experiment Plots.

Crop [†]	Variable [‡]	SS (Trace)	Pseudo- F	P-value (perm.)	Variance explained	
					Prop.	Cum. Prop.
Corn	-	-	-	-	-	-
Soybean	PAR	7071.441	1.8966	0.0471	0.0794	0.0794
	H ₂ O	7824.207	2.2144	0.0130	0.0878	0.1672
Wheat	PAR	16542.100	4.9417	0.0001	0.1834	0.1834
	N _{MIN}	5529.253	1.7047	0.0176	0.0613	0.2447

[†] For each crop, order of variables is in decreasing proportion of variance explained.

[‡] Eight variables were included in the analysis, only those variables that were significant at the $P < 0.08$ level of probability (9999 permutations) are included in the table.

number of crops in a rotation. Our results also show that increasing crop diversity can have significant impacts on the availability of light and soil resources within the cropping system, and that these impacts vary depending on the identity of the main crop. In wheat, differences in weed abundance and diversity among crop diversity treatments appeared driven mainly by the presence of cover crops and their impacts on the availability of light. However, in corn and soybean, there were few effects of crop diversity on any attribute of the weed community, despite significant differences in resource levels among treatments. In contrast to the effects of cover crops, the rotation of main crops had relatively little effect on weed communities.

The importance of cover crops in driving the crop diversity-ecosystem function relationships observed in this study is further supported by the observation that there were more differences among weed communities in crop diversity treatments in wheat compared to corn and soybean. The suppressive effects of cover crops have been shown to vary with cover crops biomass (Akemo et al., 2000; Barberi and Mazzoncini, 2001), which was much higher in wheat compared to corn and soybean. By the time weeds were harvested (August-September) cover crop biomass in wheat in treatments 2, 5, and 6 averaged 159, 254, and 277 g m⁻², respectively, compared to the same treatments in corn and soybean which each averaged less 12 g m⁻². Differences in cover crop biomass between crops was likely due to the earlier planting of cover crops in wheat (March) compared to corn and soybean (July).

The impacts of cover crops on weed abundance and resource levels in this study are consistent with observations from other agronomic studies showing that management systems that include cover crops often have lower weed abundance and

higher soil fertility (Teasdale 1996, Mutch et al. 2003, Drinkwater et al. 1998, Drinkwater et al. 2000, Snapp et al. 2005). Because there were no fertilizers or herbicides used in this study, the effects of cover crops on weeds and resource levels in wheat can be attributed to the cover crops themselves rather than associated management practices (Doucet et al. 1999, Drinkwater et al. 2000). The weed suppressive effects of cover crops have been shown to be weed species-specific (Creamer et al., 1996; Moonen & Barberi, 2004), perhaps explaining the reduced species richness and diversity in treatments planted with cover crops (treatments 2, 5, and 6; Figures 4.3-4.6), and the strong associations between certain weed species and the diversity treatments. The three cover crop species used in this study have all been shown to have allelopathic properties (Creamer et al. 1996, Davis and Liebman 2003); though it is unclear whether, and to what extent allelopathy, rather than competitive interactions, was responsible for the observed effects on weed suppression in this study.

The impact of cover crops on resource levels and competitive outcomes observed in our study are also consistent with observations from diversity studies performed in grassland systems that report strong species-specific effects on ecosystem functions (Tilman et al. 1997, Schlöpfer and Schmid 1999, Lambers et al. 2004, Hooper et al. 2005). In some of these studies leguminous forbs have been shown to contribute to substantial over-yielding in other species through their effects on soil N availability (Lambers et al. 2004). In contrast, there was no evidence in this study that weeds benefited from the increased N provided by the legume cover crops or rotation with soybean, as there were no differences in weed biomass among crop diversity treatments

in corn and soybean, and differences in weed abundance among treatments in wheat appeared due to suppression rather than facilitation.

There is evidence in the ecological literature that experimental communities containing more species are more resistant to colonization and establishment by new species (Fargione and Tilman 2005), and it is hypothesized that the suppression of colonization is due to species-rich communities having fewer unexploited niches (Levine and D'Antonio 1999). While our study did not manipulate the number of crop species in a single year beyond one main crop and two cover crop species (i.e. treatment 6), the presence of cover crops in wheat certainly led to reduced resource availability—light levels at ground level were lower in these treatments, which likely led to the reduced species abundance and lower species diversity at higher levels of crop diversity. Reduced resource availability due to cover crops also may have reduced colonization by weed species from surrounding areas or from the soil seed bank (Kitajima and Tilman 1996).

Rotation of crops (temporal diversity) appeared to have relatively little effect on the abundance and composition of the weed community. The relative lack of a rotation effect was somewhat surprising given that many agronomic studies have reported significant effects of rotating crops on weed abundance and diversity (Liebman and Dyck 1993, Kegode et al. 1999, Cardina et al. 2002, Legere and Samson 2004, Westerman et al. 2005). However these results are not without precedent. A number of recent studies have reported little or no effect of crop rotation on weed communities (Doucet et al. 1999, Barberi and Lo Cascio 2001), particularly when the effects of associated management practices are taken into account. For instance, Doucet et al.

