Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis

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Abstract. Our increasing dependence on a small number of agricultural crops, such as corn, is leading to reductions in agricultural biodiversity. Reductions in the number of crops in rotation or the replacement of rotations by monocultures are responsible for this loss of biodiversity. The belowground implications of simplifying agricultural plant communities remain unresolved; however, agroecosystem sustainability will be severely compromised if reductions in biodiversity reduce soil C and N concentrations, alter microbial communities, and degrade soil ecosystem functions as reported in natural communities. We conducted a meta-analysis of 122 studies to examine crop rotation effects on total soil C and N concentrations, and the faster cycling microbial biomass C and N pools that play key roles in soil nutrient cycling and physical processes such as aggregate formation. We specifically examined how rotation crop type and management practices influence C and N dynamics in different climates and soil types. We found that adding one or more crops in rotation to a monoculture increased total soil C by 3.6\% and total N by 5.3\%, but when rotations included a cover crop (i.e., crops that are not harvested but produced to enrich the soil and capture inorganic N), total C increased by 8.5\% and total N 12.8\%. Rotations substantially increased the soil microbial biomass C (20.7\%) and N (26.1\%) pools, and these overwhelming effects on microbial biomass were not moderated by crop type or management practices. Crop rotations, especially those that include cover crops, sustain soil quality and productivity by enhancing soil C, N, and microbial biomass, making them a cornerstone for sustainable agroecosystems.

Key words: agricultural biodiversity; crop rotation; meta-analysis; microbial biomass; monoculture; soil carbon; soil nitrogen; sustainable agroecosystems.

INTRODUCTION

Plant diversity influences a range of ecosystem processes including primary productivity, pest suppression, decomposition, nutrient cycling, and soil organic matter (SOM) dynamics (Hooper et al. 2000, Tilman et al. 2002, Zak et al. 2003, Orwin and Wardle 2005). In order to obtain some of the benefits of plant diversity, agricultural producers frequently use crop rotations, a practice that involves the sequential planting of crops over time. Producers have been aware for centuries that increasing crop diversity through time by crop rotation can help mitigate weed, insect, and pathogen pressure, and that rotating grains with legumes enhances crop yields (Bullock 1992, Copeland and Crookston 1992, Gurr et al. 2003, Smith et al. 2008). Because of these mostly aboveground benefits of crop rotation, it is estimated that ~82\% of U.S. cropland is in rotation (Padgitt et al. 2000). Recently, producers have been looking to rotations for the kinds of belowground benefits observed in spatially diverse natural communities, including enhanced SOM concentrations and microbial activity; yet, compared to aboveground responses, relatively little is known about belowground responses to crop rotation.

Although relationships between crop yields and crop rotations have been well-established (Copeland and Crookston 1992, Bullock 1992, Gurr et al. 2003, Smith et al. 2008), rotation effects on SOM dynamics, soil microbial populations, and other belowground dynamics remain uncertain (Drinkwater et al. 1998, Sanchez et al. 2001, Tonitto et al. 2006). For example, studies have shown that crop rotations increase (Russell et al. 2006, Varvel 2006, Murphy et al. 2011), decrease (Wang et al. 2006, Coulter et al. 2009, Benjamin et al. 2010), or have no effect on SOM concentrations (Gijsman et al. 1997, Soon et al. 2007, Snapp et al. 2010). The source of this variation is currently unknown, although contributing factors may include variable responses to rotation under different management, climatic, and edaphic conditions (Wardle 1992, Jobbagy and Jackson 2000, Amundson et al. 2003, Müller and Höper 2004, Fierer et al. 2009). Crop management decisions alone are likely to influence microbial and SOM dynamics via their effects on the number of rotation crops, their planting patterns, and residue biochemistry.

