

Effects of Crop Diversity on Agroecosystem Function: Crop Yield Response

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ABSTRACT

Understanding the role of diversity in the functioning of ecosystems has important implications for agriculture. Previous agricultural research has shown that crop rotation and the use of cover crops can lead to increases in yield relative to monoculture; however, few studies have been performed within the broader context of diversity–ecosystem function theory and in the absence of chemical inputs. We performed a field experiment in SW Michigan, USA, in which we manipulated the number of crop species grown in rotation and as winter cover crops over a 3-year period to test if varying the number of species in a rotation affected grain yield, a critical metric of ecosystem function in row-crops. The experimental design was unique in that no fertilizer or pesticides were used, and the only management variable manipulated was number of species in the rotation, thus providing a strong comparison to grassland diversity–ecosystem function experiments. Treatments included continuous monocultures of three row-crops, corn *Zea mays* L., soybean *Glycine max* (L.) Merr., and winter wheat *Triticum aestivum* L., and 2- and 3-year annual rotations with and without cover crops (zero, one, or two legume/small grain species), encompassing a range of crop diversity from one to six

species. Crop yields and weed biomass were measured annually for 3 years and plant available soil nitrogen was measured over the course of the growing season in the final year of the study. In all 3 years, corn grain yield increased linearly in response to the number of crops in the rotation. Corn yields in the highest diversity treatment (three crops, plus three cover crops) were over 100% higher than in continuous monoculture and were not significantly different from the county average for each of the 3 years despite the absence of chemical inputs. Corn yields in the diversity treatments were strongly correlated with the availability of inorganic soil nitrogen, which was likely influenced by the number of different legume species (crops and cover crops) present in the rotation. In soybean and winter wheat, yield differences among crop diversity treatments were also significant, but of lower magnitude (32 and 53%, respectively), and showed little direct relationship to the number of crop species grown in a rotation. Results demonstrate that agricultural research motivated by ecological theory can provide important insights into the functioning of agroecosystems and enhance our understating of the linkages between diversity and ecosystem function. Importantly, these results suggest that reduced chemical inputs do not necessarily result in yield penalties and provide support for incorporation of crop or species diversity when determining how ecosystem services can be included in food, fiber, and biofuel production.

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INTRODUCTION

The intensification of modern agricultural production systems has led to increases in world food production at the expense of cropping system and wild-land diversity and environmental health (Kleijn and Verbeek 2000; Tilman and others 2001; Robertson and Swinton 2005). Conversion of species-rich wild-lands to large-scale, industrial agricultural production, often as monocultures, has reduced the potential for species interactions important in community and ecosystem-level regulation of nutrient cycling and pest populations, which must now be replaced by inputs of synthetic fertilizer and pesticides (for example, Drinkwater and others 1998; Pimentel and others 2005). The environmental impacts associated with such inputs have led many to question the sustainability of conventional agricultural practices (Matson and others 1997; Tilman 1999; Robertson and others 2004). As agriculture changes to meet the food, fiber, and fuel demands of a growing global population, development of alternative management practices that maintain yields while minimizing the need for external inputs will be a necessary step to ensure economic and environmental sustainability (Hill and others 2006).

The relationship between species diversity and ecosystem function may have substantive implications for the development of cropping systems that are economically and ecologically sustainable (Liebman and Davis 2000; Mäder and others 2002). Although there are many agricultural examples that suggest diversity may play a role in agroecosystem function, most of these examples are from comparisons of simple and complex rotations, tropical and subsistence-based farming systems (compare Altieri and others 1983; Vandermeer 1989; Trenbath 1999; but see Trenbath 1974), or temperate systems in which crop diversity is not the only factor that is manipulated (Vyn and others 2000; Pedersen and Lauer 2003; Gan and others 2003; Porter and others 2003). Consequently, the relationship between crop diversity and agroecosystem function remains poorly understood. In contrast, there is considerable empirical evidence of a positive relationship between species diversity

and ecosystem function from temperate grassland studies which manipulate species richness in space by varying numbers of species planted into plots contemporaneously (Tilman and others 1996; Mäder and others 2002; Hooper and others 2005). Although the particular mechanisms driving the relationship between diversity and ecosystem functions such as nutrient cycling and productivity in experimental grassland assemblages are often debated, the effects appear to operate most strongly at relatively low levels of diversity (Huston 1997; Tilman 1999; Lambers and others 2004; Hooper and others 2005). Because row-crop systems are managed to maintain a relatively low number of species (usually a single crop), increased diversity in cropping systems, through the sequential addition of crop species (that is, crop rotational 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 rotational diversity (hereafter crop diversity) was manipulated through the establishment of sequential monocultures of row and cover crop species. Crops were grown without external chemical inputs of pesticides or fertilizer to avoid the confounding effects of differential inputs and maximize our ability to detect biological effects of crop system diversity on ecosystem functions. Crop yields, weed abundance, and soil nitrogen were measured over the course of the study to determine how crop diversity affects these important ecosystem variables relevant to row-crop production.

MATERIALS AND METHODS

Site Description

The study was conducted at the Biodiversity Experimental Plots (hereafter BExP, <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. The BExP was designed explicitly to test hypotheses related to the functional role of diversity in cropping systems, which, because of logistical and design issues, could not be examined

on the main LTER experimental site. 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 (Crum and Collins 1995). 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>).

