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Review paper

Meta-analysis approach to assess effect of tillage on microbial biomass and enzyme activities

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ABSTRACT

Measures of soil biology are critical for the assessment of soil quality under different agricultural management practices. By modifying soil microclimate, tillage exerts the most important control on soil microbial communities. The objective of this study is to assess the effect of tillage on soil microbial biomass and enzyme activities. A meta-analysis was conducted utilizing 139 observations from 62 studies from around the world; the selected effect size (ES) was $\log_n$ of the response ratio (RR), the mean of the tilled treatment divided by the mean of the no-till control. This ES was calculated for seven different microbial properties – microbial biomass carbon (MBC) and nitrogen (MBN), metabolic quotient (qCO_2), fluorescein diacetate (FDA), dehydrogenase (DHA), β-glucosidase, and urease. Microbial biomass, metabolic quotient and enzyme activities were evaluated due their prevalent usage in evaluation of soil quality and use in soil quality indices. Overall, microbial biomass and all of the enzyme activities were greater under no-till compared to tillage. One exception to this was that under chisel tillage, there was no difference in MBC between the tilled plots and no-till. The qCO_2 was greater under tillage than under no-till indicating more active microbes in tilled soil, perhaps compensating for the reduced quantity. In contrast, when looking at only long-term experiments, qCO_2 was similar under both tillage and no-till, which may indicate that eventually microbes in no-till plots become as active as those in tilled plots even with the larger microbial community. The findings of this study illustrate that no-till and even reduced tillage, such as chisel tillage, promote larger microbial communities and greater enzymatic activity.

1. Introduction

The primary purpose of tillage in agricultural systems is to enhance crop production through weed control and seedbed preparation. Tillage systems are described based on the degree of soil inversion and percentage of residues remaining on the soil surface following tillage operations. The use of moldboard plow fully inverts the soil, while less intensive tillage vertically disrupts soil without inversion. Conventional intensive tillage practices leave less than15% residue on the surface while conservation tillage practices leave more than 30% of residue as a soil cover at the time of planting of the next cash crop (CTIC, 2015). The negative effects of tillage on soil erosion, degradation of soil structure, soil macro organisms and loss of nutrients and soil organic matter have led to increasing usage of conservation practices. Currently, conservation agricultural practices, such as non-tillage, are practiced on nearly 155 million hectares worldwide, which comprise 11% of the arable cropland in the world (Kassam et al., 2014). North and South America are the greatest adopters of conservation practices with no-tillage adoption rates of nearly 32% and 45%, respectively (Friedrich et al., 2012).

Management practices influence the soil environment and therefore the habitat of soil microorganisms in various ways. Soil organic matter (SOM) dynamics are highly dependent on the microbial community (Acosta-Martinez et al., 2003; Alvaro-Fuentes et al., 2013). The final product of decomposition that remain in the soil, microbial residues, may be resistant to further degradation

Abbreviations: RR, response ratio; LRR, log response ratio; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; qCO_2, metabolic quotient; FDA, fluorescein diacetate; DHA, dehydrogenase; β-glu, β-glucosidase.

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thereby protecting SOM through biochemical stability or physical protection within soil aggregates (Six et al., 2006; Jastrow et al., 2007; Schimel and Schaeffer, 2012). Improving the understanding on the rates of decomposition as influenced by management is also fundamental to improve SOM management in cropping systems (Scow, 1997; West and Post, 2002). Crop rotations influence the type and quantity of crop residues being returned to the soils (Karlen et al., 1994; McDaniel et al., 2014); N fertilization increases plant growth and subsequent organic matter inputs and N availability for soil microorganisms and as well as influencing the pH of the soil near the application zone (Geisseler and Scow, 2014). In contrast, tillage can influence microbes by changing both the soil microclimate as well as access to organic matter inputs. The soil microclimate is typically cooler and moister in no-till soils compared to the drier and warmer soils under more intensive tillage (Johnson and Hoyt, 1999; Martens, 2001). Access to organic matter is greater with tillage as organic residues are broken into smaller pieces, which increases the available surface area for microbial colonization (Johnson and Hoyt, 1999; Balesdent et al., 2000). Changes in the soil environment and soil microbial communities as a result of tillage then influences soil quality. The soil biological parameters investigated in this meta-analysis (microbial biomass, metabolic quotient, and enzymatic activities) were selected as they are commonly utilized in assessments of soil quality and as components of soil quality indices (Bastida et al., 2008).

Reviews by Johnson and Hoyt (1999) and Martens (2001) have both reported greater microbial abundance under no-till soils with a more favorable microclimate compared to soils under conventional tillage; similar results were reported by Kaschuk et al. (2010), Das et al. (2014), and (Balota et al., 2004). The degree to which microbial biomass increased under no-till compared to conventional tillage differed greatly, however, with a 17% increase reported by Das et al. (2014) and a 98% increase reported by Balota et al. (2004). While microbial biomass is often reported to be greater under no-tillage systems, no differences due to tillage have also been reported in de Gennaro et al. (2014). Despite a relative consensus of greater amounts of microbial biomass C under no-till, measures of microbial activity vary much more widely. Microbial activity measured through the metabolic quotient (microbial respiration/microbial biomass or qCO2) was reported smaller under no-tillage compared to conventionally tilled systems (Balota et al., 2004) suggesting that microbes are more active under conventional tillage. On the other hand, Babujia et al. (2010) found no differences between conventional tillage and no-till practices. Other approaches used to understand microbial activity is through quantification of the functional role microbes play in the cycle of nutrients. Typically, this has been quantified through the rates of enzymatic activity. However, understanding of their dynamics in soil systems as influenced by tillage is less clear and contradictory (Gil-Sotres et al., 2005; Laudicina et al., 2012).