(1999) reported that after nine years of a corn-soybean-wheat rotation following planting to corn in the tenth year weed communities were similar to continuous corn. The lack of associated herbicide applications in our system may have decreased the diversity and strength of stress and mortality factors that weeds were subjected to, and that would have otherwise been present, in diversified crop rotations under chemical management (Liebman and Gallandt 1997, Westerman et al. 2005). The lack of a consistent rotation effect may also indicate that rotation alone is not a significantly strong filter on the assembly of weed communities (Booth and Swanton 2002, Cardina et al. 2002).

Differences in weed community composition among crops were likely due, in part, to the timing of seedbed disturbance associated with primary tillage, and variation in germination and emergence times among weed species (Keever, 1979, Crawley, 2004). Other studies have noted similar differences between the weedy flora in fall and spring-sown crop species (Andersson and Milberg 1998; Hald 1999b; Hallgren et al. 1999; Squire et al. 2000). Additional evidence for the importance of the timing of seedbed disturbance comes from the observation that weeds in corn and soybean tend to be similar to those in spring-tilled fallows, while weeds in winter wheat tend to be similar to those in fall-tilled fallows (Appendix A4.1).

The design of the experiment did not allow us to test all possible combinations of crops or crop diversity—for instance, there was no cover crop monoculture or corn-wheat rotation. Because growers are not likely to grow cover crops alone (without an associated crop), or rotate corn and wheat in succession; such treatments would not reflect potentially realistic cropping situations. Therefore our conclusions regarding the

importance of crop diversity *per se* are necessarily constrained by the desire to maintain realistic cropping sequences. However, within this constraint, increasing crop diversity *per se* appeared to have few significant impacts on the abundance, diversity, and composition of the weed community. However, because this is a long-term study, treatment effects may develop over time.

The observation that cover crops, rather than crop rotation or diversity *per se* appeared to be the main driver of weed abundance does not negate the importance of increasing crop diversity as a weed and crop management tool (Westerman et al. 2005), particularly given the observed effects of crop diversity on soil resource levels. Results of a study examining the response of grain yields to increasing crop diversity showed that yields in diverse corn and soybean rotations were maintained at levels comparable to those in conventionally managed systems, despite having higher weed abundance (Smith Chapter 5). Together, these two studies suggest that increasing crop diversity may reduce the need for intensive weed management, not because weed abundance is reduced, but because increased resource availability decreases the impacts of crop-weed competition (Blackshaw et al. 2002).

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CHAPTER 5

CROPPING-SYSTEM DIVERSITY AFFECTS ECOSYSTEM FUNCTION IN ROW CROPS

ABSTRACT

Understanding the role of diversity in the functioning of ecosystems has important implications for agriculture. We show that increasing the diversity of a row crop system, both spatially and temporally by altering crop rotation and cover crops, increases crop productivity (yield) in the absence of chemical inputs (herbicides, pesticides, fertilizer). The effects of cropping system diversity were manifest most strongly in maize and were likely due to the diversity of legumes in the cropping sequence and their effects on available inorganic soil nitrogen. Weed abundance was independent of crop diversity and yield. These results demonstrate how ecological theory is relevant to the management of agricultural ecosystems, and suggests additional strategies for managing agricultural systems with biological inputs.

INTRODUCTION

While the intensification of modern agricultural production systems has led to increases in world food production (Matson et al. 1997, Tilman et al. 2001), increased production has come at the expense of cropping system and wild-land diversity and environmental health (Pimentel et al. 1992, Matson et al. 1997, Green et al. 2005, Robertson and Swinton 2005). Conversion of species-rich wild-lands to large-scale agricultural production, often as monocultures, have reduced the potential for species interactions important in community and ecosystem-level regulation of pest populations and nutrient cycling, which must now be replaced by chemical inputs of pesticides and fertilizer (Drinkwater et al. 1998, Tilman et al. 2001, Robertson and Swinton 2005,

Hooper et al. 2005). The environmental impacts associated with such inputs have led many to question the sustainability of conventional agricultural practices (Pimentel et al. 1992, Matson et al. 1997, Tilman 1999, Tilman et al. 2001, Reganold et al. 2001, Green et al. 2005).

