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Assembly of weed communities along a crop diversity gradient

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Summary

1. Increasing cropping system diversity is one strategy for reducing reliance on external chemical inputs in agriculture and may have important implications for agro-ecosystem functions related to the regulation of weed populations and community assembly. However, the impacts of cropping system diversity on weed communities have not been evaluated formally in a study comparable with those performed in experimental grasslands, where much of the evidence regarding diversity–ecosystem function has been reported. We performed a field experiment in Michigan, USA, in which we manipulated the number of crop species grown in rotation and as winter cover crops over a 3-year period and in the absence of fertilizer and pesticides, to determine the impact of crop diversity on the abundance, composition and structure of the weed community.

2. Crop diversity treatments 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 2- and 3-year annual rotations with and without cover crops (zero, one or two legume/small grain species). Weed communities were measured each year at peak biomass, with soil resources and light availability being measured over the course of the growing season in the final year of the study.

3. The effects on weed communities of the crop diversity treatments were dependent on rotation phase. In winter wheat, weed abundance and diversity (species richness, H' and D) were lowest in the two highest crop diversity treatments. Across all phases of the rotation, weed community structure was affected more by crop identity than crop diversity *per se*.

4. In general, the effects of crop diversity on weed communities were mainly the result of the presence of cover crops, which had strong effects on soil resource and light levels, particularly in winter wheat.

5. *Synthesis and applications.* Increasing crop diversity in the absence of external chemical inputs can result in changes in soil resource availability without a concomitant increase in the abundance of weeds or a shift to weed communities that are more difficult to manage.

Introduction

Mounting concern over the economic and ecological sustainability of conventional agricultural management

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practices has led to interest in developing alternative cropping systems that are less reliant on synthetic chemical inputs. Ecological theory and experimental evidence suggest that taxonomic diversity plays an important role in the functioning of ecosystems (reviewed in Hooper *et al.* 2005). Increasing cropping system diversity has been advocated as a potential means of decreasing the need for intensive chemical inputs for weed control (Liebman & Gallandt 1997;

Kegode, Forcella & Clay 1999; Liebman & Staver 2001; Westerman *et al.* 2005). However, ecological context can affect diversity–ecosystem function relationships (Schläpfer & Schmid 1999). Many of the agricultural examples suggestive of the role of diversity come from tropical and subsistence-based farming systems (cf. Altieri, Letourneau & Davis 1983; Vandermeer 1989; Trenbath 1999; but see Trenbath 1974). Much of the recent experimental evidence linking plant diversity and ecosystem function has come from studies done in natural and synthetic grasslands, which differ in many ways from agriculturally managed systems (Levine & D'Antonio 1999; Tilman *et al.* 2001; Hooper *et al.* 2005). It is therefore unclear whether the relationships between biological diversity and ecosystem function reported in these systems can be used to develop lower input practices in temperate row-crop agro-ecosystems.

There are a number of reasons why diversity experiments performed in grasslands may have limited relevance to row-crop agro-ecosystems. Plant diversity manipulations in grasslands often span relatively large gradients in diversity, involve high densities of individuals and are rarely subjected to annual soil disturbances (Hector *et al.* 1999; Hooper *et al.* 2005). High densities coupled with low disturbance rates allow the potential for strong interactions among species (Cousens 1985). Inter- and intraspecific 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 assembly and productivity (Tilman *et al.* 1997; Schläpfer & Schmid 1999; Lambers *et al.* 2004; Hooper *et al.* 2005). In contrast, most temperate agricultural systems include only a limited number of crop species and potential species combinations (Jolliffe 1997; Schläpfer & Schmid 1999). Row spacing, planting densities and agricultural management practices, such as cultivation and the applications of fertilizer and herbicides, reduce the density of individuals and the potential strength of species interactions (Weiner, Griepentrog & Kristensen 2001; Cardinale & Palmer 2002). In addition, much of the diversity in cropping systems comes about through crop rotation (Liebman & Dyck 1993; Liebman & Staver 2001). As a result, many of the interactions among crop species are temporally separated, in contrast with grassland systems where many species interact directly (Tilman 1999).

Many studies have compared weed communities in simple and complex cropping systems (cf. Liebman & Dyck 1993; Barberi & Lo Cascio 2001; Moonen & Barberi 2004; Teasdale *et al.* 2004; Smith & Gross 2006). However, there have been no studies in agricultural systems that explicitly manipulate crop diversity, span a relatively broad range of crop diversity and do not include management practices, such as compost and other fertilizer inputs and herbicide applications, that can potentially confound or obscure the effects of diversity *per se* (Liebman & Dyck 1993; Doucet *et al.* 1999; Schläpfer & Schmid 1999).