Evaluating the effect of tillage on microbial biomass and activity with a meta-analysis approach will provide a quantitative analysis of the global response of microbial soil characteristics to different tillage practices. A meta-analysis is a statistical method of combining results from multiple data sets to evaluate the magnitude of the effect size as well as patterns of response and sources of heterogeneity (Gurevitch and Hedges, 1999; Borenstein et al., 2009; Koricheva et al., 2013). With this approach, we can also evaluate other possible sources of variability simultaneously influencing microbial properties. We expect minimally disturbed or no-tillage soils to have a larger microbial community as evidenced by greater microbial biomass C (Johnson and Hoyt, 1999; Balota et al., 2004; Das et al., 2014). Further, the reduced rates of soil disturbance are expected to reduce microbial enzymatic activity likely linked to slow rates of C and N mineralization from SOM. Specifically, the objectives of this study were to use a meta-analysis approach to 1) determine the effect size of tillage compared to no-till on microbial biomass and enzyme activities involved in the C and N cycles and 2) evaluate the influence of other sources of variability on the magnitude and direction of the effect size.

2. Materials and methods

2.1. Data collection and database

Data was collected through a process of data mining of the scientific literature using Thomas Reuters Web of Science v.5.16.1. We looked for peer-reviewed articles evaluating the effect of soil management practices on microbial biomass and activity. Keywords used for the initial search included “microbial biomass”, “microbial activity”, and “soil management”. This initial search produced 1242 articles, which were further refined by including “tillage” as another keyword to 380 articles. The literature search was restricted to peer-reviewed papers that were published between January 2000 and December 2014. The reference list from review papers on soil organic matter dynamics and soil microbial properties were further scrutinized to select additional peer-reviewed articles that had not been picked up by the initial search. Fig. 1 shows a flow chart illustrating the steps in data collection.

To construct the database, results from a publication were included if it met the following criteria for quality control and to ensure appropriate data collection: 1) Studies reported results on a minimum of one of the following soil biological parameters: microbial biomass (measured through chloroform-fumigation extraction (CFE), chloroform-fumigation incubation (CFI) or phospholipid fatty acids (PLFA) and microbial activity (measured through metabolic quotient and enzymatic activity of fluorescein diacetate (FDA), dehydrogenase, β-glucosidase, and urease) as affected by at least a no-till control and an alternative type of tillage used as treatments, 2) Articles reported data collected from field trials in grain-based studies, 3) Articles had clear specifications of experimental design and a minimum of two replications, 4) Articles included details on the length of the study, 5) Information on the location of the experimental site was provided so that additional environmental characteristics such as mean annual temperature and precipitation and soil texture could be obtained either from the same article or from additional secondary sources. A total of 62 peer-reviewed journal articles were included in the database. Multiple treatment pairs from the same study were included as separate observations when they could be categorized within separate subgroups for one or more moderating variables. A total of 137 treatment pairs were extracted; however, each treatment pair provided data for only a few microbial parameters evaluated within this study. The number of observations for each microbial property differed with 89 for microbial biomass C (MBC), 46 for microbial biomass N (MBN), 29 for metabolic quotient (qCO_2), 19 for fluorescein diacetate (FDA), 43 for dehydrogenase (DHA), 53 for β-glucosidase (β-glu), and 19 for urease. The locations for the studies included were far-ranging, and there were a minimum of three studies on every