Several studies have shown that the chemical diversity and complexity of SOM inputs strongly influence long-term SOM dynamics (Johnson et al. 2007, Fornara and Tilman 2008), whereas others have suggested that the
effects of residue complexity are mostly short term (Maul and Drinkwater 2010, Gentile et al. 2011), and that all residues become chemically similar once processed by microbes (Grandy and Neff 2008, Fierer et al. 2009, Schmidt et al. 2011). Even if this latter view is correct, residue complexity or biochemistry may regulate SOM dynamics indirectly by influencing the size, structure, and function of soil biological communities (Waldrop et al. 2004, Allison et al. 2009, Strickland et al. 2009, Tiemann and Billings 2011, Wickings et al. 2012). Given the critical role that soil fauna and microbes play in processing plant inputs and directly contributing cells and by-products to SOM (Simpson et al. 2007, Grandy and Neff 2008, Liang et al. 2011), the frequently reported positive effects of rotations on soil faunal (Ryszkowski et al. 1998) and microbial (Lupwayi et al. 1998, Wu et al. 2008, Xuan et al. 2012) abundance and diversity may increase SOM. In fact, microbial biomass is typically used as an early indicator of changes in nutrient cycling and SOM dynamics, because microbial biomass C and N pools have been shown to be more sensitive to agricultural management than bulk soil C and N pools (Joergensen et al. 1995).

Although crop rotations dominate the U.S. agricultural landscape, these rotations are typically short (e.g., corn–soybean rotations) and there remain regions where monocultures (the planting of a single crop over time) are common (Padgett et al. 2000). Further, the increasing demand for biofuel crops is pressuring U.S. agricultural producers to reduce their crop rotation diversity (Groom et al. 2008). In other regions, specifically China and Brazil, agriculture is undergoing expansion and mechanization, which often reduces agricultural plant species diversity (Bullock 1992). Given these threats to crop rotation diversity, and the inconsistent empirical relationships between crop rotation and key soil C and N cycling processes, the overriding goal of our study was to examine whether rotations influence soil C and N concentrations and microbial biomass pools relative to monocultures. We used a meta-analysis approach to synthesize the crop rotation effects across multiple studies and explore the sources of variation in global soil responses to agricultural diversification (Stewart 2010). Our specific objectives were to address how the number and types of crops in rotation, soil management practices such as tillage and fertilization intensity, and climatic and edaphic factors influence SOM dynamics and microbial biomass.

**Materials and Methods**

**Data collection**

We initially searched the literature in 2012 using ISI Web of Knowledge v.5.6 (available online). The initial search terms were “Crop” and “Soil,” which were subsequently refined by “Rotation” and “Continuous.” This initial search resulted in 1719 articles, from which we selected only those that included a monoculture treatment, were in place for a minimum of three years, and reported the effects of crop rotations on total soil C or N, microbial biomass C or N, or a combination of these variables. Studies that included a fallow period in rotation, characterized by no crop production and frequently intensive tillage or herbicide use to control weeds, were excluded from our analysis because of the wide variation in specific fallow management practices. We included both field and vegetable crops in our analysis, and expanded our search by checking the reference and citation lists of studies that met our basic criteria.

Data were extracted from both tables and figures in publications meeting our search criteria using DataThief v.1.6 (Tummers 2006). The response variables used in our meta-analysis are total soil organic C (TC), total soil nitrogen (TN), microbial biomass C (MBC), and microbial biomass N (MBN). Response variables that were measured more than once during a growing season were averaged for an overall annual value. Many studies included a wide range of sampling depths with varying intervals at which the response variables were measured. Thus, to obtain an integrated estimate of relative soil responses to rotation, all data reported at multiple depths were converted to a single, depth-weighted mean (sensu Johnson and Curtis 2001) with maximum depth of sampling treated as a moderating variable (moderating variables will be described further). Bulk density values were measured by rotation treatment in only 19% of our studies, or 85 out 454 total observations. Because of the limited data, the inconsistent and nonsignificant response of bulk density to crop rotation treatments (e.g., Holford 1990, Coulter et al. 2009; Appendix B: Fig. B1), and limitations to converting soil C concentrations to stocks using modeled estimates of bulk density (Heuscher et al. 2005, Don et al. 2011), we chose to report our data on a concentration basis. Analysis of soil C and N on a concentration basis provides direct evidence of cropping systems effects on key soil processes related to long-term productivity and sustainability, the primary objective of our analysis. Soil C accrual rates were calculated as the change in soil C concentration (rotation soil C minus monoculture soil C) divided by the number of years since the experimentally paired monoculture and rotation fields were established in each study.