Experimental Design

Crop diversity treatments at the BExP were initiated in spring 2000 and included 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 per year). We considered the total number of different crop species present within a year (annual diversity) and over the entire 3-year rotation (rotational diversity) to represent the overall level of crop diversity in each treatment. The six diversity treatments thus ranged from one to three crop species annually and one to six species over a 3-year rotation period and included: (1) continuous monoculture, (2) continuous monoculture w/ one cover crop species annually, (3) two-crop rotation, (4) three-crop rotation, (5) three-crop rotation with one cover crop species annually, and (6) three-crop rotation with two cover crop species annually (Table 1). The crop species and rotation sequences used in the treatments were selected with the goal of maintaining relevance to current production practices; consequently, only three of the possible sequences were included in the design of the two-crop rotation (treatment 3): corn–soybean, soybean–corn, and soybean–winter

wheat. The three-crop rotations (treatments 4–6) were all planted in the same sequence: corn–soybean–winter wheat. Each phase (entry point) of the two- and three-crop rotations was present every year, allowing comparisons of diversity effects to be made for each of the three crop species across years.

The cover crops planted varied depending on the grain crop and included red clover (*Trifolium pratense* L.), crimson clover (*Trifolium incarnatum* L.), and cereal rye (*Secale cereale* L.) (Figure 1). In treatments 2 and 5, which had only a single cover crop, red clover was sown into corn in July and into wheat in March. In soybean, cereal rye was sown in October (treatment 2 only) and crimson clover was sown in July (treatment 5 only). For the highest diversity treatment (3 spp/yr; treatment 6) each crop was grown with two cover crops: red clover was planted into corn and wheat as above; crimson clover was planted into soybean (June). The cereal rye cover was sown in October into plots to be planted to corn and soybean the following year. One result of increasing diversity of the cropping system was that the period during which crops were present on the soil was extended (Figure 1).

The diversity treatments were randomly applied to plots in three linear blocks; in the fourth block, treatments were arranged in 4 × 5 blocks and planted in sequential order of decreasing diversity. Treatments within this block were considered randomized in subsequent analyses. Individual plots measured 9.1 m × 27.4 m with no buffer strips between plots. Replicate blocks were separated by 8 m grass buffers that were routinely mowed. All plots were chisel plowed and soil-finished prior to planting the grain crop. Corn and soybean were planted in late April or May and winter wheat was planted in late September or

Table 1. Crop Diversity Treatments at the KBS Biodiversity Experimental Plots (BExP)

Treatment	Description	No. crop species					
		Annually			Over rotation		
		Crops	Cover	Total	Crops	Cover	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

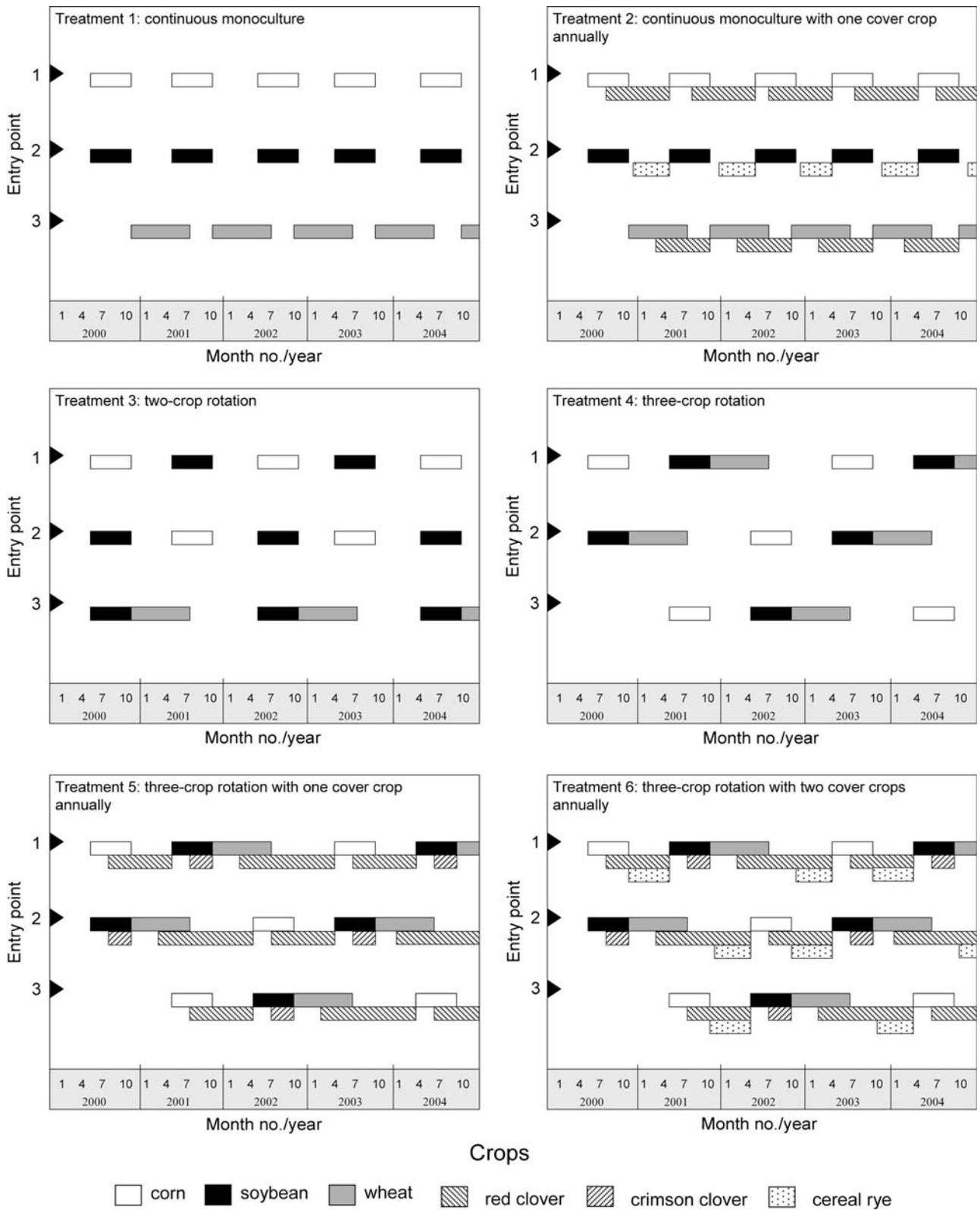


Figure 1. Schematic representation of the six crop diversity treatments at the KBS Biodiversity Experimental Plots (BExP). Bars indicate approximate length of time, from crop sowing to harvest/incorporation into the soil, that each species is present in each of the three entry points. Months are 1, January; 4, April; 7, July; 10, October

early October. No external chemical inputs (pesticides or fertilizer) were applied to any of the treatments; periodic inter-row cultivations (cultivation/rotary hoeing) were performed in corn and soybean early in the season to control weeds.