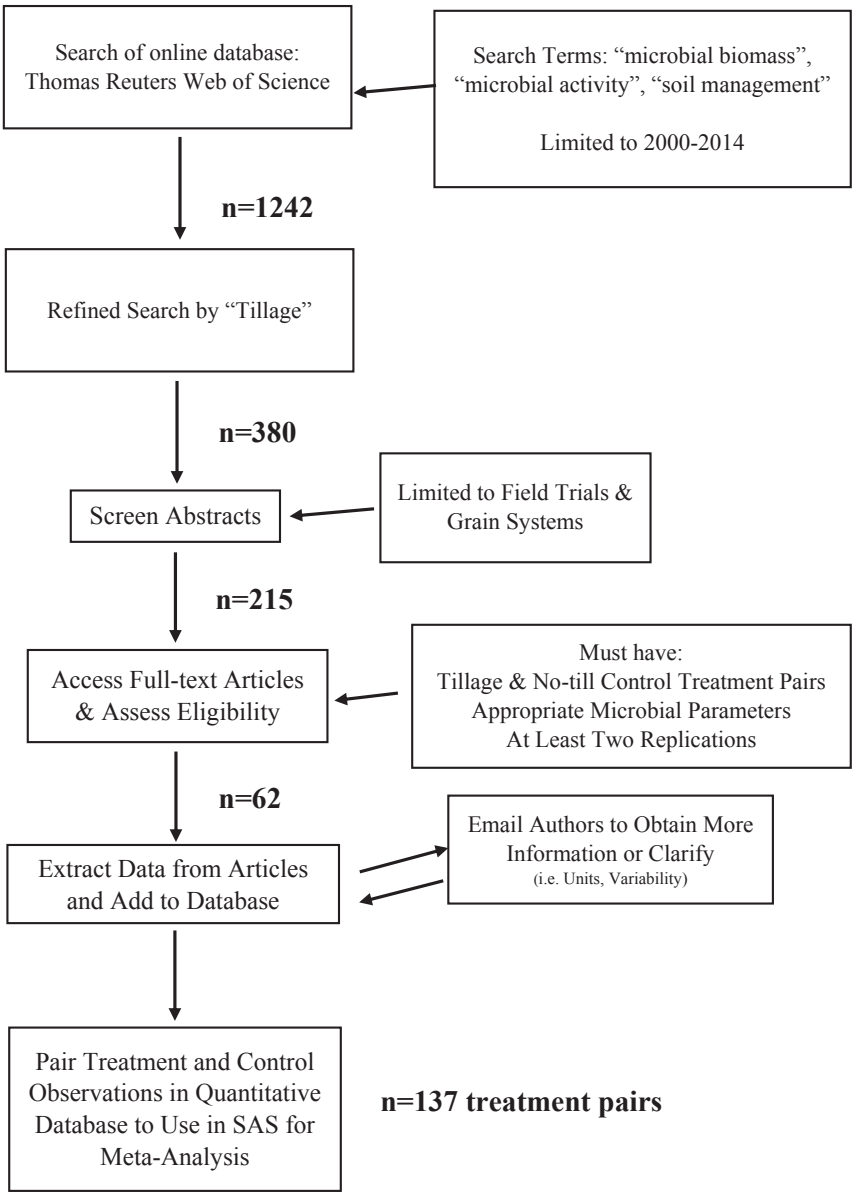

Fig. 1. Meta-analysis data collection flow chart. Outline of the steps in the data collection process as well as the number of journal articles included at each step.

continent excluding Antarctica.

Mean estimates for the response variables were extracted from tables, figures, and text. The PlotDigitizer software (http://plotdigitizer.sourceforge.net/) was utilized to extract data from figures. The tillage treatments were further characterized by tillage implements and depth of tillage. Additional classification variables that can help explain the variability in the data set and were included in the database were related to crop management practices including length of rotation and number of species within crop rotation, legume or cover crop use, and average annual nitrogen fertilizer rate. Study parameters such as duration of the experimental plots and depth of sampling were also recorded. When measurements for multiple sampling depths were available, a weighted average of the mean was reported. Environmental factors included in the database consisted of mean annual temperature and precipitation, soil organic carbon content, and soil texture. Many studies also reported data on multiple sampling dates; in such cases, the spring sampling date was included in the database where possible. If no spring sampling was reported, a fall sampling date was included in the database; the date of sampling was also recorded in the database. Measures of variability were recorded and converted to standard deviations as much as possible; a minimum of 50% and up to 89% of the SDs of treatment pairs for the seven microbial properties were available from the articles. Where missing, authors were contacted and as a last resort, standard deviations were estimated based on the average CV for the known data.

2.2. Data analysis

The statistical analysis was performed using methods for meta-analysis (Hedges et al., 1999) in the SAS statistical software

(version 9.4, SAS Institute Inc., Cary, NC). Meta-analysis use in agronomy and soil sciences has increased in the recent years (Miguez and Bollero, 2005; Gardner and Drinkwater, 2009; Kallenbach and Grandy, 2011; Geisseler and Scow, 2014; McDaniel et al., 2014) and has helped to make quantitative inferences on the effect of management practices on soil properties studied across multiple experimental sites, locations and climatic regimes. In this meta-analysis, we quantified the magnitude of the effect of tillage on the dependent variables identified as the response ratios (RR) between microbial properties (microbial biomass C, qCO_2, and soil enzymatic activity) in tillage treatments and a control or non-tillage treatment with the following equation:

$$RR = \overline{Y}_{till}/\overline{Y}_{no-till}. \quad (1)$$

A RR greater > 1 suggests a stronger effect of the tillage than non-tillage treatments on microbial soil properties. To normalize the data set, we then used a natural logarithmic transformation

$$LRR = \ln(RR). \quad (2)$$

The variance (υ_i) for each study was calculated using the following equation from Hedges et al. (1999).

$$\upsilon_i = \frac{SD^2_{till}}{n_{till} * \overline{Y}^2_{till}} + \frac{SD^2_{no-till}}{n_{no-till} * \overline{Y}^2_{no-till}}. \quad (3)$$

using the squared standard deviation (SD^2), sample size (n) and squared means ($\overline{Y}^2$) of the tillage and no-tillage treatment pairs.