We report data recorded from 3 years (2002–04) of a long-term cropping system diversity study established in 2000 to examine the direct effects of crop diversity on ecosystem functions and processes in annual row-crop agriculture. We examined five main questions. (i) Does increasing crop diversity affect the overall abundance of weeds? (ii) Does crop diversity affect the diversity and structure of weed communities? (iii) Does the phase of the rotation affect these relationships? (iv) Does variation in the diversity of cover crops and row-crops have similar impacts on crop diversity–weed community relationships? (v) Are the effects of crop diversity on weed communities mediated through changes in soil (specifically N and H_2O) or above-ground (light) resources?

Materials and methods

STUDY SITE

The study was conducted at the biodiversity experiment plots (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). The mean annual temperature at the LTER site is 9·7 °C. Annual precipitation is 890 mm, with about half in the form of snow (http://lter.kbs.msu.edu/siteDescription.html, accessed 29 August 2004).

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. Crop diversity treatments 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 2- and 3-year annual rotations with and without cover crops (zero, one or two legume/small grain species). The six crop diversity treatments had one to three crop species annually and one to six species over a 3-year period (Table 1) and included: (1) continuous monoculture (one sp.), (2) continuous monoculture with one cover crop annually (two spp.), (3) two-crop rotation (two spp.), (4) three-crop rotation (three spp.), (5) three-crop rotation with one cover crop annually (two spp. annually, five spp. over a 3-year rotation) and (6) three-crop rotation with two cover crop species annually (three spp. annually, six spp. over a 3-year 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) were all planted in the same sequence: corn–soybean–wheat. Each phase (hereafter referred to as crop) of the two- and three-crop rotations was present every year, allowing

Table 1. Crop diversity treatments at the KBS LTER BEP. Treatments were established in 2000 and included monocultures and two- and three-crop rotations of corn, soybean and wheat, with and without grass and legume cover crops

| | No. crop species | | | | | |
| | Annual | | | Sum over rotation | | |
Diversity treatment no. and description	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	1–2	3	3	3	6

comparisons to be made among the six crop diversity treatments for each of the three main row-crop species.

Cover crops used in the experiment included red clover *Trifolium pratense* L., crimson clover *Trifolium incarnatum* L. and cereal rye *Secale cereale* L., varying depending on the main crop. In treatments receiving a single cover crop (treatments 2 and 5), *T. pratense* was sown into corn in July and wheat in March, and *S. cereale* was sown into soybean (treatment 2 only) in October. For the highest diversity treatment (treatment 6), each crop was grown with two cover crops: *T. pratense* was planted into corn and wheat and, in July, *T. incarnatum* was planted into soybean. *Secale cereale* was 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 from low to high diversity in a 4 × 5 block. Replicate blocks were separated by 8-m grass buffers. Individual plots measured 9·1 × 27·4 m with no buffer strips between plots. All plots were chisel ploughed and soil finished prior to planting the main crop. Planting date was dependent on weather conditions; however, corn and soybean were planted in late April or May, respectively, and winter wheat in late September–early October. No external inputs (herbicides, insecticides 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

Above-ground weed and cover crop biomass was harvested at peak biomass (August–September) from two 0·25 × 1-m quadrats encompassing the same number of rows and inter-row areas in two central locations in each plot. Weed species composition was determined from a 0·5 × 2-m quadrat that included the area harvested. The sampling location was changed each year to avoid harvesting weeds from areas that had been harvested the previous season. Harvested biomass was separated to species, dried at 65 °C for 48 h, and weighed to the nearest 0·01 g.

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 × 9-m area 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 1 M KCl (20 g) and the rest air-dried and archived. Nitrogen (NO_3^- and NH_4^+) was analysed with an Alpkem 3550 continuous-flow colorimetric analyser (OI Analytical, College Station, TX). Soils were stored at 4 °C and processed within 48 h of collection. In addition, N mineralization rates (28 day incubation at 25 °C) were determined from soils sampled in 2002 and November 2004.

To determine how crop diversity affected seasonal patterns of light environment, the percentage of photosynthetically active radiation (PAR) at the soil surface was measured with an AccuPar LP-80 Ceptometer (Decagon Devices Inc., Pullman, WA) on three dates in 2004: 23 July (mid-season), 22 August (late season) and 19 September (post-season). Measurements were taken at solar noon ± 2 h by placing the ceptometer at ground level parallel to the crop row at two locations within the central 3 × 5-m area 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, crop diversity and year of sampling on weed biomass, weed species richness (number of species per m²) and weed diversity. The initial model included four factors (block, crop, crop diversity and year) and the

factorial combinations of crop, crop diversity and year. Data were analysed as a randomized compete block with repeated measures using PROC MIXED (Little *et al.* 1996) in SAS (SAS Version 8·02; SAS Institute, Cary, NC; SAS Institute 1999). Separate analyses were performed for each crop and for each crop × year when higher order interactions were significant. Treatment means were compared with Tukey's Honestly Significant Difference (HSD) test at the $P < 0.05$ level of probability when main effects were significant. In all analyses, crop, crop diversity and year were considered fixed effects; the block effect was considered random.