Plant Sampling

Crop yields were determined annually with a plot combine using standard practices (http://lter.kbs.msu.edu/Data/LTER_Metadata.jsp?Table=KBS032-001). Winter wheat was harvested in July and soybean and corn was harvested in October and November, respectively. Crop yields (Mg ha^{-1}) were calculated assuming 13% (wheat and soybean) or 15% (corn) moisture. Annual average yield data for the county (Kalamazoo County) and state of Michigan were obtained from the USDA Agricultural Statistics Data Base (<http://www.nass.usda.gov/index.asp>) to provide a local and regional conventional baseline to compare to yields in this experiment.

Aboveground weed biomass was harvested at peak biomass (August–September) from two 0.25×1 m quadrats placed perpendicular to the crop rows located near the center of each plot. The location of sampling was changed each year to avoid areas that had been harvested the previous season. Harvested weed biomass was dried at 65°C for at least 72 h and weighed to the nearest 0.01 g.

Soil Nitrogen

Inorganic soil nitrogen (NO_3^- and NH_4^+) was measured at three times in 2004 to assess the availability of N at several stages of the growing season. Sampling dates were 28 June, 23 August, and 16 November, approximately 1 month after planting, and 1 month prior to and after harvest, respectively, of corn and soybean. Soils were sampled to a depth of 25 cm (four-2 cm diameter cores) within the central 3×9 m of each plot from both the rows and inter-row areas. 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 1 M KCl (20 g) and the rest air-dried and archived. Inorganic nitrogen (NO_3^- and NH_4^+) was determined with an AlpKem 3550 continuous-flow colorimetric analyzer (OI Analytical, College Station, TX, USA). Soils were stored at 4°C after collection and were processed within 48 h 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 3 years (2002–2004). To analyze differences among treatments we used a three factor (diversity treatment, block, year) repeated-measures ANOVA, with year as the repeated factor (SAS Proc Mixed procedure) followed by a Tukey test at $P = 0.05$. To place our crop diversity results within a broader agronomic context, we used a single-sample *t*-test to statistically compare our annual BExP treatment yields to those obtained by local producers. Because yields at the county level (Kalamazoo County) tended to be higher than those at the state level, we focused our analyses on county yields, but provide state-level yields for comparison. To determine yield responses across the entire 3-year sequence of each treatment, total grain yields (yields of all harvestable grain produced over the study period) were assessed and analyzed with a two-factor (diversity treatment and block) ANOVA. BExP crop yields in 2004 were also analyzed using total numbers of crop species, weed biomass, and total available inorganic soil N as independent variables in separate linear regressions. Weed biomass data was $\log_{10}(X + 0.01)$ transformed prior to analysis to improve homoscedasticity.

RESULTS

Crop Yield

The number of species in the rotation (crop diversity) affected yields in all three crops (Table 2; Figure 2A–C). However, the strongest effects of crop diversity were in corn, where over-yielding (% increase in yield compared to the monoculture) was over 100% in some treatments. Over the 3 years, corn yields in the highest diversity 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 (Figure 2A). In all 3 years, there was a significant positive linear relationship between the number of crop species in the rotation and corn yield. The slope of this relationship increased each year, suggesting an increasingly strong diversity effect with time (Figure 3). Removal of treatment 1 (the only treatment that did not include a legume) from the analysis resulted in only a slight change in the relationship between crop species richness and corn yield; the relationship was non-significant in 2002, but remained significant ($P < 0.05$) and

Table 2. Repeated Measures ANOVA for the Effects of Crop Diversity on Crop Yields and Weed Biomass in the KBS Biodiversity Experiment Plots (BExP) over 3 Years (2002–2004)

	Crop yields		Weed biomass	
	F-value (df)	P > F	F-value (df)	P > F
<i>Corn</i>				
Diversity (D)	15.22 (5,15)	<0.0001	1.66 (5,15)	0.2054
Year (Y)	0.19 (2,36)	0.8294	4.26 (2,36)	0.0219
D*Y	2.07 (10, 36)	0.0537	1.48 (10,36)	0.1880
<i>Soybean</i>				
Diversity (D)	6.55 (5,15)	0.0020	2.07 (5,15)	0.1269
Year (Y)	162.47 (2,40)	<0.0001	13.22 (2,40)	0.0006
D*Y	1.82 (10,40)	0.0888	1.00 (10,40)	0.4591
<i>Wheat</i>				
Diversity (D)	5.01 (5,15)	0.0067	17.81 (5,15)	<0.0001
Year (Y)	112.15 (2,33)	<0.0001	30.44 (2,33)	<0.0001
D*Y	4.61 (9,33)	0.0005	13.15 (9,33)	<0.0001

Significant effects are bolded.