The relationship between species diversity and ecosystem function may have substantive implications for the development of agriculture that is more sustainable (Matson et al. 1997, Liebman and Davis 2000, Mader et al. 2002, Robertson and Swinton 2005). Considerable empirical evidence suggests a link between important ecosystem functions such as nutrient cycling and productivity and the number of species in a community (Tilman et al. 1996, Mittelbach et al. 2001, Mader et al. 2002, Hooper et al. 2005). While the particular mechanisms driving the relationship between diversity and ecosystem function in experimental assemblages are often debated, they appear to operate most strongly at relatively low levels of diversity (Huston 1997, Tilman 1999, Schwartz et al. 2000, Lambers et al. 2004). Because plant diversity in annual row crop systems is already low (usually a single crop), theory thus suggests that increased diversity might be expected to have particularly large effects on ecosystem function in these systems.

Here we report the results of a study established in 2000 in which cropping system diversity is manipulated, both temporally and spatially, through the rotation of both row and cover crops grown without external chemical inputs [of pesticides, herbicides, or fertilizer]. Crop yields, weed abundance, and soil nitrogen were measured over the course of the study to determine how crop diversity affects ecosystem processes related to row-crop production. We grew corn, soybean, and

wheat in combinations of 1-3 crop species annually and 1-6 species over a 3-year rotation period to provide a wide range of plant community diversities.

MATERIALS AND METHODS

Study site

The study was conducted at the Biodiversity Experimental Plots (hereafter BEP, <http://lter.kbs.msu.edu/experimentalDesign.html>) at the W. K. Kellogg Biological Station LTER (Long-term Ecological Research) site of Michigan State University in SW Michigan, USA. Soils at the study site are a mixture of Kalamazoo (fine-loamy, mixed, mesic Typic Hapludalfs) and Oshtemo (coarse-loamy, mixed, mesic Typic Hapludalfs) sandy loams (Sanchez et al. 2001). Annual precipitation at the KBS LTER site is 890 mm⁻¹ and mean annual temperature is 9.7 °C (<http://lter.kbs.msu.edu/siteDescription.html>).

Treatment systems were initiated at the BEP in 2000 and consisted of three row crops, corn (*Zea mays* L.), soybean (*Glycine max* (L.) Merr.), and winter wheat (*Triticum aestivum* L.) grown in continuous monoculture and in two and three-year annual rotations with and without cover crops (zero, one, or two legume/small grain species). The six treatment systems range in diversity from one to three crop species annually and one to five species over a three-year period and include: (1) continuous monoculture (1 spp), (2) continuous monoculture w/ one cover crop annually (2 spp), (3) two-crop rotation (2 spp), (4) three-crop rotation (3 spp), (5) three-crop rotation with one cover crop annually (2 spp annually; 4 spp over 3 yr rotation), and (6) three-crop rotation with two cover crop species annually (3 spp annually; 5 spp over 3 yr rotation). In the two-crop rotation (system 3), only three of the possible sequences were included

in the design: corn-soybean, soybean-corn, and soybean-wheat. The three-crop rotations (systems 4-6) are all planted in the same sequence: corn-soybean-wheat. Each phase of the two and three-crop rotations is present every year, allowing comparisons to be made among the six diversity treatments for each the three main crop species.

Cover crops vary depending on the main crop and include red clover (*Trifolium pratense* L.), crimson clover (*Trifolium incarnatum* L.), and cereal rye (*Secale cereale* L.). In treatments receiving a single cover crop (systems 2 and 5), *T. pratense* is sown into corn in July and wheat in March, and *S. cereale* is sown in soybean (system 2 only) in October. For the highest diversity treatment (system 6) each crop is grown with two cover crops: *T. pratense* is planted into corn and wheat as above, and *T. incarnatum* is planted into soybean. *Secale cereale* is added to corn and wheat in October.

Diversity treatments were randomly applied to plots in three linear blocks; in the fourth block, treatments were arranged in 4 x 5 blocks and planted in sequential order of decreasing diversity. Individual plots measure 9.1m x 27.4 m with no buffer strips between plots. Replicate blocks were separated by grass buffers. All plots are chisel plowed and soil-finished prior to planting the main crop. Corn and soybean are planted in late April or May and winter wheat is planted in late September or early October. No external inputs (herbicides, pesticides, or fertilizer, including manure and compost) were applied to any of the treatments after 2001; periodic inter-row cultivations (cultivation/rotary hoeing) are performed in corn and soybean early in the season to control weeds.

Sampling

Crop yield was determined annually using standard practices with a plot combine. Wheat was harvested in July and soybean and corn was harvested in October and November, respectively. Crop yields (Kg ha^{-1}) were calculated assuming 13 % (wheat and soybean) and 15 % (corn) moisture. Average yields in a nearby conventionally managed (full inputs of herbicides, pesticides, and fertilizer) corn-soybean-wheat rotation at the KBS LTER were calculated in a similar manner and are presented in the results to provide a local conventional baseline with which to compare those in the BEP. Yields for each crop in the conventional system are the average of the six years that each crop was present in the rotation over the time period from 1989 to 2002.