We chose to investigate several different measures of weed community diversity because each emphasizes different aspects of community structure (Magurran 1988) and the predicted effects of crop diversity on weed community structure are somewhat unclear (Liebman & Staver 2001). The diversity measures analysed were Shannon diversity, $H' = -\Sigma p_i(\log p_i)$, where p_i is the proportion of biomass accounted for by species *i* per sample (Magurran 1988), Evenness, $E = H'/\ln(\text{species richness})$, and Simpson's index of diversity, $D = 1 - \Sigma p_i^2$ (McCune & Grace 2002). Weed biomass and species richness data were log- and square-root transformed, respectively, to reduce heteroscedasticity. Analysis of variance was used to analyse treatment effects on soil resource and light data.

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, all species abundances were $\log(x + 1)$ transformed. A dissimilarity matrix using Bray–Curtis coefficients was then calculated from the transformed species abundance values. Very rare species (those occurring in fewer than 5% of the plot years) were deleted prior to analysis.

We 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 2002–2004. For the multivariate linear model, three factors (block, crop diversity and year), and the interaction between crop diversity and year were analysed using a randomized complete block design with repeated measures. The 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-selection stepwise multivariate multiple regression (McArdle & Anderson 2001; Anderson 2003) was performed to characterize weed community structure 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 & Grace 2002) on $\log(x + 0.1)$-transformed species composition and abundance data from 2004. Ordination was performed for each crop separately to improve our ability to detect differences among treatments. Correlations between the NMDS ordination axes scores, soil resource and light levels were also calculated to examine the strength of the relationship between community structure and abiotic variables using the PC-ORD software package (McCune & Mefford 1999).

For each crop, species-level responses to the diversity treatments were analysed with indicator species analysis (ISA; Dufrene & Legendre 1997) using crop diversity treatment as the grouping variable. ISA combines information regarding abundance and faithfulness of occurrence of a species in a particular group or treatment (McCune & Grace 2002). Indicator values (IV) were calculated by multiplying the relative abundance and relative frequency of each species in each crop diversity treatment in 2004. For each species, the significance of the highest indicator value (corresponding to the crop diversity treatment with which it was most associated) was tested with a Monte Carlo procedure (1000 permutations) at the $P < 0.05$ level of probability. ISA was also performed on weed presence/absence data across diversity treatments, using crop as the grouping variable, to determine the strength of species association with each crop.

Back-transformed data are presented in all tables and figures; in figures, box-plots are used to indicate the range of variability in the observations.

Results

WEED BIOMASS

Weed biomass was affected by crop, crop diversity, year of sampling and the interaction between all three factors (three-way interaction, $F_{29,109} = 2.56$, $P = 0.0002$). Subsequent repeated-measures analyses for each crop showed that most of the effects across crops were driven by a significant crop diversity–year interaction in wheat ($F_{9,33} = 13.15$, $P < 0.0001$). In all 3 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 6, Tukey HSD, $P < 0.05$; Fig. 1). While there was a significant effect of year on weed biomass in both corn and soybean (corn $F_{2,36} = 4.26$, $P = 0.02$; soybean $F_{2,40} = 13.22$, $P < 0.001$), there was no significant crop diversity effect or crop diversity–year interaction for either crop ($P > 0.05$).
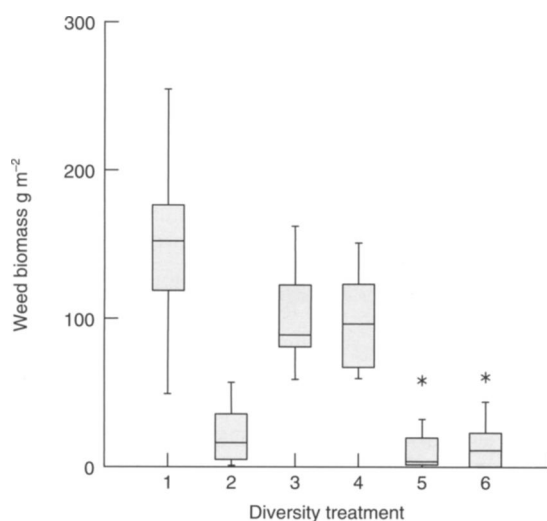
Fig. 1. Box-plots showing variation around the median for weed biomass in winter wheat for each crop diversity treatment from 2002 to 2004 (see Table 1 for a description of the diversity treatments). The black line within the grey box represents the median; the grey box represents 50% of the data; whiskers represent the 10th and 90th percentiles; asterisks indicate outliers; $n = 12$. Treatments 2, 5 and 6 had cover crops.