The first step in this meta-analysis was the evaluation of total group heterogeneity in which the null hypothesis of no heterogeneity is tested using the Q_t statistic (Hedges et al., 1999). The LRRs were weighted using the inverse of the variance

$$w = 1/\upsilon_i. \quad (4)$$

If the test for Q_t is significant ($\alpha \leq 0.05$), it suggests that the effect of tillage varied among observations and that the introduction of additional moderator variables may help explain such variability (Miguez and Bollero, 2005). To allow for inferences beyond the only the studies included in this meta-analysis, a mixed model was used with study as a random effect and the moderator variables as fixed. For a mixed model, the means are weighted using the inverse of the total variance where the total variance is the sum of the with-in studies variance (υ_i) calculated in equation (3) and the between-studies variance ($\widehat{\sigma}^2_\theta$)

$$w^* = 1\Big/\left(\upsilon_i + \widehat{\sigma}^2_\theta\right) \quad (5)$$

The calculation of $\widehat{\sigma}^2_\theta$ followed the steps outline in Cooper and Hedges (1994), whereby the data was first analyzed in a fixed model using weights based only on the inverse of with-in studies variance from equation (4). The results of the fixed model were used to estimate between studies variance using the following equation

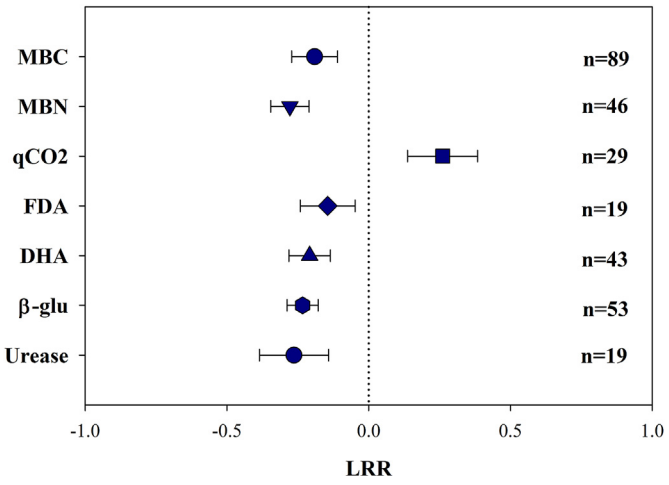

Fig. 2. Overall mean log response ratios for the seven microbial properties included in the meta-analysis: microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), metabolic quotient (qCO_2), fluorescein diacetate (FDA), dehydrogenase (DHA), β-glucosidase (β-glu), and urease. Values less than zero indicate a decrease in microbial biomass due to treatment and values more than zero indicate an increase in microbial biomass with tillage treatment compared to no-till control.

$$\widehat{\sigma}^2_\theta = \left[\frac{RSS}{k-p-1}\right] - \sum\frac{\upsilon_i}{k}. \quad (6)$$

where RSS is the residual sum of squares from the fixed model analysis, k is the number of studies used in the analysis for a particular moderator variable, ρ is the number of regression parameters, and $\sum \upsilon_i/k$ is the average of the with-in study variances. The final step is to run the analysis as a mixed model using weights based on the total variance from equation (6). Because not all observations included data on each moderator variable and the sums of squares were partitioned differently, an estimate of total variance was calculated separately for each moderator variable.

When the test of the moderator variable yielded P values ≤ 0.05 for categorical variables, we generated mean effect sizes and 95% confidence intervals. Means with confidence intervals not overlapping zero were considered significantly different.

The distribution of LRR for each microbial property was visually examined using the funnel plots to ensure that data points belonged to the same population distribution and to avoid publication bias. The funnel plot is a scatter plot of the LRR against the sample size or the variance. The general assumption is that effect sizes belonging to the same population have comparable magnitudes. In the effect size vs variance relationship, the former tends to be more variable in experiments with small sample sizes, but variability is reduced as sample sizes increase rendering to a funnel-shaped plot (Borenstein et al., 2009). Funnel plots for each soil microbial parameter are included in the Appendix (Figure A.1). Asymmetrical funnel plots indicate that there may be publication bias. Most of the plots were fairly balanced around the mean, but MBN and qCO_2 funnel plots both show some asymmetry at higher variance levels; therefore, there may be some publication bias for these two variables.

A sensitivity analysis was also conducted to evaluate the effect of changes to the analysis on the results. Different approaches to the analysis were conducted, such as study treated as fixed vs.

Table 1
Significance of the tests for management factors impacting the effect of tillage in the mixed model analysis for microbial biomass carbon, microbial biomass nitrogen, and metabolic quotient. DF is degrees of freedom. Probability values less than 0.05 are italicized and in bold.

Source	Microbial biomass carbon			Microbial biomass nitrogen			Metabolic quotient		
	DF	Error DF	*p* Value	DF	Error DF	*p* Value	DF	Error DF	*p* Value
Tillage implement	3	37	***0.024***	2	16	0.574	2	17	0.088
Depth of tillage	1	22	***0.013***	1	9	0.694	1	6	0.119
Rotation type	4	37	0.876	3	18	0.228	2	16	0.0587
Legume	1	43	0.741	1	21	0.338	1	18	0.400
Cover crop	1	42	0.941	1	19	0.666	1	17	0.110
N fertilizer rate	1	17	0.560	1	11	0.616	1	5	0.142
Sampling timing	2	34	0.939	2	20	0.521	2	13	0.765
Sampling depth	1	43	0.298	1	20	0.297	1	17	0.608
Study duration	2	40	0.471	2	20	0.687	1	18	***0.003***
Temperature	1	43	0.173	1	21	0.908	1	18	0.305
Precipitation	1	43	0.104	1	21	0.344	1	18	0.678
Soil organic carbon	1	39	0.745	1	21	0.387	1	18	0.061
Percentage clay & silt	1	32	0.130	1	16	0.295	1	18	***0.031***