Aboveground weed biomass was harvested at peak biomass (August-September) from two 0.25 x 1 m quadrats placed in two central locations in each plot. The location of sampling was changed each year to minimize edge effects and to avoid harvesting weeds from areas that had been harvested the previous season. Harvested weed biomass was separated to species, dried at 65° C for 48 hrs and weighed to the nearest 0.01g.

Inorganic soil nitrogen (NO_3^- and NH_4^+) was measured at the end of the growing season (November) in 2002 and at three times (28 June, 23 August, and 16 November) in 2004. Soils were sampled to a depth of 25 cm (four 2 cm diameter cores) within the central 3 x 9 m of each plot from both the rows and inter-rows. Aggregated samples were sieved through a 4 mm screen to remove stones and large pieces of organic material. Following sieving, a portion of each aggregated sample (20-30 g) was

processed for gravimetric soil moisture analysis. The remaining sample was subdivided; 20 g of each sample was processed for N extraction with 100 ml of 1M KCL (20 g) and the rest air-dried and archived. Nitrogen (NO_3^- and NH_4^+) was analyzed with an Alpkem 3550 continuous-flow colorimetric analyzer (OI Analytical, College Station, TX, USA). Soils were stored at 4° C and were processed within 48 hrs of collection.

Statistical analyses

Within each crop, separate analyses were performed to determine the effect of cropping system diversity on yield and aboveground weed biomass across the three years (2002-2004). To analyze differences among treatments we used a three factor (diversity system, block, year) repeated-measures ANOVA, with year as the repeated factor (SAS Proc Mixed procedure) followed by a Tukey-Kramer Test at $P = 0.05$. Weed biomass data was $\log_{10}(X + 0.01)$ transformed prior to analysis to improve homoscedasticity. Crop yield (2004) was also analyzed using weed biomass and total available inorganic soil N as independent variables in separate linear regressions.

RESULTS AND DISCUSSION

Cropping system diversity affected yields in all three crops (Table 5.1). However, the strongest effects of diversity were observed in corn, where over-yielding (% increase in yield compared to the monoculture) was over 100% in some treatments. Yields in the highest diversity corn treatment averaged 6.9 Mg ha^{-1} (111 bu A^{-1}) compared to 3.4 Mg ha^{-1} (54 bu A^{-1}) in the lowest diversity treatment. In addition, corn yields in the most diverse treatments (four and five species) were higher than those in

the conventionally managed treatments on nearby plots, which averaged just under 6 Mg ha⁻¹ (95.5 bu A⁻¹) over six years from 1989 to 2002 (Figure 5.1).

In soybean and wheat, yield differences among cropping systems were also significant (Table 5.1) but of lower magnitude (32 and 53 %, respectively). Grain yields in soybean in the highest diversity treatments (systems 4-6) were also higher than those in the conventionally managed system, which averaged just under 2.2 Mg ha⁻¹ (33 bu A⁻¹) (Figure 5.1). In contrast, yields in wheat at all levels of diversity were substantially lower than those in the conventional system (3.6 Mg ha⁻¹). The significant treatment effect in wheat was due to low yields in the monoculture (system 1); the other diversity systems did not differ from one another (Tukey-Kramer Test, $P > 0.05$).

The reasons for the particularly strong diversity effects in corn compared to soybean and wheat were unclear, but may be due to differences in row-spacing, time of planting or physiological differences of C4 grasses compared to legumes and C3 species (Loomis and Connor 1992). C4 grasses also had strong responses to experimental manipulations of diversity in a grassland ecosystem (Lambers et al. 2004). Because the responses to cropping system diversity were most pronounced in corn, we focus on this crop to examine potential mechanisms responsible for the observed diversity effects.

We found no evidence that the observed yield differences were due to reduced weed-crop competition in these diversity treatments. Weed abundance was independent of cropping system diversity over the three years for which we had data ($P = 0.205$) (Table 5.1); nor was there any relationship between weed biomass and corn yield ($r^2 = 0.04$, $P = 0.34$). We did not detect any differences in weed abundance in corn among treatments with and without cover crops, which suggests that cover crops provided few

Table 5.1: Repeated measures ANOVA for the effects of cropping system diversity on crop yields and weed biomass in the KBS Biodiversity Experiment Plots (BEP) over three years (2002-2004). Significant effects are bolded for clarity.