SPECIES RICHNESS AND DIVERSITY

Weed species richness was affected by the interaction of crop, crop diversity and year (three-way interaction, $F_{29,109} = 4.36$, $P < 0.0001$). Subsequent repeated-measures analysis revealed significant crop diversity–year interactions in all three crops (two-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 crop diversity treatments were only significant in 2003 ($F_{5,15} = 3.99$, $P = 0.0168$), with treatment 2 (continuous monoculture with cover crop) having lower weed species richness than treatment 4 (three-crop rotation, Tukey HSD, $P < 0.05$). In soybean, differences among crop diversity treatments were significant only in 2003 ($F_{5,19} = 5.82$, $P = 0.002$); treatments 5 and 6 (three-crop rotation with one and two cover crop species, respectively) had fewer species than treatment 3 (two-crop rotation) (Tukey HSD, $P < 0.05$). In contrast, there were significant differences in weed species richness among treatments planted to wheat in all 3 years, and the differences among crop diversity treatments increased over time (Fig. 2). In general, wheat grown in treatments that included cover crops (treatments 2, 5 and 6) had lower weed species richness compared with treatments without cover crops (Tukey HSD, $P < 0.05$). Species richness did not differ between treatments 1, 3 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 analysed. Weed species evenness was affected by crop and year of sampling (crop $F_{2,51} = 17.18$, $P < 0.0001$; year $F_{2,109} = 4.92$, $P = 0.009$) but not crop diversity, and was lower in soybean compared with corn and wheat. In contrast, analysis of the Shannon and Simpson's diversity indices revealed a three-way interaction between crop, crop diversity and year of sampling (three-way interaction, H' $F_{29,109} = 2.0$, $P = 0.006$; D $F_{29,109} = 1.86$, $P = 0.012$). Separate repeated-measures analyses for each crop revealed that crop diversity treatment effects on both diversity measures were similar and 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, $P < 0.05$; Fig. 3).

COMMUNITY COMPOSITION AND STRUCTURE

A total of 54 different weed species was observed over the 3 years of this experiment; of these, 34 were observed in corn, 31 in soybean and 47 in wheat. The crop effect 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 (Fig. 4). ISA indicated that species that were significantly associated with winter wheat included broadleaf and grass species such as *Polygonum aviculare* L. and *Panicum dichotomiflorum* Michx. Species associated with corn and soybean included broadleaf species such as *Stellaria media* (L.) Vill. and *Chenopodium album* L. Overall, more weed species showed significant associations with winter wheat than corn or soybean (see Table S1 in the supplementary material).
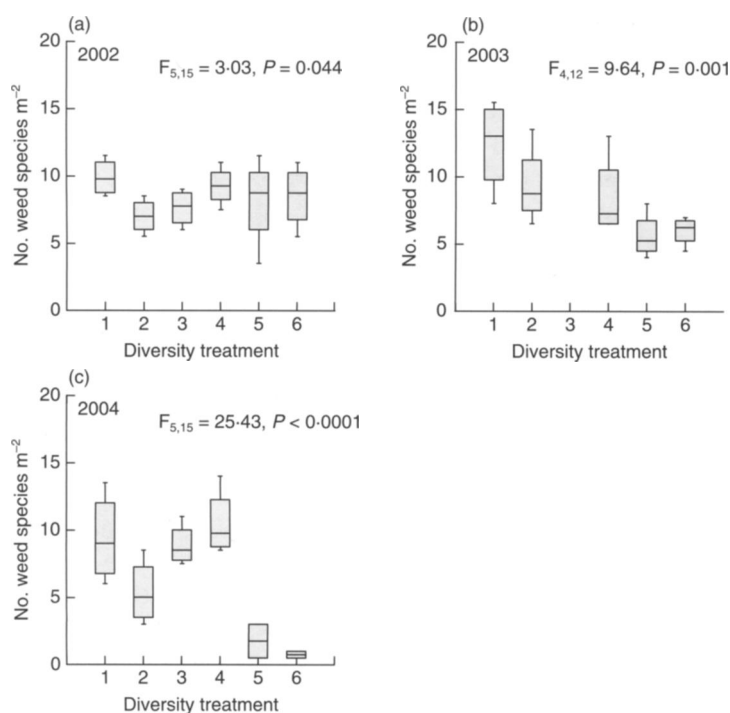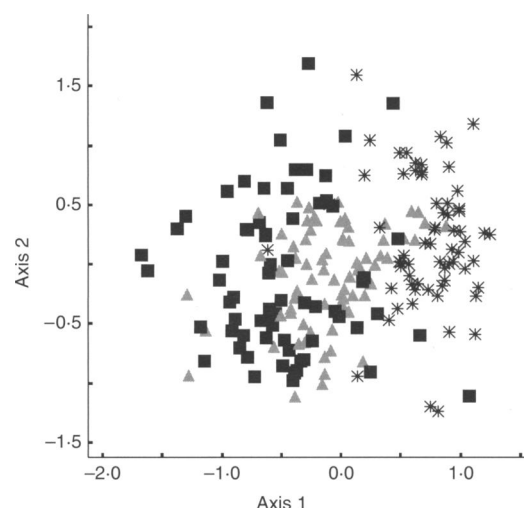