The environmental and edaphic moderating variables that we examined include soil texture, mean annual temperature (MAT), and mean annual precipitation (MAP). Additionally, we included as moderating variables crop and soil management practices that may influence rotational diversity effects on soil C and N, including the number of crops in the rotation, tillage practices (conventional, reduced, or no-till), fertilizer rate, duration of the experiment, and depth of soil sampling. When climatic data, MAT, and MAP were
not made available in publications, they were estimated from regional online climate sources.

**Data analysis**

In our meta-analysis, the effect size or response ratio (R) represents the influence of adding one or more crops to a monoculture crop. We used MetaWin v.2.1 to calculate R and 95% bias-corrected confidence intervals (CI) with 9999 iterations (Johnson and Curtis 2001, Knorr et al. 2005, Tonitto et al. 2006). MetaWin is available online. The R values of the response variables (SOC, TN, MBC, MBN, C:N, MBC:TC, MBN:TN, and MBC:MBN) within each study were calculated as:

\[
\ln R = \ln \bar{X}_c - \ln \bar{X}_w = \ln \frac{\bar{X}_c}{\bar{X}_w}
\]

where \(\bar{X}_c\) and \(\bar{X}_w\) are, respectively, the experiment (rotation) and control (monoculture) mean calculated for that observation. Many studies had one or more factors crossed with crop rotation in their experiment. For each of these studies, we treated individual experimental units as separate observations (k). For instance, when a crop rotation study included both conventional and no-till treatments, we treated each tillage level as a separate k. Thus, some studies had multiple effect sizes. We used funnel plots to determine that there was no evidence of publication bias (Philibert et al. 2012). Because many publications did not include measures of variance, we used an unweighted meta-analysis where all studies had a variance equal to 1. Effect sizes were considered significant (at \(P < 0.05\)) when 95% CIs did not overlap with zero or other treatment 95% CIs (Adams et al. 1997).

Moderating variables were analyzed using MetaWin v.2.1 in a procedure similar to ANOVA. The categorical moderating variables we analyzed were: tillage (yes or no); N fertilizer (yes or no); number of crops (2 through 5+); monoculture crop type used as control (corn, soy, sorghum, wheat, and miscellaneous); cover crops (yes or no); and number of legumes (0 through 3). Total group heterogeneity (\(Q_f\)) was partitioned into within-group (\(Q_w\)) and between-group (\(Q_b\)) heterogeneity, similar to partitioning variation in an ANOVA. The \(Q_b\) is similar to the model sums of squares and \(Q_w\) the error sums of squares. However, in order to maintain a robust ANOVA for the effects of categorical variables, a minimum of 10 k was required (Kullenbach and Grandy 2011). Categorical moderating variable levels were sometimes combined into a new category in cases where \(k < 10\) (e.g., miscellaneous or 3+ crops), and were run again. The continuous moderating variables we analyzed were: years since the beginning of the experiment; N fertilizer rate; maximum sampling depth; percentage sand; percentage clay; MAT; and MAP. We suspected that changes in SOM pools due to rotations may also be related to changes in soil C inputs, and these are typically related to crop yields and residue production. Thus, additional moderating variables included relative differences in yields and residue inputs between monoculture and rotation calculated using the equation for \(R\).

**RESULTS**

In total, 122 publications were included in this meta-analysis, providing 454 observations. These studies encompassed crop rotation experiments from all over the world (North America, 65%; South America, 8%; Australia, Asia, and Europe, 7%; and Africa 6% of all studies; Appendix A) and included ranges in MAT from 0° to 27°C and in MAP from 265 to 2200 mm. The average duration of the crop rotation experiments was 18 years (range 3–98 years). Most of the studies (59%) compared a monoculture to a two-crop rotation, with the maximum number of six crops in rotation (Mitchell and Entry 1998). Soil TC and TN data were normally distributed, whereas MBC and MBN had nonnormal distributions (Fig. 1). The R distributions were normal for all four variables. Adding one or more crops in rotation to a monoculture generally increased soil C and N pools, and had substantially larger effect on MBC and MBN (Fig. 2). Rotation increased TC by 3.6% and TN 5.3%, and MBC by 20.9% and MBN by 26.1%. There was no significant rotation effect on the soil C:N ratios (Fig. 2). The MBC:TC and MBN:TN ratios were increased 10% and 24%, respectively (Fig. 2).