	Crop yields		Weed Biomass	
	F-value (df)	<i>P</i> > F	F-value (df)	<i>P</i> > F
<i>Corn</i>				
System	15.22 (5,15)	<0.0001	1.66 (5,15)	0.2054
Year	0.19 (2,36)	0.8294	4.26 (2,36)	0.0219
System*year	2.07 (10, 36)	0.0537	1.48 (10,36)	0.1880
<i>Soybean</i>				
System	6.55 (5,15)	0.0020	2.07 (5,15)	0.1269
Year	162.47 (2,40)	<0.0001	8.87 (2,40)	0.0006
System*year	1.82 (10,40)	0.0888	1.00 (10,40)	0.4591
<i>Wheat</i>				
System	5.01 (5,15)	0.0067	17.81 (5,15)	<0.0001
Year	112.15 (2,33)	<0.0001	30.44 (2,33)	<0.0001
System*year	4.61 (9,33)	0.0005	13.15 (9,33)	<0.0001

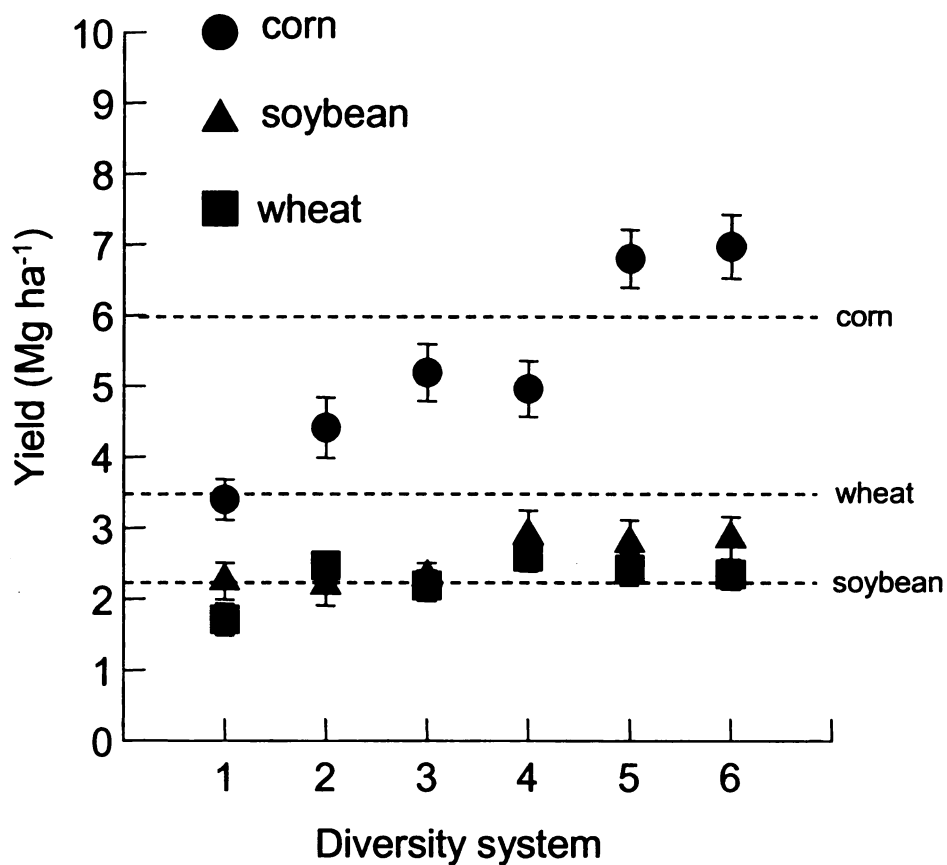


Figure 5.1: Crop yields averaged across three years (2002-2004) in the BEP experiment. Values are means (± 1 SE, $n = 12$). Dotted lines indicate yields (six year average) for each crop in a nearby conventionally managed corn-soybean-wheat rotation. The diversity system treatments are: (1) continuous monoculture, (2) monoculture with one cover crop annually, (3) two crop rotation, (4) three-crop rotation, (5) three-crop rotation with one cover crop annually, and (6) three-crop rotation with two cover crops annually.

additional weed control benefits beyond those of mechanical cultivation (Knezevic et al. 2002).

In contrast, we found strong evidence for differential facilitation of soil nitrogen availability across these diversity treatments. Early season soil nitrogen levels in 2004 had a significant positive effect on corn yield ($r^2 = 0.67$, $P < 0.001$) (Figure 5.2), and was highest in the most diverse systems (systems 4 and 5) and lowest in the least diverse system (continuous monoculture, system 1) (Tukey-Kramer Test, $P < 0.05$). Available soil nitrogen levels remained high in the diverse treatments through the mid-season sampling (23 August) ($F_{5,15} = 4.31$, $P = 0.012$) but decreased to levels that were equivalent across the diversity treatments by the end of the growing season (16 November) ($P = 0.1213$).