Fig. 2. Box-plots showing variation around the median for number of weed species in winter wheat for each crop diversity treatment from 2002 to 2004 (see Table 1 for a description of the diversity treatments). The black line within the grey box represents the median; the grey box represents 50% of the data; whiskers represent the minimum and maximum values; $n = 4$. Treatments 2, 5 and 6 had cover crops.
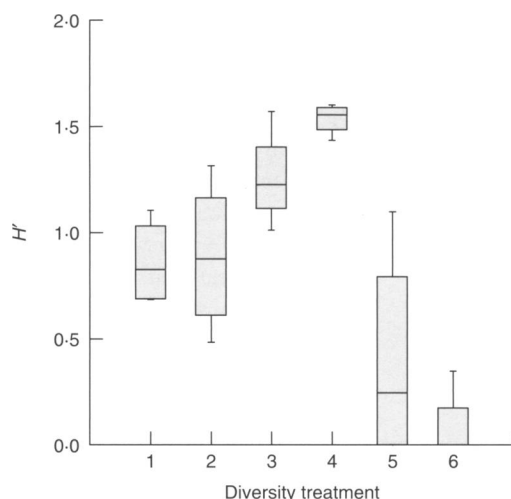
Fig. 3. Box-plots showing variation around the median for Shannon diversity (H') of the weed community in 2004 in crop diversity treatments planted to winter wheat (see Table 1 for a description of the diversity treatments). The black line within the grey box represents the median; the grey box represents 50% of the data; whiskers represent the minimum and maximum values; $n = 4$. Treatments 2, 5 and 6 had cover crops.
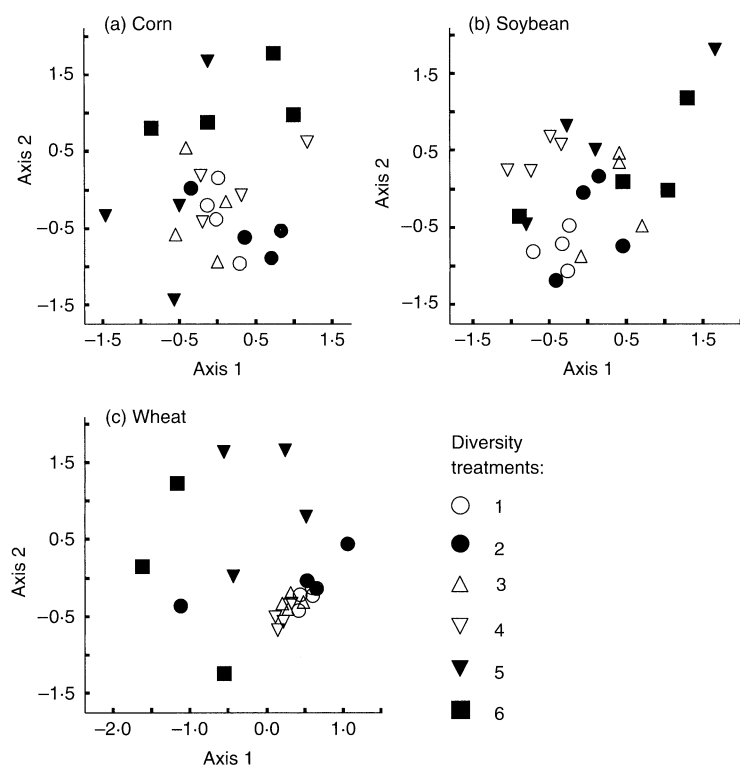

Fig. 4. Plot scores for the first two most explanatory axes of NMDS analysis of weed composition (presence/absence) from 2002 to 2004 in six cropping system diversity treatments (Table 1) at the BEP at the LTER at KBS, Hickory Corners, Michigan, USA. NMDS: stress = 17·992, $P < 0·05$, cumulative r^2 for axes 1 and 2 = 0·638. Symbols: triangles, corn; squares, soybean; crosses, winter wheat.

In addition to the strong effects of crop, we were also able to detect significant crop diversity effects on weed community structure. The distance-based multivariate analysis indicated that, for each crop, weed community structure was affected by crop diversity, year of sampling and their interaction (see Table S2 in the supplementary material). NMDS ordination of the species abundance data from 2004 showed that, for each crop, treatment replicates with higher crop diversity tended to ordinate separately from replicates with lower crop diversity (Fig. 5). This was particularly evident in wheat; replicates without cover crops clustered together and were distinct from those with cover crops, which were fairly homogeneously dispersed in ordination space (Fig. 5c).