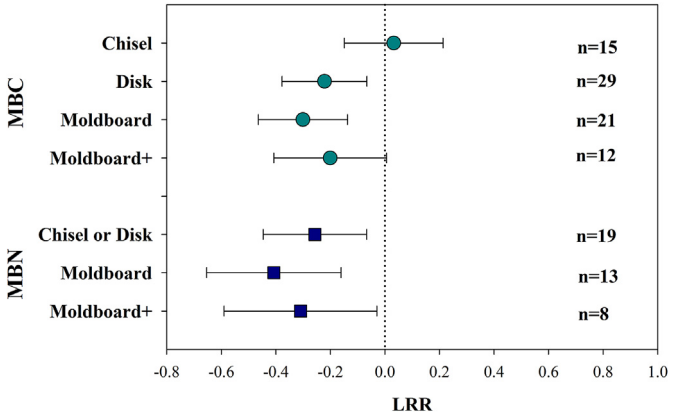

Fig. 3. Mean log response ratios (LRR) and 95% confidence intervals for tillage implements for microbial biomass carbon (MBC) and nitrogen (MBN). Values less than zero indicate a decrease in microbial biomass due to treatment and values more than zero indicate an increase in microbial biomass with tillage treatment compared to no-till control.

random, unweighted vs. weighted, removal of influential data. These were compared to evaluate the robustness of the conclusions drawn from the results. The sensitivity analysis indicated that results from the weighted analysis of a mixed model were different from the simpler models, which indicates that the more complex models are necessary.

3. Results

3.1. Overview of microbial properties

The forest plots in Fig. 2 show the mean log response ratio and the 95% confidence intervals for each of the investigated microbial properties. The mean log response ratios were negative for all of the microbial properties with the exception of qCO_2. The negative mean LRRs ranged from −0.28 for MBN to −0.14 for FDA, while the lone positive mean LRR of qCO_2 was 0.26. The positive LRR for qCO_2 indicates that qCO_2 was greater under tillage than no-till. When the LRR is negative as for microbial biomass and the enzymatic activity, the measured property was greater under the no-till control than the tillage treatment.

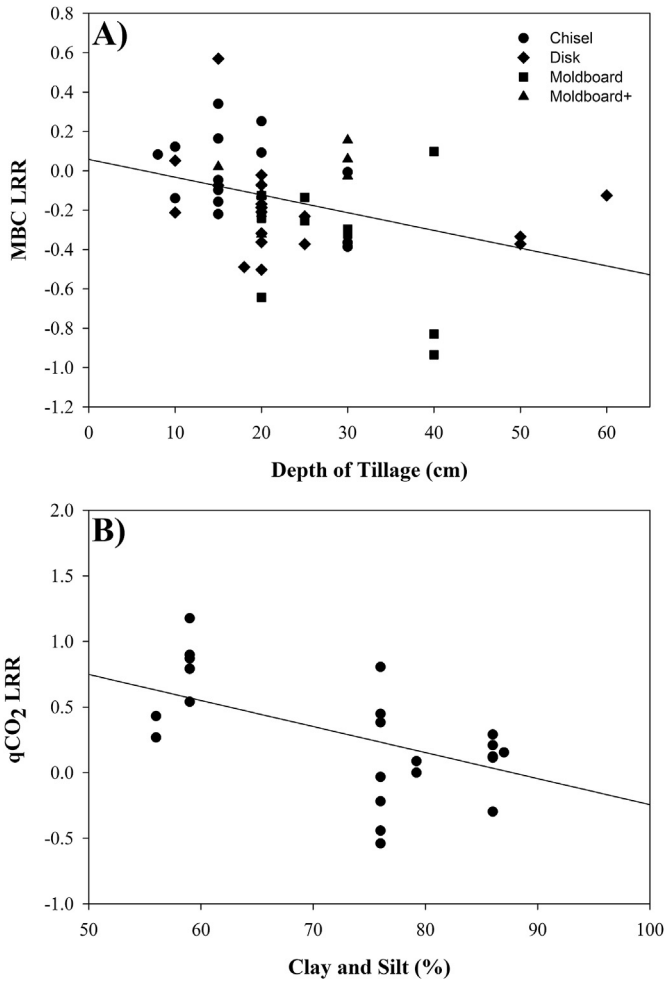

Fig. 4. Scatter plot with linear regression graph of the natural logarithm of response ratio [tillage mean/no-tillage mean (LRR)] for a) microbial biomass carbon (MBC) versus depth of tillage operations (n = 54) and b) metabolic quotient (qCO_2) versus percentage of clay and silt (n = 25).