Differences in inorganic nitrogen availability and crop yields among the treatments appeared to be driven primarily by the diversity of legume species in the cropping sequence (Drinkwater et al. 1998). These results parallel those from studies in grasslands that have attributed diversity effects to the identity and functional traits of the species (Hooper and Vitousek 1998, Diaz and Cabido 2001, Lambers et al. 2004). In many of these experiments legumes were identified as important drivers of positive diversity-productivity relationships due to their stimulation of over-yielding in non-nitrogen fixing species (Lambers et al. 2004, Hooper et al. 2005). Corn yields increased when the number of legume species in the rotation increased from zero to one (system 1 vs. 2) and from one to two (system 5; Figure 5.1). Effects were similar whether the diversity increase was due to the inclusion of soybean or *Trifolium* cover crops in the

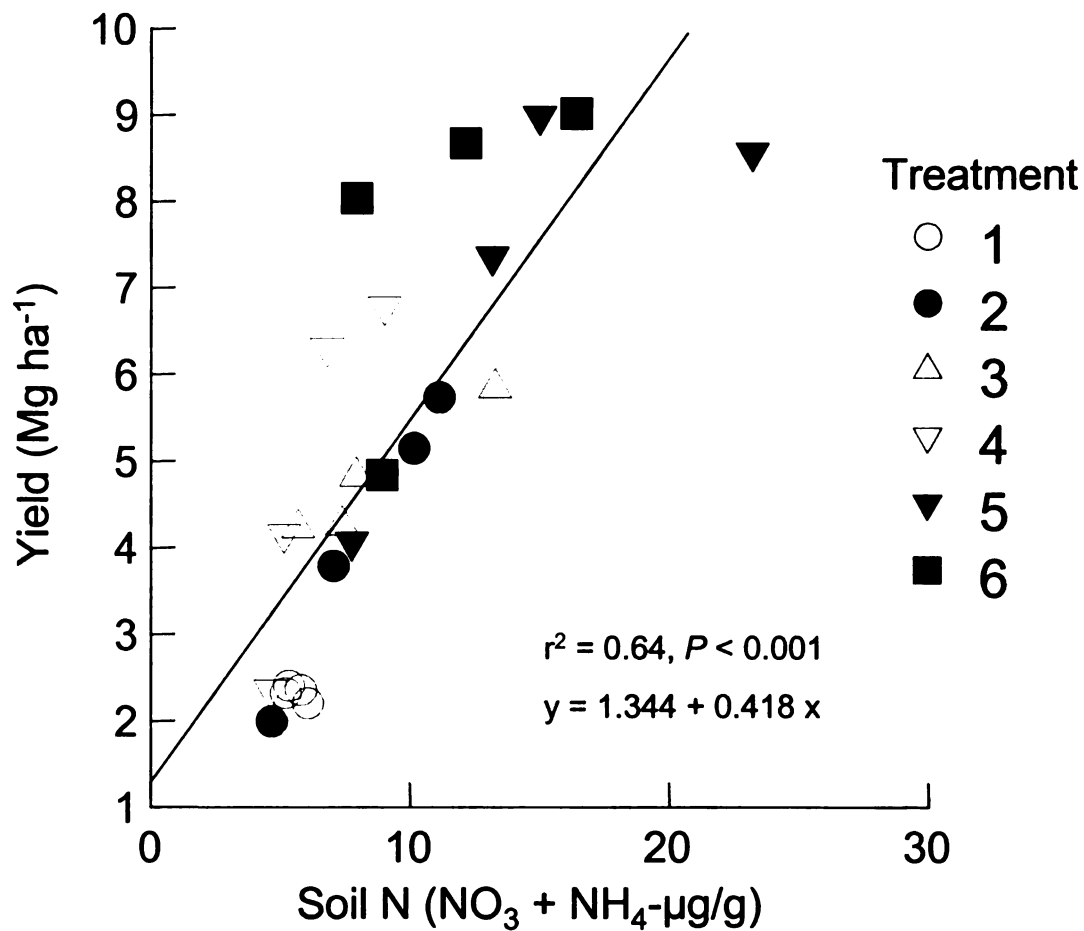


Figure 5.2: Relationship between corn grain yields (October) and early season inorganic soil nitrogen (June) in 2004. Refer to figure 1 for a description of the diversity treatments.

rotation. Increases in the diversity of non-legume crops did not affect yields appreciably (i.e. system 2 vs. systems 3 and 4).

Despite the observed significant effect of legumes on ecosystem processes in this experiment, the fact that continuous monocultures did not out-yield the higher diversity treatments in any of the crops implies that there are benefits to increasing diversity *per se*, beyond simply the inclusion of species of large-effect (Lambers et al. 2004). Other factors may also have contributed to some of the observed effects of cropping system diversity on yields, such as disease and insect pests (Andow 1991, Zhu et al. 2000). Though we did not measure disease or insect damage, we saw no obvious signs of disease or insect damage among the treatments.

It would be naive to suggest that many growers and agricultural researchers are unaware of the beneficial effects that crop rotation and cover crops have on crop performance (Robertson and Swinton 2005). And indeed, many agricultural studies have been performed to examine these effects (Liebman and Dyck 1993, Drinkwater et al. 1998). However, such studies are rarely performed within the broader context of diversity-ecosystem function studies, or not confounded with the application of fertilizer or pesticide inputs (Doucet et al. 1999).