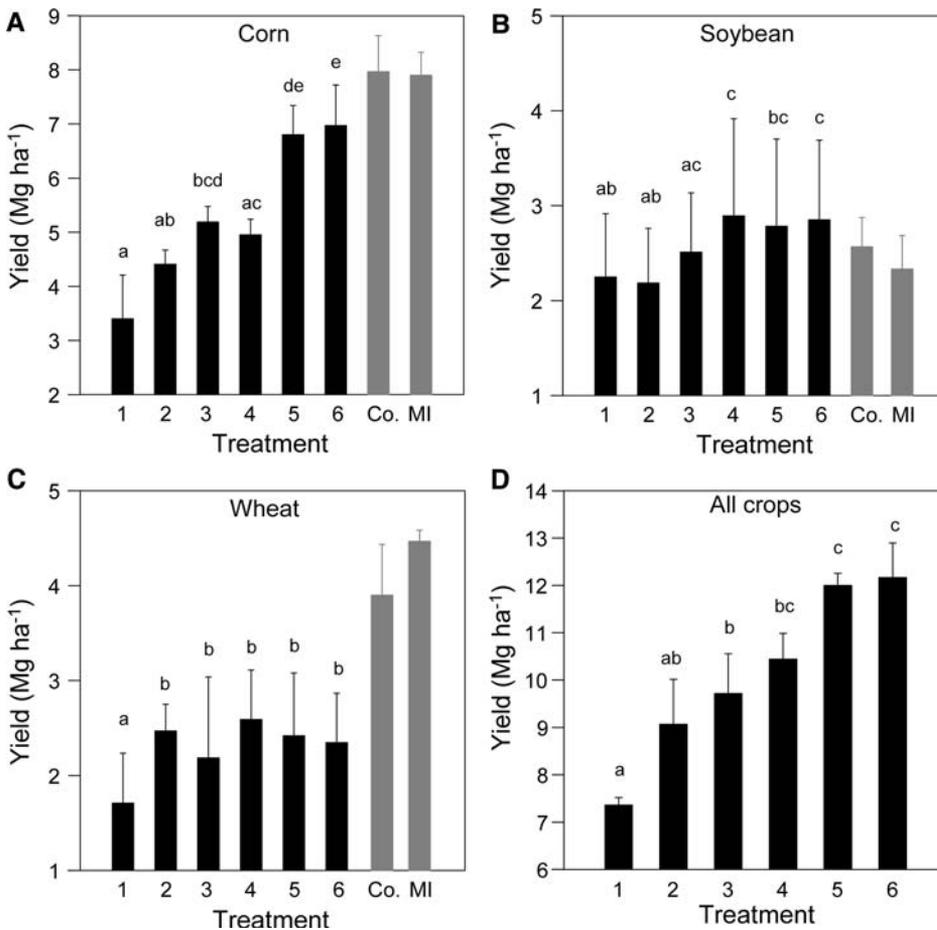


Figure 2. Comparisons of average grain yields for (A) corn, (B) soybean, and (C) winter wheat across crop diversity treatments in the BExP (black bars), Kalamazoo County (Co.), and the State of Michigan (MI). Values are means of treatment averages ± SE, *n* = 3 years. BExP treatments are listed in order of increasing diversity (number of species in rotation; see Table 1 for details). Panel D is total grain yields of all crops summed over the study period. Among the BExP treatments, bars sharing the same letter are not significantly different from each other at the *P* = 0.05 level (Tukey HSD) based on analysis of treatment means, *n* = 12 (panels A–C) and *n* = 4 (panel D)

positive in both 2003 ($r^2 = 0.56$, slope = 0.75) and 2004 ($r^2 = 0.43$, slope = 0.86).

Corn yields generally increased with the number of legume species in the rotation; having one

legume (crop or cover crop; treatment 1 vs. 2–4) increased corn yields from 1.0 to 1.8 Mg ha⁻¹ compared to the monoculture. Increasing from one to two legume species in the rotation resulted

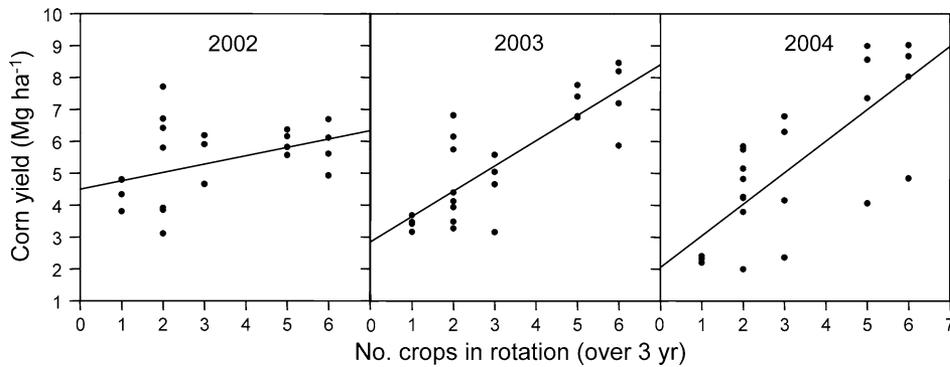


Figure 3. Regression between corn yield and crop diversity (number of crops over a 3-year rotation) in the BExP plots across years.

Regression analyses-(2002): $P = 0.048$, $r^2 = 0.17$, $\hat{y} = 4.5 + 0.26x$; (2003): $P < 0.001$, $r^2 = 0.67$, $\hat{y} = 2.8 + 0.79x$; (2004): $P < 0.001$, $r^2 = 0.58$, $\hat{y} = 2.0 + 0.99x$

in an additional increase of 1.8 to 2.6 Mg ha⁻¹ (Tukey HSD, $P < 0.05$; treatments 2–4 vs. 5 and 6) (Figures 2 and 4). Effects were similar whether the diversity increase was due to the inclusion of soybean or *Trifolium* cover crops. The number of non-legume crops in the rotation did not affect corn yields appreciably (that is, treatment 2 vs. treatments 3 and 4). Interestingly, corn yields in the most diverse treatment (treatment 6) were not significantly different from the Kalamazoo county average for conventionally managed corn each of the 3 years (t -test, $df = 3$; 2002: $t = -2.9$, $P = 0.63$; 2003: $t = -1.3$, $P = 0.28$; 2004: $t = -1.1$, $P = 0.35$).