There were few continuous variables moderating the crop rotation effect (Table 1). Fertilization rate showed a positive correlation with the crop rotation effect on soil C:N ratio (\(P = 0.027\)). Soil clay content was positively correlated with the rotation effect on MBC:TN (\(P = 0.029\)). Climatic variables showed the most significant correlations with the rotation effect (Table 1). Mean annual temperature correlated positively with rotation effects on TC (\(P = 0.045\)), MBN (\(P = 0.023\)), and MBC:TN (\(P = 0.035\)). Mean annual precipitation also correlated positively with TC (\(P < 0.001\)), TN (\(P = 0.008\)), and MBN (\(P = 0.018\)), but negatively with the rotation effect on the MBC:MBN ratio (\(P = 0.008\)).

The number of crops included in a rotation had a significant effect on TC (\(P = 0.025\)) and TN (\(P = 0.015\)) (Fig. 3, Table 2). Increasing the number of crops in rotation from two to three increased TC from 1.9% to 7.5%, but adding more than three appeared to have diminishing returns on TC (3.7% for four crops, and 7.7% for five or more crops). Adding one crop to a monoculture (i.e., two crops) increased TN by 2.9%, whereas adding an additional crop increased TN by 10.7%. Similar to TC, TN had diminishing increases at three and four crops in rotation, at 6.6% and 11.1%, respectively. The rotation effect on MBC or MBN did not differ as the number of species in rotation increased (Table 2). The monoculture crop under comparison to rotation also significantly influenced the rotation effect.
on TC (P = 0.004; Fig. 4, Table 2), but not on other variables. Soybeans showed the greatest response to rotation, with an 11% increase in TC, whereas introducing a rotation into corn monocultures did not increase TC. The crop rotation management factor with the strongest effects on TC and TN was the inclusion of a cover crop (Figs. 5 and 6, Table 2). Cover crops increased TC by 7.8% and TN 12.8% relative to monocultures, whereas rotations without cover crops did not significantly influence TC and TN. However, three-crop rotations without cover crops increased TN by 7.8% (Fig. 6). Given that virtually all of the cover crops included a legume, it was impossible to separate the benefits of using cover crops, per se, from the benefits of using legumes as cover crops. In contrast to TC and TN, the crop type (monoculture or whether cover crop was included) exerted little control over the rotation effect on MBC and MBN (Table 2).

**DISCUSSION**

**Rotation effects on total soil and microbial biomass C and N**

Our meta-analysis provides insights into how crop rotation influences total soil C and N pools, as well as the more rapid cycling MB pools that directly influence potential productivity and other key ecosystem services (Insam et al. 1991, Jonasson et al. 1996, Liang et al. 2011b). Across all studies, we found that adding one or more crops in rotation to a monoculture increased soil C by 3.6% and MBC by 20.7%, while increasing total soil N by 5.3% and MBN 26.1%. This stronger response in the MBC and MBN pools probably reflects the sensitivity of soil microbes to the quantity and quality of organic matter incorporated into the soil.

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**Fig. 1.** Total number of observations reported for soil total carbon (C), total nitrogen (N), microbial biomass carbon (MBC), and microbial biomass nitrogen (MBN) for monoculture and crop rotation.

**Fig. 2.** Overall mean change in soil C and N pools from crop rotation. The number of observations for each pool is shown in parentheses. Error bars are 95% bias-corrected confidence intervals.
biochemistry of crop inputs (Carter 1986, Sparling 1992, Motta et al. 2007). Further, observed increases in MBC and MBN, as well as in the proportion of total soil C and N in the MBC and N pools, point to a proportional shift of C and N into SOM pools with rapid cycling times, which is likely to be accompanied by a general increase in potential soil biological activity. This is supported by those studies reporting that rotations increased enzyme activities (e.g., Klose and Tabatabai 2000, Ekenler and Tabatabai 2002, Dodge and Tabatabai 2003, Dodge and Ali Tabatabai 2005, Acosta-Martinez et al. 2007) and faunal densities (Ryszkowski 2000, Ekenler and Tabatabai 2002, Dodge and Tabatabai 2003). Moreover, along with increasing nutrient cycling rates, MB dynamics probably underlie the greater accumulation of soil C and N under rotation compared to monocultures. Emerging concepts of SOM formation argue that the majority of SOM is composed of microbial by-products and microbial necromass, the material from dead cells (Simpson et al. 2007, Liang and Balser 2010, Schmidt et al. 2011). Viewed in this light, the accumulation of soil C and N over time is closely related to the production of microbial products.