Results of this study show that increasing diversity in cropping systems can lead to significant increases in ecosystem functions related to crop production, and offers further supporting evidence that ecosystem functioning is related to both the number and types of species in a community. In addition, our results further challenge the conventional notions that high external inputs are always necessary to maintain high yields and that environmentally friendly farming strategies will necessarily reduce

farmer's profits (Banks 2004). However, while our results suggest that farmers could reduce their reliance on agricultural inputs by adopting the most diverse cropping systems studied here, a thorough economic analysis will be necessary to determine whether or not the reduced expenditures on chemical pesticides and fertilizers offset the cost of cover crops and the yield reduction during the wheat phase of the rotation.

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CHAPTER 6

CONCLUSIONS AND FUTURE DIRECTIONS

The results from the research presented in this dissertation provide compelling support for the positive role that increasing cropping-system diversity can play in the functioning and production of row-crop agricultural systems. We were able to demonstrate that by manipulating crop rotation and cover crops with complementary resource use requirements and functional traits there are significant positive impacts on soil resources and crop yields. In contrast to the effects on crop yields, manipulation of diversity with crops that have complementary resource use requirements and functional traits appeared to have relatively few impacts on the abundance, composition, and diversity of the weed community when the impacts of cover crops were taken into account. Together these two main results suggest that increasing row crop diversity may reduce the need for intensive weed management, not because weed abundance is reduced, but because increased resource availability decreases the impacts of crop-weed competition.

There are relatively few studies that have looked at the role of diversity in agricultural systems and these too have generally shown beneficial effects of increasing agroecosystem diversity on soil fertility and crop productivity (Vandermeer 1989, Drinkwater et al. 1998, Altieri 1999, Reganold et al. 2001, Westerman et al. 2005). Our results are particularly compelling because we constrained the crop diversity treatments in both the LFL and the BEP studies to reflect potentially realistic cropping situations. In addition, in the BEP study, we varied only biological diversity and not other

components of cropping system management that could potentially be used by growers to further increase crop yields and/or fertility in these systems.

The results of this dissertation help further our understanding of the factors that determine the abundance and composition of weed communities and influence ecosystem processes in row-crop agricultural systems. Results of this dissertation also demonstrate the potential for crop diversity to be used as a management tool and suggest that growers may have viable alternatives to the use of synthetic chemical inputs for weed and crop management.

Future directions

More work will be needed to determine the mechanisms underlying the crop yield responses to increasing diversity observed in this study. This will likely require a detailed study of the soil microbial community to determine whether more diverse cropping systems have a greater number and/or diversity of beneficial soil microorganisms and/or are more resistant to soil pathogen attack (Zak et al. 2003). Determining the relationship between crop diversity and insect pest abundance may also yield clues to the importance of crop diversity in this system; results from past studies comparing numbers of herbivore pests in simple and diverse agroecosystems have been equivocal (Andow 1991, Tonhasca and Byrne 1994, Norris and Kogan 2000).

Future studies of diversity in agricultural systems should address the role of disturbance in mediating diversity-ecosystem function relationships (Huston 1979, Cardinale and Palmer 2002). While management-related disturbances were minimized in the BEP study (i.e. no herbicide applications), tillage and inter-row cultivation were both used to prepare the seed bed and manage weeds early in the growing season. Both

of these factors can have significant impacts on weed communities (Menalled et al. 2001, Davis et al. 2005) and may have contributed to the lack of response to crop diversity we observed in the weed community in both the LFL and BEP studies.

No till-cropping systems may be a more appropriate agricultural system within which to test general theories regarding diversity and ecosystem function because the lack of annual disturbance under no-till cropping may increase the potential for competitive and facilitative interactions among crops and weeds. No-till systems tend also to require more herbicide inputs than tilled systems because weeds cannot be managed mechanically (Donald et al. 2001). Therefore manipulations of diversity that decrease the need for weed management in no-till systems may have particularly significant implications for the development of more sustainable agriculture practices.

While this dissertation addresses the role of diversity in row crop agroecosystems typical of the US Midwest, additional studies will be needed to address whether other types of agricultural systems may also be amenable to management through manipulations of crop diversity. There are many examples of diversified cropping systems in tropical agroecosystems (Vandermeer 1989, Vandermeer et al. 1998, Altieri 1999); however, there are far fewer examples of manipulations of diversity in temperate agricultural systems that do not involve corn, soybean, and wheat (but see Zhu et al. 2000).