In soybean and winter wheat, the effects of the crop diversity treatments on grain yields were

significant (Table 2), but were of lower magnitude than those in corn (highest yielding treatments were 32 and 53% higher than the monocultures, respectively). Soybean grain yields in treatments with at least two species in the rotation were equal to or greater than the county average in 2002 (t -test, $df = 3$, $t > 0$, $P \leq 0.05$) and comparable in treatments 1–5 in 2004 (t -test, $df = 3$, $t < 0$, $P > 0.05$). The significant crop diversity treatment effect in winter wheat was due to low yields in the monoculture (treatment 1); the other diversity treatments did not differ from one another (Tukey HSD, $P > 0.05$). With the exception of treatment 6 in 2002, yields each year in winter wheat at all levels of crop diversity were significantly lower than the county average (t -test, $df = 3$, $t < 0$, $P < 0.05$).

Aggregate yields collected over the entire 3-year sequence of each diversity treatment (total grain yields) may provide a more appropriate analog to the common metrics assessed in other plant diversity–ecosystem function studies. Total grain yields, yields of all harvestable grains produced over the course of the study, varied with the level of crop diversity ($F_{5,15} = 18.63$, $P < 0.0001$), and were over 60% greater in the highest diversity treatment compared to the lowest diversity treatment (Figure 2D).

Weed Biomass

Weed abundance differed among crop diversity treatments in wheat, but was independent of diversity in corn and soybean over the 3 years (ANOVA, $P > 0.05$) (Smith and Gross 2007; Table 2). In wheat, within-year differences in weed biomass among treatments were due to treatments with cover crops having lower weed biomass compared to those without (Tukey HSD, $P < 0.05$). There was no relationship in any of the 3 years between weed biomass and grain yield in corn and winter wheat ($P > 0.05$); however, there was a

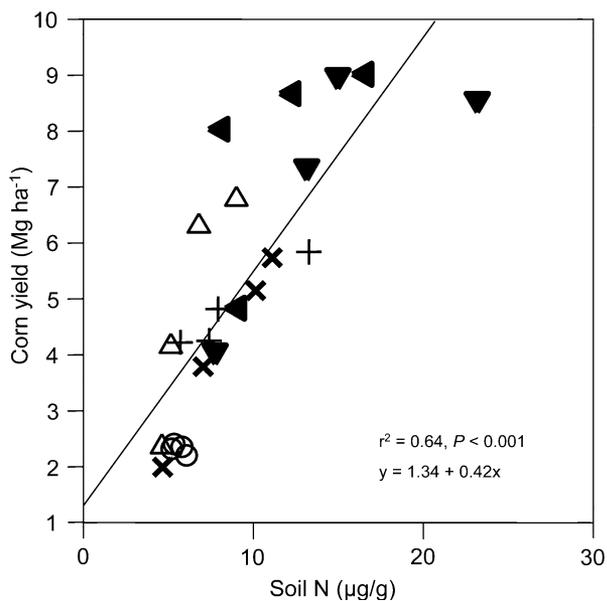


Figure 4. Relationship between corn grain yields and early season (June) inorganic soil nitrogen in 2004. Symbols are treatments: 1 (○), 2 (×), 3 (+), 4 (△), 5 (▼), and 6 (◀). Refer to Table 1 for a description of the diversity treatments

significant negative linear relationship between weed biomass and grain yield in soybean in 2002 ($r^2 = 0.23$, $P = 0.02$) and 2004 ($r^2 = 0.30$, $P = 0.01$).

Soil Nitrogen

Early season soil nitrogen levels in 2004 were positively related to grain yield in corn ($r^2 = 0.64$, $P < 0.001$) (Figure 4), and were highest in the higher diversity treatments (treatments 4 and 5) and lowest in the least diverse treatment (continuous monoculture, treatment 1) (Tukey HSD, $P < 0.05$). Available soil nitrogen levels remained high in the diverse corn treatments through the mid-season sampling (23 August) ($F_{5,15} = 4.31$, $P = 0.01$), but decreased to levels that were equivalent across the diversity treatments by the end of the growing season (16 November) ($P = 0.12$). Soil nitrogen levels measured on 28 June were independent of diversity in soybean ($P = 0.26$), but in winter wheat were significantly higher in treatment 2 (continuous monoculture with one cover crop) than treatments 3–6 (Tukey HSD, $P < 0.05$). However, there was no relationship between early season soil nitrogen availability and grain yield in soybean ($P = 0.92$) or winter wheat ($P = 0.23$).

DISCUSSION

Increasing the diversity of crop species in a rotation had significant effects on grain yield in this experiment, but effects were often crop-species specific. In corn, yields increased linearly with increasing diversity of the rotation and in the highest diversity treatment were not significantly different from the county average for conventionally managed corn in each of the 3 years. This similarity in yields is remarkable given the absence of synthetic chemical inputs (fertilizer or pesticides) in the BExP, and suggests that diverse cropping systems can provide an ecosystem service that replaces (or reduces) reliance on chemical inputs in some systems. Other agronomic studies have reported corn yields that were similar (Poudeh and others 2002; Delate and Cambardella 2004; Pimentel and others 2005; Smith and Gross 2006) or only moderately reduced (<10%; Porter and others 2003; but see Teasdale and others 2007) in diverse organic and low-input cropping systems when compared to those in conventional-input systems. Grain yields in soybean and wheat also were lower in the monocultures than in any of the multiple species treatments, but beyond

that there was no effect of species diversity on crop yields. The different responses of the three crop species to diversity suggest that species traits will influence how crops respond to increasing diversity and its impacts on ecosystem services in row-crop systems (Porter and others 2003). Despite the differences among crops in their response to diversity, total grain yields harvested over the course of the study were greatest in the highest diversity treatments (Figure 2D), suggesting that increases in over-all productivity (in terms of grain yield) may compensate for the decreased corn frequency in the higher diversity rotations.