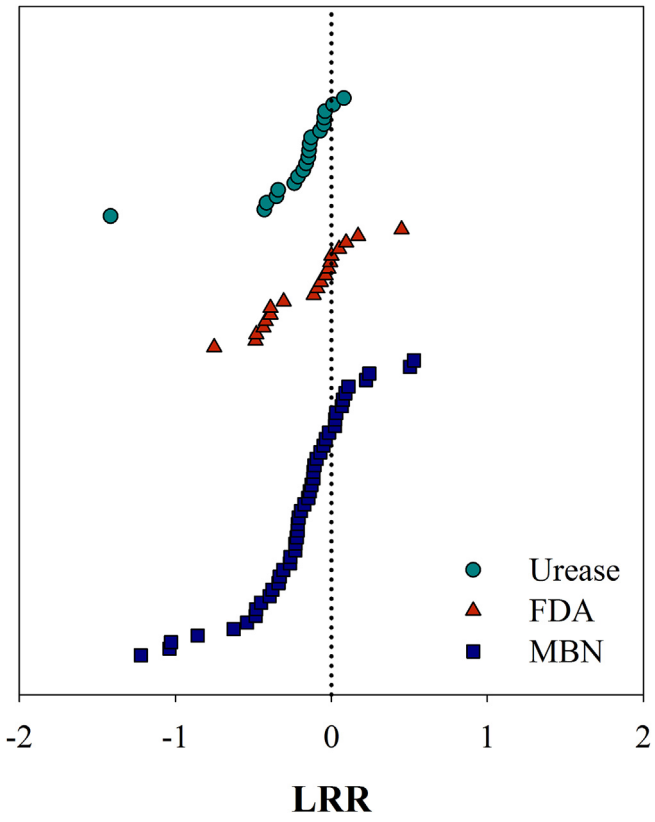

Fig. 5. Natural log response ratios (LRR) of 46 microbial biomass nitrogen (MBN), 19 fluorescein diacetate (FDA), and 19 urease observations. Values less than zero indicate a decrease in microbial biomass due to tillage and values more than zero indicate an increase in microbial biomass with tillage treatment compared to no-till control.

3.2. Microbial biomass

The test for heterogeneity for MBC was significant ($Q_t = 959$, $df = 89$, $p < 0.0001$), which indicates that the response ratios were not homogenous across all observations and other factors may be influencing the effect of tillage. Further analysis tested the influence of the moderator variables in Table 1, which revealed tillage implement and tillage depth significant at $\alpha = 0.05$ for MBC. The forest plot presented in Fig. 3 shows the means and 95% confidence interval for the different levels of tillage implements. A LRR with a value of 0 indicates that there was no difference between the tillage treatment and no-till for MBC. When the LRR is negative, MBC was greater for the no-till control than the tillage treatment. When the LRR is positive, MBC was greater under tillage than no-till.

For MBC, the four subgroups of tillage implements tested were chisel, disk, moldboard, and moldboard+. The level moldboard + refers to the use of moldboard plow plus another implement, either chisel or disk tillage. There were a minimum of 12 observations for each of these subgroups. For the more intensive levels of tillage (moldboard and moldboard+), MBC was reduced under tillage compared to no-till. Microbial biomass carbon under chisel tillage did not differ from MBC under no-till; in contrast, the results for disking are very similar to those of the more intensive tillage with less MBC under tillage than no-till. While both chisel and disk tillage are typically considered to be less intensive than moldboard tillage, in some cases, disk tillage sometimes inverts the soil in a similar manner to moldboard plow, especially when set to deeper tillage depths and/or with multiple passes. Like tillage implement type, the depth of tillage was significant and was able to

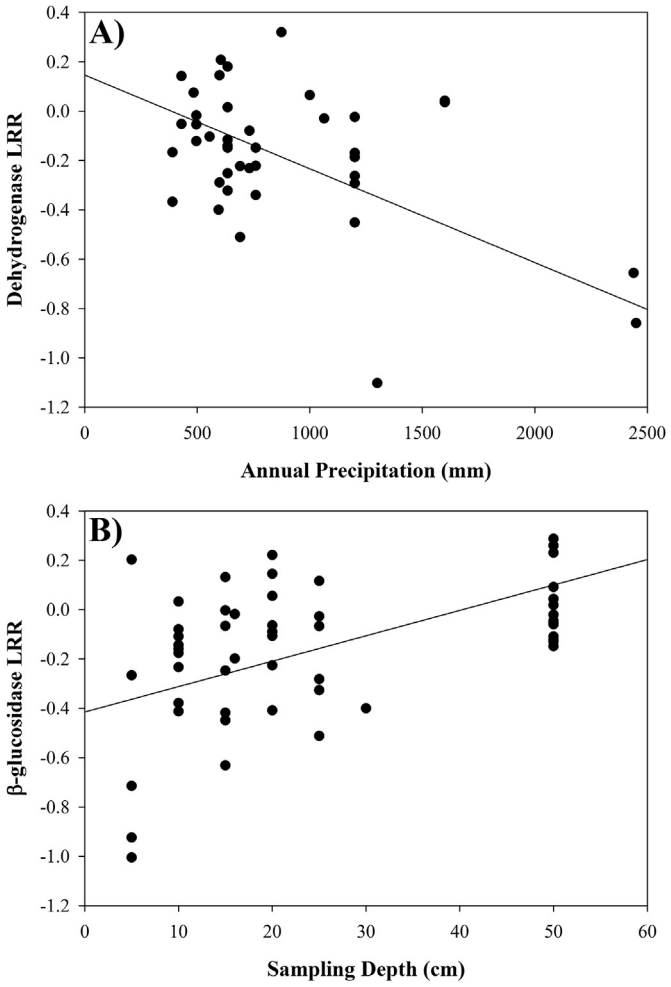

Fig. 6. Scatter plot with linear regression graph of the natural logarithm of response ratio [tillage mean/no-tillage mean (LRR)] for a) dehydrogenase (DHA) versus mean annual precipitation (mm) (n = 43) and b) β-glucosidase (β-glu) versus sampling depth (cm) (n = 53).