**Influence of crop type on the rotation effect**

The key variable influencing soil total C and N responses to rotations was whether or not they included a cover crop. Cover crops are grown between periods when cash crops are produced (e.g., fall through spring in northern temperate regions), in order to increase biomass inputs to soil, decrease erosion, disrupt pest cycles, and retain inorganic N. In our study, cover crops accounted for most of the rotation effect on total soil C and N, increasing soil TC by 8.5% (Fig. 5) and soil TN by 12.8% (Fig. 6). One possible explanation for the pronounced effects of cover crops is their enhanced belowground productivity compared to cash crops. Most cover crops never reach maturity and are produced in the fall and early spring when low temperature and light availability are likely to promote high ratios of root to shoot production (Marcelis et al. 1998). The few studies available show that cover crop root productivity can be equal to or greater than aboveground productivity (Sainju et al. 1998, Gardner and Sarrantonio 2012), and even small increases in root inputs over long time periods may increase soil C and N. Root inputs are regarded as more important to SOM formation than shoot inputs in new conceptual models (Schmidt et al. 2011, Cotrufo et al. 2013), a hypothesis supported by Rasse et al. (2005) who estimated using meta-analysis that 2.4 times more SOM is derived from roots than from shoots. Roots are produced belowground in close proximity to soil microbes and soil mineral surfaces; these close associations between roots, microbes, and minerals can directly affect decomposer community structure and function and encourage physical SOM stabilization. Roots are also chemically distinct from shoots (Silver and Miya 2001, Baumann et al. 2011) and thus may be decomposed differently, in a way that makes them contribute more to SOM formation. Additionally, roots exude labile C com-

### Table 1. Pearson correlation coefficients between moderating continuous variables and the crop rotation effect size ($R$).

<table>
<thead>
<tr>
<th>Continuous moderating variable</th>
<th>TC</th>
<th>TN</th>
<th>MBC</th>
<th>MBN</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Years since beginning of experiment</td>
<td>0.003 (383)</td>
<td>0.05 (250)</td>
<td>-0.073 (144)</td>
<td>0.17 (83)</td>
<td>0.032 (228)</td>
</tr>
<tr>
<td>N fertilization rate</td>
<td>-0.063 (260)</td>
<td>-0.105 (176)</td>
<td>-0.02 (88)</td>
<td>-0.061 (59)</td>
<td><strong>0.172 (164)</strong>*</td>
</tr>
<tr>
<td>Depth of sampling</td>
<td>0.041 (409)</td>
<td>0.059 (238)</td>
<td>0.052 (139)</td>
<td>-0.052 (77)</td>
<td>0.074 (219)</td>
</tr>
<tr>
<td>Sand (%)</td>
<td>-0.025 (184)</td>
<td>0.013 (125)</td>
<td>0.075 (67)</td>
<td>0.042 (32)</td>
<td>0.047 (116)</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>-0.008 (187)</td>
<td>-0.106 (128)</td>
<td>0.102 (72)</td>
<td>0.28 (36)</td>
<td>0.015 (119)</td>
</tr>
<tr>
<td>Mean annual temperature</td>
<td>0.15 (162)**</td>
<td>0.151 (84)</td>
<td>0.002 (64)</td>
<td><strong>0.364 (39)</strong>*</td>
<td>0.163 (83)</td>
</tr>
<tr>
<td>Mean annual precipitation</td>
<td><strong>0.212 (249)</strong>***</td>
<td><strong>0.22 (143)</strong>*</td>
<td>0.043 (89)</td>
<td><strong>0.32 (54)</strong>*</td>
<td>0.073 (133)</td>
</tr>
<tr>
<td>Relative yield difference</td>
<td>-0.01 (33)</td>
<td>-0.174 (30)</td>
<td>-0.234 (12)</td>
<td>0.033 (14)</td>
<td>0.119 (18)</td>
</tr>
<tr>
<td>Relative residue inputs</td>
<td>-0.025 (75)</td>
<td>-0.113 (43)</td>
<td>-0.218 (20)</td>
<td>-0.12 (11)</td>
<td>0.156 (36)</td>
</tr>
</tbody>
</table>