An important ecosystem service provided by crop diversity that could impact grain yields is the availability of nutrients, particularly soil nitrogen (Drinkwater and others 1998; Mäder and others 2002). The diversity treatments in the BExP likely impacted soil nitrogen availability through at least two major mechanisms: (1) changes in the intensity of nitrogen export from soil reservoirs due to differential crop uptake and (2) differences in biological nitrogen fixation related to the inclusion and frequency of legumes. The relative importance of each mechanism to the observed yield responses appeared to be crop dependent. In corn, nitrogen availability was higher early in the growing season in the more diverse treatments and this was strongly correlated with grain yields. Corn is an effective competitor for nitrogen; export by corn of the nitrogen provided by previous soybean and leguminous cover crops may have reduced availability to subsequent crops, particularly in the lower diversity treatments where corn occurred more frequently. In contrast to corn, soybean, because it can fix its own nitrogen, is typically not highly responsive to added nitrogen (Reese and Buss 1992), which may explain its lack of responsiveness to increased diversity in this study. The lack of responsiveness in wheat is more difficult to explain, but may be due to asynchronies in the timing of nitrogen availability relative to crop demand (Boman and others 1995). The fact that weed abundance was not greater in treatments with greater available nitrogen suggests also that weeds were unable to take advantage of the increased nitrogen availability, likely due to the effectiveness of the mechanical control early in the growing season (Mohler and others 1997).

Differences in inorganic nitrogen availability and corn yields among the treatments appeared to be driven primarily by the number of legume species in the cropping sequence, suggesting that crop-functional traits were important determinants of

ecosystem function in this system. These results parallel those from rotation studies in agricultural systems (Drinkwater and others 1998; Gentry and others 2001) and 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; Spehn and others 2002; Lambers and others 2004). In many of these experiments legumes were identified as important drivers of positive diversity–productivity relationships due to their stimulation of overyielding in non-nitrogen fixing species, particularly those with the C4 photosynthetic pathway (Spehn and others 2002; Lambers and others 2004; Hooper and others 2005).

Another potentially important ecosystem service provided by crop diversity that could impact grain yields is weed suppression (Liebman and Dyck 1993). In row-crops, yields are often correlated with variation in weed biomass (Weiner and others 2001). Crop diversity could influence weed biomass or composition by increasing the prevalence of stress and mortality factors that affect weeds or by changing resource use by crops and weeds such that crops preempt resources used by weeds (Liebman and Gallandt 1997; Liebman and Staver 2001). However, we found little evidence that the observed yield differences in relation to crop diversity were due to effects on weed biomass across these treatments. We detected no differences in weed abundance among diversity treatments in corn and soybean despite the fact that weed management practices differed among the three crops (inter-row cultivation in corn and soybean, no cultivation in winter wheat). Treatment differences in weed abundance in winter wheat due to the presence of cover crops were not related to yields.

Crop Species Richness and the “Rotation Effect”

The beneficial impacts of crop rotation and leguminous cover crops on crop yields are well known (for example, Bullock 1992; Drinkwater and others 1998; Pimentel and others 2005). In general, yield increases attributable to crop rotation have been shown to depend on crop, climate, soil type, and associated management practices, and can vary from zero to over 50% (Crookston and others 1991; Vyn and others 2000; Pedersen and Lauer 2003; Gan and others 2003; Porter and others 2003). However, what is not well understood are the mechanisms driving these impacts (Bullock 1992; Whiting and Crookston 1993) or the relative importance of crop diversity per se in contributing

to the more general “rotation effect” commonly reported by agronomists. An important distinction of the BExP from more traditional studies of crop rotation is that in this experiment only crop species diversity was varied—there were no chemical or other management differences between treatments which could potentially confound diversity responses (Doucet and others 1999; Porter and others 2003; Anderson 2005). Additionally, our treatments systematically varied crop diversity across a greater range of diversity levels than are examined in most rotation studies.

In this experiment, legumes appeared to have particularly strong effects on ecosystem functions that influence corn yields. The strong influence of legumes is recognized in the plant species richness literature from unmanaged ecosystems and it is not unrealistic to assume that legumes may have an even stronger potential to influence ecosystem processes in agricultural systems where large amounts of nitrogen are exported annually through harvest.

Aspects of the design of the diversity treatments make it difficult to clearly distinguish between the influence of strong functional group effects and species richness as the primary mechanisms contributing to the yield responses observed in this study. For example, treatments 2 and 3 both include legumes in the same frequency (that is, a legume is alternating with a non-legume). Whether a two-species treatment without a legume would have produced yields comparable to these treatments is unknown. Another potential criticism of the design is that crop species richness may be confounded with the inclusion of legumes in ways that increase the time in which treatments are under nitrogen-fixing plants as species richness increases. This point, however, is likely not a significant issue as the treatments also differ in the extent to which nitrogen contributions derived from the legumes remain within the system or are exported with harvested biomass. For example, although treatment 5 contains a total of three legume species (soybean and two leguminous cover crop species) the frequency with which a non-harvested legume is present on the soil in this treatment is only slightly greater than that of treatment 2 (Figure 1). Despite the potential limitations of the experimental design, evidence for an effect of crop diversity beyond that of simply rotating one crop with another comes from the fact that yields of all three crops grown in the continuous monocultures with cover crops (treatment 2, two species total) were similar to those in the two-crop rotation (treatment 3, two species total).