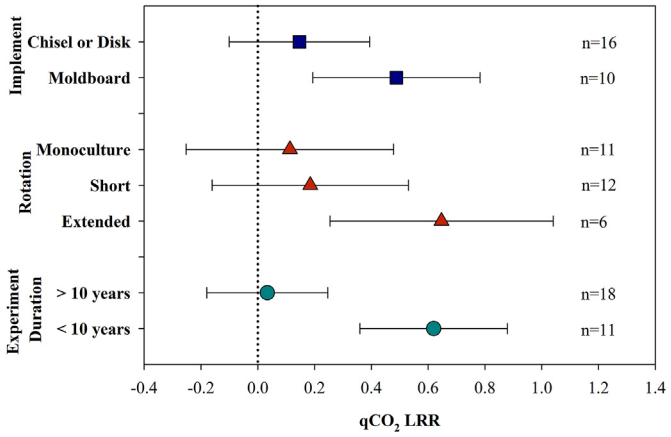

Fig. 7. Mean log response ratios (LRR) of metabolic quotient (qCO_2) and 95% confidence intervals for three moderator variables – tillage implement, rotation length, and experiment duration. Values less than zero indicate a decrease in microbial biomass due to treatment and values more than zero indicate an increase in microbial biomass with tillage treatment compared to no-till control.

Table 2
Significance of the tests for management factors impacting the effect of tillage in the mixed model analysis for the enzymatic activities of fluorescein diacetate (FDA), dehydrogenase (DHA), β-glucosidase, and urease. DF is degrees of freedom. Probability values less than 0.05 are italicized and in bold.

Source[a]	Fluorescein diacetate			Dehydrogenase			β-glucosidase			Urease		
	DF	Error DF	*p* Value	DF	Error DF	*p* Value	DF	Error DF	*p* Value	DF	Error DF	*p* Value
Tillage implement	1	10	0.618	2	15	0.581	2	28	0.321	–	–	–
Depth of tillage	–	–	–	1	13	0.290	1	9	0.057	1	3	0.709
Rotation type	2	10	0.180	1	20	0.957	2	24	0.952	–	–	–
Legume	1	11	0.590	1	20	0.594	1	30	0.791	–	–	–
Cover CROP	1	11	0.548	1	20	0.629	1	31	0.944	–	–	–
N fertilizer rate	–	–	–	1	8	0.487	1	20	0.925	–	–	–
Sampling timing	2	10	0.751	2	19	0.887	2	28	0.653	–	–	–
Sampling depth	1	10	0.935	1	20	***0.021***	1	30	***0.031***	1	6	0.717
Study duration	1	11	0.447	1	19	0.155	2	30	0.141	–	–	–
Temperature	1	10	0.648	1	20	0.117	1	31	0.804	1	8	0.724
Precipitation	1	10	0.265	1	20	***0.001***	1	31	0.364	1	8	0.610
Soil organic carbon	1	8	0.476	1	20	0.316	1	29	0.264	1	7	0.400
Percentage clay & silt	1	8	0.180	1	14	***0.013***	1	24	0.263	1	5	0.185

[a] Some moderator variables were not analyzed for FDA or urease due to too few observations ($k < 7$).

explain some of the variation (Table 1). The slope statistically differed from zero with the 95% confidence interval of −0.02 to −0.002. Fig. 4A shows the scatter plot and regression line. As the depth of tillage increased, the LRR decreased; therefore, deeper tillage reduced MBC compared to no-till more so than shallower tillage.

The test for heterogeneity for MBN was also significant ($Q_t = 852$, df = 45, $p < 0.0001$). When moderator variables were evaluated for their contribution to the variation, none of the moderator variables tested were significant (Table 1). The mean effect size for MBN was −0.19 with a 95% confidence interval of −0.42 to −0.14, indicating like MBC, a reduction in MBN under tillage compared to no-till. However, Fig. 5 shows that although no moderator variable was significant, there is still a great deal of variability within the observations. The forest plot in Fig. 3 shows the LRRs for tillage implements for MBN and all of the 95% confidence limits for the different tillage implement subgroups are below zero, indicating that MBN under tillage is less than no-till for all tillage implements. However, it is important to note that for MBN, chisel and disk tillage were combined together into one subgroup. Since disk tillage differed from chisel tillage for MBC, it is possible that this is possible that this is also true for MBN; however, because of the low number of observations for disk tillage, these two subgroups were combined together so this could not be further tested.

3.3. Metabolic quotient

Metabolic quotient is the ratio of basal respiration to microbial biomass and is an indicator of how active the microbial community is. The test for heterogeneity was significant for qCO_2 ($Q_t = 451$, df = 28, $p < 0.0001$). Both study duration and the percentage of clay and silt in the soil were significant and may be able to explain some of the variation (Table 1). The metabolic quotient in experiments that had been in place for more than 10 years were similar under both tillage and no-tillage systems as the LRR was near zero (Fig. 7). In contrast, shorter experiments in place for less than 10 years showed a marked difference between tillage and no-till. With a mean LRR of 0.62, qCO_2 was greater under no-till than tillage in the first 10 years of experiments. Soil texture was also an important contributor to variation within the dataset as the percentage of clay and silt was significant with a slope with a 95% confidence interval of −0.04 to −0.002 (Fig. 4B). Under sandier soils, the qCO_2 was greater under no-till compared to tilled, but as the percentage of fine particles increased, the smaller the difference between till and no-till became. While not significant at $\alpha = 0.05$, forest plots for both rotation and tillage implement are shown in Fig. 7. All three of the rotations showed a fairly large amount of variability, but the key difference is that under the extended rotation, qCO_2 under no-till was greater than under till as the confidence interval does not cross zero; the extended rotation consisted of at least a three year rotation with a minimum of three crop species. Likewise for tillage implement, qCO_2 under moldboard tillage was less than no-till, but for chisel or disk tillage there was little difference between tillage and no-till.