Associations between certain weed species and the crop diversity treatments were reflected in the indicator species analysis performed on data from each crop in 2004. In corn, the analysis indicated that *Poa compressa* L. was most associated with treatment 3 (two-crop rotation, ISA, IV = 53·6, $P = 0·028$). In soybean, three weed species showed strong associations with particular crop diversity treatments. *Taraxacum officinale* G.H. Weber ex Wiggers and *Digitaria sanguinalis* (L.) Scop. were both strongly associated with the soybean phase of the three-crop rotation without cover crops (treatment 4, ISA, *T. officinale* IV = 70·8, $P = 0·003$; *D. sanguinalis* IV = 53·3, $P = 0·042$), and *Setaria faberi* Herrm. was associated with soybean grown in continuous monoculture (treatment 1, ISA, IV = 47·7, $P = 0·023$). Indicator species analysis identified five weed–crop diversity treatment associations in wheat. *Chenopodium album, Oxalis stricta* L. and *T. officinale* were associated with the wheat phase in treatment 4

(three-crop rotation without cover crops, ISA, *C. album* IV = 84·0, $P = 0·001$; *O. stricta* IV = 70·3, $P = 0·001$; *T. officinale* IV = 49·0, $P = 0·006$); *Elymus repens* (L.) Gould was associated with the wheat phase in treatment 3 (two-crop rotation, IV = 61·3, $P = 0·029$); and *Digitaria ischaemum* (Schreb.) Schreb. ex Muhl. was associated with treatment 1 (continuous monoculture, IV = 51·2, $P = 0·001$).

SOIL RESOURCES AND LIGHT

In 2002, 2 years after the crop diversity treatments had been initiated, there were indications of treatment effects on soil resources; however, these were variable and depended on the crop (ANOVA, crop by crop diversity interaction, $F_{10,51} = 2·91$, $P = 0·006$). Across plots that had been sown to winter wheat in autumn 2001, soil N measured in November 2002 was significantly higher in treatment 2 (monoculture with cover crops) compared with treatments 3, 4 and 5 (Tukey HSD, $P < 0·05$). However, there were no differences in soil N among plots sown to corn and soybean. Treatment effects were also not apparent among plots that were sown to wheat in October (a month prior to sampling) ($P = 0·093$).

Two years later (4 years after treatments were initiated) crop diversity treatment effects were more pronounced but still variable among crops. Soil N pools measured in June 2004 showed a significant effect of crop diversity in corn and wheat but not in soybean (interaction $F_{10,51} = 2·98$, $P = 0·005$) (Fig. 6a–c). In August, crop diversity treatment effects on soil N pools were still significant in corn and wheat. In corn, soil N pools were higher in treatment 5 than treatments 1, 3 and 4;

Fig. 5. Plot scores for the first two most explanatory axes of NMDS analysis of weed abundance and composition in six diversity treatments (Table 1) in corn (a), soybean (b) and winter wheat (c) in 2004. 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, $P < 0·05$, $r^2 = 0·711$.
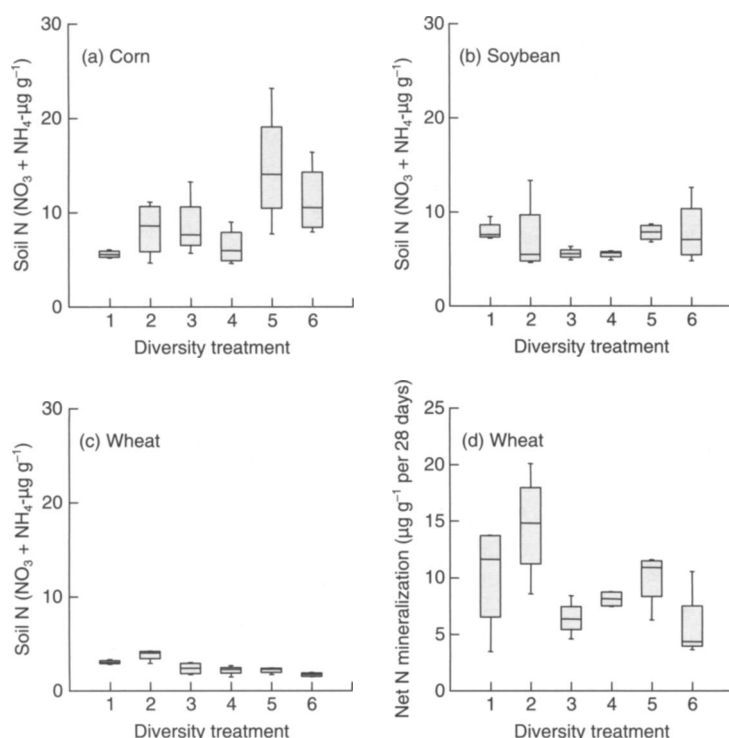
Fig. 6. Box-plots showing variation around the median for inorganic N pools (NO_3-N + NH_4-N) measured in June 2004 in (a) corn, (b) soybean and (c) winter wheat and (d) net mineralization after 28 days in winter wheat for each crop diversity treatment in 2004 (see Table 1 for a description of the diversity treatments). The black line within the grey box represents the median; the grey box represents 50% of the data; whiskers represent the minimum and maximum values; $n = 4$. Treatments 2, 5 and 6 had cover crops. Note different y-axis scale in (d).