**Notes:** Response variables are abbreviated as C, soil total carbon; N, total nitrogen; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen, and their ratios. Values in the cells are the correlation coefficients $r$, with the number of observations given in parentheses. Asterisks indicate significance.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
pounds into the soil as rhizodeposits, which are quickly incorporated into microbial biomass and may help promote both higher microbial growth efficiency and higher rates of biomass production (Kong et al. 2011). Thus, even relatively small increases in cover crop root inputs over time could increase SOM concentrations.

Another possible explanation for the large influence of cover crops on the rotation effect may be linked to the fact that the majority of cover crops in this analysis were leguminous (97%). Several studies have shown that adding a legume in rotation significantly increases bulk soil C and N pools (Drinkwater et al. 1998, Spehn et al. 2000, Jarecki and Lal 2003, Grandy and Robertson 2007, Carranca et al. 2009), perhaps due to the high-quality residues promoting microbial growth efficiency and aggregation (Six et al. 2006, Grandy and Robertson 2007, Bradford et al. 2013, Cotrufo et al. 2013, Frey et al. 2013). Several other studies comparing cover crop types have found inconsistent results, some suggesting that overall cover crop biomass is the major driver of soil C accumulation, whereas others point to the importance of using cover crop combinations that include both legumes and nonlegumes (Kuo et al. 1997, Sainju et al. 2003, 2005, 2006, Fageria et al. 2005, Villamil et al. 2006). Although we cannot resolve these uncertainties via direct comparison with leguminous vs. nonleguminous cover crops, our analyses highlight the importance of legumes as cover crops for soil C accumulation across a wide variety of rotations, soil types, and climate regimes.

In addition to the inclusion of cover crops, the monoculture crop under comparison also strongly influenced soil responses to rotation. For example, rotations did not increase soil C compared to corn monocultures, but rotations did increase soil C when compared to soy (11%), sorghum (7.9%), and wheat (2.9%) monocultures. The large soil C response with monoculture soybeans reminds us that we cannot make generalizations about the benefits of legumes for soil ecosystem services. Although our inquiry shows that legumes as cover crops build soil C and N pools, legumes clearly differ in their effects on soil processes, which is probably related to wide variation in their productivity, residue chemistry, and physiology. The poor performance of soybeans in rotation may be attributed to limited biomass inputs as well as to the chemical composition of these inputs (Conley et al. 2011). For example, in comparison to soybeans, corn produces more biomass inputs, and these inputs are more chemically recalcitrant. Thus, in order to maximize total soil C gains, a producer must consider both the characteristics of the monoculture crop currently under continuous production and that of the rotated crop(s).

Table 1. Effect size of response variable

<table>
<thead>
<tr>
<th></th>
<th>MBC:TC</th>
<th>MBN:TN</th>
<th>MBC:MBN</th>
</tr>
</thead>
<tbody>
<tr>
<td>−0.008 (115)</td>
<td>0.04 (66)</td>
<td>−0.113 (72)</td>
<td></td>
</tr>
<tr>
<td>0.162 (72)</td>
<td>−0.075 (47)</td>
<td>0.114 (51)</td>
<td></td>
</tr>
<tr>
<td>−0.003 (113)</td>
<td>−0.079 (62)</td>
<td>0.085 (69)</td>
<td></td>
</tr>
<tr>
<td>0.202 (54)</td>
<td>0.275 (27)</td>
<td>−0.037 (32)</td>
<td></td>
</tr>
<tr>
<td>−0.112 (56)</td>
<td>0.413 (28)*</td>
<td>−0.143 (36)</td>
<td></td>
</tr>
<tr>
<td>−0.099 (55)</td>
<td>0.386 (30)*</td>
<td>−0.315 (39)</td>
<td></td>
</tr>
<tr>
<td>−0.082 (68)</td>
<td>0.202 (36)</td>
<td>−0.357 (54)**</td>
<td></td>
</tr>
<tr>
<td>−0.411 (10)</td>
<td>−0.011 (14)</td>
<td>−0.142 (7)</td>
<td></td>
</tr>
<tr>
<td>−0.352 (15)</td>
<td>−0.321 (11)</td>
<td>0.281 (11)</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Number of observations (k), Qb (between-group heterogeneity) statistics, and P values for soil C and N pools and each of the categorical moderating variables.