Additionally, the positive linear relationship observed between crop diversity and corn yield (even with the removal of treatment 1 from the analysis), and the differences in total harvestable grain yield among the diversity treatments, imply that there are benefits to the cropping system (in terms of yield) of increasing crop diversity *per se*, and that effects cannot be attributed solely to the inclusion of legumes (Bullock 1992; Huston 1997; Lambers and others 2004).

Anderson (2005) reported that in a crop diversity study conducted with conventional inputs, a consequence of increased crop diversity was that certain crops improved the water and nutrient use efficiency of following crops. Although the mechanisms responsible for these types of interactions in agroecosystems remain illusive (Stevenson and van Kessel 1996; Anderson 2005), it is possible that similar interactions occurring among crop species contributed to the diversity effects observed in our study. Other factors that could be affected by crop diversity, and that could have contributed to some of the effects of crop diversity on yields observed in this study, include disease and insect pest suppression (Andow 1991; Bullock 1992; Whiting and Crookston 1993; Zhu and others 2000; Anderson 2005). Although we observed no apparent signs of differential disease or insect damage among the crop diversity treatments, we did not expressly measure these variables and it is possible that these factors may have manifest themselves in ways that were not visually apparent while still impacting plant performance and yield. A follow-up experiment, where corn was grown in the greenhouse with soils collected from the low and high diversity treatments, did not find any evidence of soil-borne pathogens in this system (Nichols and Gross, unpublished). Diseases and pathogens, or other factors that limit yield (or crop health) and vary with crop diversity, may become more apparent over time.

CONCLUSIONS

Although this experiment was not designed to assess the full gamut of potential agroecosystem services that diversity might provide, the results presented here show that increasing crop diversity in row-crop ecosystems can lead to significant increases in ecosystem functions related to crop production and affect grain yield, particularly in corn. These data are consistent with observations on the effects of increasing species and functional group diversity on ecosystem processes in grasslands, and suggest that agricultural systems can be

used to test basic ecological theory, and that such theory can contribute to a more mechanistic understanding of biologically based management systems (Robertson and others 2004). Determining whether or not diversity contributes to agro-ecological sustainability will require careful assessment of external inputs associated with production in diverse systems (such as non-renewable fuel used to operate equipment) and potential outputs such as greenhouse gas emissions and nutrient outflow (Mosier and others 1998; Swinton and others 2006).

Our results are consistent with earlier work showing that synthetic chemical inputs are not always necessary to maintain high yields in agricultural ecosystems (Pimentel and others 2005; Smith and Gross 2006). More importantly, we show that yield penalties associated with low chemical use can be offset by managing for higher plant species diversity. In addition to their relevance to food production systems, these results have implications for the development of sustainable fuels, and suggest that increasing crop diversity may offset the need for agricultural inputs, identified as an important limit to the potential benefits of crop-based biofuels (Hill and others 2006). The effects of cropping system diversity were less dramatic in soybean and winter wheat than in corn, and understanding why these effects varied among crops will be important. Further experiments will be necessary to determine the exact mechanisms by which crop diversity mediates yield responses in agriculturally important plant species and may reveal how wheat and soybean yields could be enhanced.

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REFERENCES

- Altieri MA, Letourneau DK, Davis JR. 1983. Developing sustainable agroecosystems. *BioScience* 33:45–9.
- Anderson RL. 2005. Improving sustainability of cropping systems in the Central Great Plains. *J Sustain Agric* 26:97–114.