Future studies should also address the role of weed diversity on crop-weed competition. For instance, do diverse weed communities compete more or less with crops? Ecological theory would suggest that a diverse weed community would utilize more available niches and fully exploit available resources and so might preempt

resources that would otherwise be available to crops (Tilman 1999). Diverse weed communities might also be more likely to contain species that are strong competitors with crops (Tilman 1999, Davis et al. 2005). Conversely, however, diverse weed communities may be able to suppress dominance among the weed species and so reduce the competitive impact on the crop. In addition, diverse weed communities may also be more efficient at sequestering nutrients early and late in the growing season by serving as 'natural cover crops' that prevent soil nutrients from being leached from the system. Particular weed assemblages might also promote beneficial insects or microbial associations that would reduce herbivory, disease transmission, or suppress populations of soil-borne pests (e.g. nematodes). The potentially beneficial effects of weeds in cropping systems have received relatively little attention (but see Schellhorn and Sork 1997, Norris and Kogan 2000), and more work in this area could prove enlightening.

The density at which weed diversity affects crop yields should also be addressed. There is some indication that at high weed density, diverse weed communities may have fewer effects on crop yields than less diverse weed communities at the same density (Gross and Smith, 2003). Future research will be needed to investigate whether or not this is a general result and the mechanism underlying this observation.

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APPENDIX A

CHAPTER 4 APPENDIX

Appendix A4.1: Indicator values (IV) of species found in spring (S) and fall-tilled (F) fallow treatments from 2002-2004. Nativity indicates whether species were introduced (I) or native (N) to the USA. Life cycle indicates whether species are annual (A), biennial (B), or perennial (P). Species in bold are significant at $P < 0.05$ %.

Species	Nativity (USA)	Life cycle, Growth form	Disturba nce	IV	P
<i>Abutilon theophrasti</i>	I	A, forb	S	90.5	0.001
<i>Amaranthus retroflexus</i>	I	A, forb	S	41.7	0.034
<i>Ambrosia artemisiifolia</i>	I	A, forb	F	65.4	0.007
<i>Arabidopsis thaliana</i>	I	A, forb	F	89.5	0.001
<i>Aster</i> sp.	U	A, forb	F	16.7	0.491
<i>Barbarea vulgaris</i>	I	B, forb	F	16.7	0.495
<i>Capsella bursa-pastoris</i>	I	A, forb	F	25	0.209
<i>Cerastium fontanum</i>	I	B/P, forb	F	16.7	0.483
<i>Chenopodium album</i>	U	A, forb	S	61.2	0.002
<i>Conyza canadensis</i>	N	A/B, forb	F	75	0.001
<i>Daucus carota</i>	I	B, forb	F	25	0.223
<i>Digitaria ischaemum</i>	I	A, C4 grass	S	56.2	0.076
<i>Digitaria sanguinalis</i>	N	A, C4 grass	S	85.9	0.001
<i>Echinochloa crus-galli</i>	I	A, C4 grass	S	8.3	1
<i>Elymus repens</i>	I	P, C3 grass	F	59.1	0.015
<i>Eragrostis cilianensis</i>	I	A, C4 grass	S	41.7	0.034
<i>Erigeron</i> sp.	N	A/B, forb	F	16.7	0.48
<i>Lepidium virginicum</i>	N	A/B/P, forb	F	16.7	0.488
<i>Mollugo verticillata</i>	N	A, forb	S	15.3	0.47
<i>Oxalis stricta</i>	N	P, forb	F	56.8	0.053
<i>Panicum capillare</i>	N	A, C4 grass	F	8.3	1
<i>Panicum dichotomiflorum</i>	N	A, C4 grass	S	67.8	0.018
<i>Plantago lanceolata</i>	I	A/B/P, forb	F	33.3	0.096
<i>Plantago major</i>	N	P, forb	F	41.7	0.023
<i>Poa</i> sp.	I	P, C3	F	41.7	0.029
<i>Polygonum aviculare</i>	I	A/P, forb	F	75	0.002
<i>Polygonum convolvulus</i>	I	A, forb	F	8.3	1
<i>Polygonum persicaria</i>	U	A/P, forb	F	12.2	0.71
<i>Portulaca oleracea</i>	N	A, forb	F	8.3	1
<i>Potentilla norvegica</i>	N	A/B/P, forb	F	25	0.223
<i>Rumex obtusifolius</i>	I	P, forb	F	32.1	0.534
<i>Setaria faberi</i>	I	A, C4 grass	S	75	0.001
<i>Setaria pumila</i>	I	A, C4 grass	S	54.7	0.077
<i>Setaria viridis</i>	I	A, C4 grass	S	66	0.006

Appendix A4.1 (cont'd).

Species	Nativity (USA)	Life cycle, Growth form	Disturba nce	IV	P
<i>Silene latifolia</i>	I	B/P, forb	F	8.3	1
<i>Solanum ptychanthum</i>	N	A, forb	S	8.3	1
<i>Solidago canadensis</i>	N	P, forb	F	33.3	0.105
<i>Stellaria media</i>	I	A/P, forb	F	25	0.225
<i>Taraxacum officinale</i>	U	P, forb	F	81.6	0.001
<i>Trifolium</i> sp.	I	B/P, forb	F	90.9	0.001
<i>Veronica</i> sp.	U	A, forb	F	15.3	0.45

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