in wheat, N pools were higher in treatment 2 than treatments 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 with crop diversity treatment (interaction $F_{10,51} = 5·21$, $P < 0·0001$), probably reflecting the recent planting to wheat (in October) in some of these treatments. Similar to 2002, soil N pools in plots sown to wheat in 2003 were higher in treatment 2 than treatments 3, 4, 5 and 6. In November 2004 net soil N mineralization varied among plots that were sown to wheat in 2003 (Fig. 6d) but not those sown to corn and soybean in 2004 (interaction $F_{10,51} = 2·89$, $P = 0·0062$). There were also significant treatment differences in N mineralization among plots that were sown to wheat in October 2004 ($F_{5,15} = 5·91$, $P = 0·003$), with treatment 2 (continuous monoculture with cover crop) having higher N pools than treatments 3, 4 and 6 (Tukey HSD, $P < 0·05$). This may reflect the relative importance of cover crops vs. soybean as an N source, as treatments 3, 4 and 6 were planted to soybean the previous spring (May 2004).

Soil moisture levels measured in late June 2004 were lowest in wheat ($F_{2,51} = 23·58$, $P < 0·0001$) but were unaffected by crop diversity ($P = 0·0708$). In late August, soil moisture levels differed among 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 with soybean and wheat (Tukey HSD test, $P < 0·05$). Across all crops, soil moisture in August was highest in treatment 1 (monoculture) and lowest in treatments 5 and 6 (three-crop rotation with cover crops). By 16 November there were no significant differences in soil moisture related to crop or crop diversity treatment (data not shown).

Light levels (% PAR) at ground level in late July differed among diversity treatments only in wheat (interaction $F_{10,42} = 2·14$, $P = 0·0426$) and were lowest in the highest diversity wheat treatments, particularly those with cover crops (Tukey HSD test, $P < 0·05$). 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 continuous monoculture (treatment 1). In wheat, they were highest in the two- and three-crop rotation without cover crops. By 19 September, light levels differed among crop 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 with those without cover crops (Fig. 7).

RELATIONSHIP BETWEEN RESOURCES AND WEED COMMUNITIES

The relationship between resource levels and weed community structure was investigated by examining correlations between resource variables (in 2004) and the NMDS ordination axes scores. Data on cover crop biomass were also included in these analyses. There
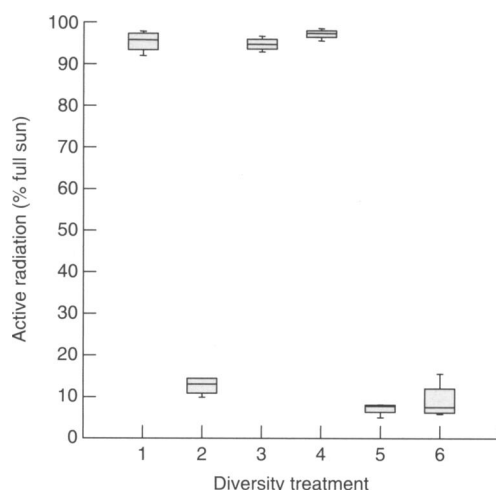
Fig. 7. Box-plots showing variation around the median for light levels at the soil surface in winter wheat for each crop diversity treatment on 19 September 2004 (see Table 1 for a description of the diversity treatments). The black line within the grey box represents the median; the grey box represents 50% of the data; whiskers represent the minimum and maximum values; $n = 4$. Treatments 2, 5 and 6 had cover crops.

was little correlation between resource levels 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 scores in wheat, the strongest of which were those related to cover crop biomass and light availability (see Table S3 in the supplementary material).

Relationships between the weed community and soil resources and light were also investigated using forward-selection stepwise multivariate multiple regression. The analysis indicated that no resource variables explained any of the variation in weed community structure in corn (smallest P-value = 0.09) (data not shown). In soybean, light level (PAR) late in the season was identified as a significant predictor of weed community structure ($r^2 = 0.08$, $P = 0.047$). When forward selection was applied, two variables, late season light and mid-season soil moisture, were identified as significant and together explained 17% of the variance in community structure in soybean (see Table S4 in the supplementary material). Grouping the separate measurements of each resource variable into four factors (H_2O, N, light and cover crop) 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 (see Table S4 in the supplementary material). Grouping the variables improved the strength of the relationship, with each of the four factors separately

explaining more than 12% of the variance in community structure (data not shown). However, forward selection of the model with the variables grouped indicated that only light was a significant predictor of community structure, explaining 24% of the variation ($P = 0.0001$).

Discussion

With respect to the five main questions addressed in this study, we found that varying the diversity of crops within a cropping system can have significant impacts on weed communities but that the effects are strongly crop-species specific. The impacts of crop diversity on light availability and soil resources, and their effects on weed communities, are also crop-species specific. In wheat, differences in weed abundance and community structure among crop diversity treatments appeared to be driven mainly by the presence of cover crops and their impacts on light availability. In contrast, 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 general, the use of cover crops, rather than crop rotation or crop diversity *per se*, was the primary determinant of weed community structure in this system.