<table>
<thead>
<tr>
<th>Moderating variable</th>
<th>Categories (levels)</th>
<th>k</th>
<th>Qb</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tillage</td>
<td>No till</td>
<td>77</td>
<td>0.01</td>
<td>0.468</td>
</tr>
<tr>
<td></td>
<td>Conv. till</td>
<td>134</td>
<td>79</td>
<td>0.762</td>
</tr>
<tr>
<td>N fertilizer</td>
<td>no</td>
<td>228</td>
<td>0.04</td>
<td>0.209</td>
</tr>
<tr>
<td></td>
<td>yes</td>
<td>57</td>
<td>31</td>
<td>0.553</td>
</tr>
<tr>
<td>No. crops in rotation</td>
<td>2</td>
<td>239</td>
<td>0.21</td>
<td>0.025</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>78</td>
<td>49</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>25</td>
<td>12</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>5+</td>
<td>26</td>
<td>8</td>
<td>0.4</td>
</tr>
<tr>
<td>Monoculture crop</td>
<td>corn</td>
<td>146</td>
<td>0.25</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>wheat</td>
<td>87</td>
<td>56</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>soy</td>
<td>34</td>
<td>18</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>sorghum</td>
<td>17</td>
<td>4</td>
<td>0.251</td>
</tr>
<tr>
<td></td>
<td>misc.</td>
<td>53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cover crop</td>
<td>no</td>
<td>264</td>
<td>0.27</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>yes</td>
<td>81</td>
<td>145</td>
<td>0.27</td>
</tr>
<tr>
<td>No. legumes</td>
<td>0</td>
<td>117</td>
<td>0.2</td>
<td>0.045</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>201</td>
<td>0.98</td>
<td>0.312</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>47</td>
<td>0.3</td>
<td>0.089</td>
</tr>
</tbody>
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Notes: Values in bold were significant at P < 0.05. “Conv. till” is conventional till; “misc.” includes miscellaneous monoculture crops.
In contrast to TC and TN, rotation effects on MBC and MBN were not influenced by cover crops or monoculture crop type. While reflecting the overall strength of the rotation effect on MB, our findings also align with others showing that MB is more sensitive than TC to aboveground plant biodiversity (Zak et al. 2003, Eisenhauer et al. 2010). For instance, Zak et al. (2003) found in a mesic grassland that increasing plant diversity from one to 16 species increased TC by 13% and MBC by 31%. Taken together, the strong rotation effect on MB coupled with the relative insensitivity of MB to factors controlling plant C inputs such as cover crops and monoculture crop type, suggests that MB dynamics are related to temporal crop biodiversity.

Climate and management control on the rotation effect

We explored a range of management-, climate-, and soil-related variables that could moderate the effects of rotations on soil C and N pools (Tables 1 and 2). Although management-related variables such as experiment duration, tillage, depth of soil sampling, and inorganic N fertilization rates had little correlation with the rotational biodiversity effect, two climatic variables, MAT and MAP, were positively correlated with the rotation effect on soil C and N. Both MAT and MAP are strongly correlated with NPP and the overall quantity of SOM inputs (Chapin et al. 2002), which are directly related to soil C and N concentrations and microbial biomass (Raich and Schlesinger 1992, Wardle 1992, Amundson et al. 2003, Fierer et al. 2009). We saw evidence of this in significant positive relationships between precipitation and MBN. Further, climate may also influence crop selection (Mendelsohn and Dinar 2003), such that varieties and species with greater production potential may be more common in regions with more favorable growing conditions.