- Andow DA. 1991. Vegetational diversity and arthropod population response. *Annu Rev Entomol* 36:561–86.
- Boman RK, Westerman RL, Raun WR, Jojola ME. 1995. Time of nitrogen application-effects on winter wheat and residual soil nitrate. *Soil Sci Soc Am J* 59:1364–9.
- Bullock DG. 1992. Crop-rotation. *Crit Rev Plant Sci* 11:309–26.
- Crookston RK, Kurle JE, Copeland PJ, Ford JH, Lueschen WE. 1991. Rotational cropping sequence affects yield of corn and soybean. *Agron J* 83:108–13.
- Crum JR, Collins HP. 1995. KBS soils. <http://lter.kbs.msu.edu/Soil/Characterization>.
- Delate K, Cambardella CA. 2004. Agroecosystem performance during transition to certified organic grain production. *Agron J* 96:1288–98.
- Diaz S, Cabido M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–55.
- Doucet C, Weaver SE, Hamill AS, Zhang JH. 1999. Separating the effects of crop rotation from weed management on weed density and diversity. *Weed Sci* 47:729–35.
- Drinkwater LE, Wagoner P, Sarrantonio M. 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. *Nature* 396:262–5.
- Gan YT, Miller PR, McConkey BG, Zentner RP, Stevenson FC, McDonald CL. 2003. Influence of diverse cropping sequences on durum wheat yield and protein in the semiarid northern Great Plains. *Agron J* 95:245–52.
- Gentry LE, Below FE, David MB, Bergerou JA. 2001. Source of the soybean N credit in maize production. *Plant Soil* 236:175–84.
- Hill J, Nelson E, Tilman D, Polasky S, Tiffany D. 2006. Environmental, economic, and energetic costs and benefits of biodiesel and ethanol biofuels. *Proc Natl Acad Sci USA* 103:11206–10.
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35.
- Hooper DU, Vitousek PM. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecol Monogr* 68:121–49.
- Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–60.
- Kleijn D, Verbeek M. 2000. Factors affecting the species composition of arable field boundary vegetation. *J Appl Ecol* 37:256–66.
- Lambers JHR, Harpole WS, Tilman D, Knops J, Reich PB. 2004. Mechanisms responsible for the positive diversity–productivity relationship in Minnesota grasslands. *Ecol Lett* 7:661–8.
- Liebman M, Davis AS. 2000. Integration of soil, crop and weed management in low-external-input farming systems. *Weed Res* 40:27–47.
- Liebman M, Dyck E. 1993. Crop rotation and intercropping strategies for weed management. *Ecol Appl* 3:92–122.
- Liebman M, Gallandt ER. 1997. Many little hammers: ecological management of crop-weed interactions. In: Jackson LE, Ed. *Agricultural Ecology*. San Diego, CA: Academic Press p 291–343.
- Liebman M, Staver CP. 2001. Crop diversification for weed management. In: Liebman M, Mohler CL, Staver CP, Eds. *Ecological Management of Agricultural Weeds*. New York, NY: Cambridge University Press p 322–74.
- Mäder P, Fliessbach A, Dubois D, Gunst L, Fried P, Niggli U. 2002. Soil fertility and biodiversity in organic farming. *Science* 296:1694–7.
- Matson PA, Parton WJ, Power AG, Swift MJ. 1997. Agricultural intensification and ecosystem properties. *Science* 277:504–9.
- Mohler CL, Frisch JC, Pleasant JM. 1997. Evaluation of mechanical weed management programs for corn (*Zea mays*). *Weed Technol* 11:123–31.
- Mosier A, Kroeze C, Nevison C, Oenema O, Seitzinger S, van Cleemput O. 1998. Closing the global N₂O budget: nitrous oxide emissions through the agricultural nitrogen cycle—OECD/IPCC/IEA phase II development of IPCC guidelines for national greenhouse gas inventory methodology. *Nutr Cycl Agroecosyst* 52:225–48.
- Pedersen P, Lauer JG. 2003. Corn and soybean response to rotation sequence, row spacing, and tillage system. *Agron J* 95:965–71.
- Pimentel D, Hepperly P, Hanson J, Doubs D, Seidel R. 2005. Environmental, energetic, and economic comparisons of organic and conventional farming systems. *Bioscience* 55:573–82.
- Poudeh DD, Horwath WR, Lanini WT, Temple SR, van Bruggen AHC. 2002. Comparison of soil N availability and leaching potential, crop yields and weeds in organic, low-input and conventional farming systems in northern California. *Agric Ecos Environ* 90:125–37.
- Porter PM, Huggins DR, Perillo CA, Quiring SR, Crookston RK. 2003. Organic and other management strategies with two- and four-year crop rotations in Minnesota. *Agron J* 95:233–44.
- Reese PF, Buss GR. 1992. Response of dryland soybeans to nitrogen in full-season and double-crop systems. *J Prod Agric* 5:528–31.
- Robertson GP, Swinton SM. 2005. Reconciling agricultural productivity and environmental integrity: a grand challenge for agriculture. *Front Ecol Environ* 3:38–46.
- Robertson GP, Broome JC, Chornesky EA, Frankenberger JR, Johnson P, Lipson M, Miranowski JA, Owens ED, Pimentel D, Thrupp LA. 2004. Rethinking the vision for environmental research in US agriculture. *BioScience* 54:61–5.
- Smith RG, Gross KL. 2006. Weed community and corn yield variability in diverse management systems. *Weed Sci* 54:106–13.
- Smith RG, Gross KL. 2007. Assembly of weed communities along a crop diversity gradient. *J Appl Ecol* 44:1046–56.
- Spehn EM, Scherer-Lorenzen M, Schmid B, Hector A, Caldeira MC, Dimitrakopoulos PG, Finn JA, Jumpponen A, O'Donovan G, Pereira JS, Schulze ED, Troumbis AY, Körner C. 2002. The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos* 98:205–18.
- Stevenson FC, van Kessel C. 1996. The nitrogen and non-nitrogen rotation benefits of pea to succeeding crops. *Can J Plant Sci* 76:735–45.
- Swinton SM, Lupi F, Robertson GP, Landis DA. 2006. Ecosystem services from agriculture: looking beyond the usual suspects. *Am J Agric Econ* 88:1160–6.
- Teasdale JR, Coffman CB, Mangum RW. 2007. Potential long-term benefits of no-tillage and organic cropping systems for

- grain production and soil improvement. *Agron J* 99: 1297–305.
- Tilman D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. *Proc Natl Acad Sci USA* 96:5995–6000.
- Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281–4.
- Tilman D, Wedin D, Knops J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–20.
- Trenbath BR. 1974. Biomass productivity of mixtures. *Adv Agron* 26:177–210.
- Trenbath BR. 1999. Multispecies cropping systems in India—predictions of their productivity, stability, resilience and ecological sustainability. *Agroforest Syst* 45:81–107.
- Vandermeer JH. 1989. *The ecology of intercropping*. Cambridge, UK: Cambridge University Press.
- Vyn TJ, Faber JG, Janovicek KJ, Beauchamp EG. 2000. Cover crop effects on nitrogen availability to corn following wheat. *Agron J* 92:915–24.
- Weiner J, Griepentrog HW, Kristensen L. 2001. Suppression of weeds by spring wheat *Triticum aestivum* increases with crop density and spatial uniformity. *J Appl Ecol* 38:784–90.
- Whiting KR, Crookston RK. 1993. Host-specific pathogens do not account for the corn soybean rotation effect. *Crop Sci* 33:539–43.
- Zhu YY, Chen HR, Fan JH, Wang YY, Li Y, Chen JB, Fan JX, Yang SS, Hu LP, Leung H, Mew TW, Teng PS, Wang ZH, Mundt CC. 2000. Genetic diversity and disease control in rice. *Nature* 406:718–22.