The suppressive effects of cover crops have been shown to vary with cover crop biomass (Akemo, Regnier & Bennett 2000) and, in our study, cover crop biomass was much higher in wheat than corn or soybean. At the time weeds were harvested (August–September), cover crop biomass in the wheat phases of treatments 2, 5 and 6 was 10–20 times higher than these same treatments in corn and soybean (160–277 g/m² compared with less than 12 g/m²). Differences in cover crop biomass among crops were probably the result of differences in planting date, as cover crops were sown in wheat earlier (March) compared with corn and soybean (July).

The impacts of cover crops on weed abundance and resource levels in this study are consistent with observations from other studies, showing that management systems that include cover crops often have lower weed abundance and higher soil fertility (Teasdale 1996; Drinkwater, Wagoner & Sarrantonio 1998; Snapp *et al.* 2005). Because neither fertilizers nor herbicides were used in this study, the observed effect 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, Janke & Rossoni-Longnecker 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 of weed communities in treatments planted with cover crops (treatments 2, 5 and 6; Figs 2 and 3) and the strong associations between certain weed species and the crop diversity treatments. The three cover crop species used in this study have all been shown to have allelopathic properties (Creamer *et al.* 1996; Davis & Liebman 2003), although it is

unclear whether, and to what extent, allelopathy, rather than direct competitive interactions, was responsible for the observed effects on weed suppression in this study.

The impact of cover crops on resource levels and weed communities observed in our study is consistent with observations from diversity studies performed in grassland systems that report strong species-specific effects on ecosystem functions (Tilman *et al.* 1997; Grime 1998; Schläpfer & Schmid 1999; Lambers *et al.* 2004; Hooper *et al.* 2005). In some of these experiments, 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, we found no evidence that weeds benefited from the increased N provided by the legume cover crops or rotations with soybean.

The ecological literature suggests that experimental communities richer in species are more resistant to invasion as a result of species-rich communities having fewer unexploited niches (cf. Levine & D'Antonio 1999; Fargione & Tilman 2005). While our study manipulated only a narrow range of crop species in a year, one main crop and one or two cover crop species, we found effects of crop diversity on invasion in wheat that appear to have been a result of differences in light availability. Light levels were lower in wheat with cover crops than monocultures, and this reduction in light may have reduced weed colonization (Kitajima & Tilman 1996).

Increasing the number of crops in a rotation (temporal diversity) had relatively little effect on the structure of the weed community. This was somewhat surprising given that many agronomic studies have reported significant effects of crop rotation on weed abundance and diversity (cf. Liebman & Dyck 1993; Cardina, Herms & Doohan 2002; Legere & Samson 2004). However, several recent studies have reported little or no effect of crop rotation on weed communities (Doucet *et al.* 1999; Barberi & Lo Cascio 2001), particularly when the effects of associated management practices are taken into account. For instance, Doucet *et al.* (1999) reported that weed communities in corn in the 10th year of a corn–soybean–wheat rotation were similar to continuous corn. The lack of associated herbicide applications in our system may have decreased the mortality factors that weeds are more typically subjected to in diversified crop rotations under chemical management (Liebman & Gallandt 1997; Westerman *et al.* 2005). The lack of a consistent rotation effect may also indicate that crop rotation alone is not a particularly strong filter on the assembly of weed communities (Booth & Swanton 2002; Cardina, Herms & Doohan 2002).

Differences in weed community composition between winter wheat and corn and soybean in our study were most probably the result of the timing of tillage and planting of each crop and variation in germination and emergence times among weed species (Keever 1979; Smith 2006). Other studies have noted similar differences between the weedy flora in autumn- and spring-sown crop species (Andersson & Milberg 1998; Hald 1999).

The observation that neither crop rotation nor diversity *per se* had strong effects on weed communities does not negate the importance of incorporating diversity within agricultural management systems. Numerous studies have shown the beneficial ecosystem-level impacts of diversified cropping systems, particularly when legumes are included (cf. Drinkwater, Wagoner & Sarrantonio 1998; but see Scherer-Lorenzen *et al.* 2003). Indeed, our results, when considered together, suggest that management aimed at enhancing crop diversity for improvement of other aspects of cropping system sustainability, such as soil fertility and natural enemy abundance, need not necessarily be accompanied by a shift towards novel or more difficult to manage weed communities. A better understanding of how crop functional characteristics constrain the assembly of weed communities in diversified cropping systems may provide additional opportunities for enhancing weed suppression across the entire rotation sequence.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article.

Table S1. Results of indicator species analysis

Table S2. Results of distance-based multivariate analysis of variance

Table S3. Correlations with NMDS axis scores

Table S4. Results of distance-based multivariate multiple regression

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