While crop selection can play a vital role in determining the impact of rotations on soils, what other management decisions might also be important? Surprisingly, we found a lack of evidence that tillage or fertilization alter the effect rotations have on soil C and N and microbial biomass C and N (Table 2). This is in contrast to studies like Snapp et al. (2010), which demonstrated that management practices, such as conventional vs. organic, had superseded the crop biodiversity effect. We expected the rotation effect on soil C to be more pronounced when coupled with other soil C-building management practices, such as no-till, but saw no evidence that tillage was mediating the effect of rotations on soil C. This might suggest that the mechanisms driving SOM and MB differences in monoculture vs. rotation are different than those responsible for variations among till vs. no-till and fertilized vs. unfertilized systems. For example, if the
rotation effect on soil C is more biologically driven, with C accrual through increased MB growth efficiency (an estimate of the amount of microbial biomass produced per unit of substrate; Frey et al. 2013) and MB contributions to SOM formation, and C accrual under no-till systems is primarily driven by physical processes, including increased aggregation and physical protection of SOM (Balesdent et al. 2000, Six et al. 2000, Kahlon et al. 2013), then increases in soil C under no-till or with rotation would be somewhat independent of each other. Different mechanisms for soil C accrual such as those just described could explain why tillage and fertilization did not modify the rotation effect observed in this study.

In spatial-biodiversity manipulation experiments, which typically use up to 10 or more plant species, soil functioning (including C accrual) is commonly found to increase with plant diversity up to a “saturation” point at a certain level of biodiversity, after which soil functioning is no longer improved by the addition of more species (Zak et al. 2003, Reich et al. 2012). This idea is important in the context of agricultural systems where rotation management decisions must ultimately be based on economics, and rotations with more than 2–3 crops may not be profitable. Our analyses help to define the crop rotational species saturation curve for several very important soil functions in the context of management. In our study, the greatest number of crop species in rotation was six (Mitchell and Entry 1998), but the saturation threshold appeared to occur after the addition of only one crop (two total crops in rotation) for increasing TC and after the addition of two crops (three total crops in rotation) for increasing TN (Fig. 3). In contrast, we found a large overall increase in MBC (20.7%) and MBN (26.1%) with crop rotation that was not moderated by the number of crops in rotation. This finding was surprising, considering the sensitivity of MB to agricultural management, and considering that in spatial biodiversity studies, increases in plant richness (even up to 16 and 60 species) tends to show increased microbial biomass (Zak et al. 2003, Eisenhauer et al. 2010). In a grassland manipulation, Zak et al. (2003) showed that the saturation point where plant diversity no longer resulted in substantial increases in soil MB was eight species. However, it is likely that the full suite of interspecies interactions that may occur when multiple species coexist in space, as well as the exploitation of different niches by these species, are not realized with temporal biodiversity. Thus the effects of increasing biodiversity in cropping systems may be more limited, with a lower saturation point than in natural, spatially diverse systems.

Consequences of rotation effects

The results of our meta-analysis highlight the benefits of crop rotations; even simple two-crop rotations, relative to monoculture, had an estimated soil C sequestration rate of 50.6 ± 22.7 mg C [g soil]⁻¹ yr⁻¹. However, as previously discussed, the increase in soil C under rotations found in this study seems to be driven largely by the inclusion of a cover crop; soil C sequestration rates under a rotation with a cover crop of 119.2 ± 18.7 mg C [g soil]⁻¹ yr⁻¹ are significantly higher than soil C sequestration rates under rotation with no cover crop, 7.8 ± 25.6 mg C [g soil]⁻¹ yr⁻¹. In the United States, where an estimated 18% of cropland is in monoculture (Padgitt et al. 2000), the addition of one or more crops to rotations currently managed as monocultures could potentially increase soil C by 0.03 to 1.7 Gg (Kern 1994). Further, considering only monoculture systems may severely underestimate the potential for increased soil C accrual with cover crops because cover crops are used on only a small proportion of all cropland in the United States, including those lands currently in rotation (Dabney et al. 2001). This suggests that even though market demands may lead to transitions from rotations to monoculture cash crops, land managers could still optimize soil C storage, as well as soil fertility and sustainability, with the use of cover crops during periods between production of cash crops.

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Literature Cited


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SUPPLEMENTAL MATERIAL

Appendix A
A table depicting details for all the studies used in this meta-analysis on crop rotation effects on soil microbial biomass and organic matter dynamics, including a full list of the references used in this meta-analysis and their DOIs (Ecological Archives A024-033-A1).

Appendix B
A figure showing meta-analysis on the crop rotation effect on bulk density (Ecological Archives A024-033-A2).