3.4. Total microbial activity

Both FDA and DHA are enzymes that are typically used as indicators of total microbial activity. The test of heterogeneity was significant for both FDA ($Q_t = 138$, df = 18, $p < 0.0001$) and DHA ($Q_t = 2862$, df = 42, $p < 0.0001$). For FDA, none of the moderator variable were significant (Table 2); the log response ratios for FDA can be seen in Fig. 5. This graph shows that there is some variability, but none of the moderator variables were able to explain it sufficiently. The mean effect size for FDA was −0.14, but the 95% confidence interval encompassed zero (−0.37 to 0.08).

Variation in DHA, in contrast to FDA, had a number of different moderator variables that were significant: sampling depth, precipitation, and percentage clay and silt (Table 2). However, the high amount of variability and a number of influential data points make interpretation of the results complicated. For both sampling depth and percentage clay and silt, sensitivity analysis revealed that although slope was significant for both (0.017 and 0.011, respectively), the removal of a single influential point made the slope no longer significant. Therefore, it is doubtful that this is a true explanation of the variation in the data. For annual precipitation, the mean of the slope is negative indicating that at locations with greater precipitation, DHA activity is greater under no-till than till, but in drier conditions, DHA activity is similar regardless of tillage practice. However, it is important to note that the 95% confidence interval for the slope was from −3.73 to 0.0013 (Fig. 6A). This confidence interval is very wide and does include zero indicating that there is a high amount of variability remaining in the data.

3.5. Carbon and nitrogen cycling

Two enzymes were included in the meta-analysis to provide insight to how the cycling of carbon and nitrogen may differ under no-till and tilled systems. β-glucosidase is an important enzyme in the carbon cycle as a cellulose. Urease was included to show the nitrogen cycle. The test for heterogeneity for β-glucosidase was, significant ($Q_t = 4467$, df = 52, $p < 0.0001$). For β-glucosidase, the moderator variable of sampling depth was significant (Table 2) with the 95% confidence interval for the slope as 2.26 to 0.0314 (Fig. 6B). For soil sampled to greater depths, the difference between tillage and no-till decreased as the LRR became closer to zero. Near the surface, β-glucosidase activity was greater under no-till than tillage.

Like FDA and MBN, the test for heterogeneity was significant for urease ($Q_t = 202$, df = 18, $p < 0.0001$), but none of the moderator variables were significant (Table 2). The LRR for all of the urease observations are in Fig. 4 and the majority of the points are just below zero indicating that urease activity was slightly greater in no-till than tillage in most of the observations. This is in agreement with the mean LRR for urease as it was −0.264 with a 95% confidence interval of −0.53 to 0.01.

4. Discussion

4.1. Impact of tillage on microbial properties

One of the key benefits of utilizing soil biological properties is their purported sensitivity of these measures to management changes (Gianfreda and Ruggiero, 2006; Joergensen and Emmerling, 2006) while also being considered to be useful indicators of soil quality (Bastida et al., 2008). Based on the overall mean LRRs for each of the parameters (Fig. 2), it is evident that all of the soil microbial parameters included in this meta-analysis have the potential to provide valuable information about the impact of tillage on soil microbial communities, but none can be considered to be more sensitive to management than the others. When selecting which of these microbial properties to measure, the decision should be based primarily on which aspect of microbial community is of interest. Microbial biomass carbon and nitrogen can only indirectly indicate the size of the microbial community, while metabolic quotient and certain enzymatic activities, such as FDA and DHA, can provide insight into the activity of the microbial community. Enzymes related to specific nutrient cycles, such as β-glu in the carbon cycle and urease in the nitrogen cycle, can show how the functional diversity of the microbial community is impacted.

Microbial biomass was reduced under tillage compared to no-till as measured by both MBC and MBN. The greater microbial biomass under no-till soils has been previously reported (Balota et al., 2004; Kaschuk et al., 2010) as there are more favorable environmental conditions under no-till for microbes leading to larger microbial biomass. An important difference from this pattern is that chisel tillage was exception to this trend, as the mean LRR for this subgroup was close to zero indicating that MBC under tillage did not differ from no-till (Fig. 3). While this does not provide information about the diversity of the microbial community, this result indicates that microbial community size is not suppressed by chisel tillage. In contrast, the impact of disk tillage on microbial biomass was not different from that of a moldboard plow, which is typically considered to disturb the soil much more than other types of tillage implements. If set to a deeper tillage depth, disk tillage can invert the soil and this may lead to similar effects on the soil microbial community as the soil inversion due to a moldboard plow. While the categorization of tillage implement is helpful, the depth of tillage is also important, especially as an explanation for the seeming discrepancy with disk tillage. As expected, the LRR for shallow tillage is near zero and the LRR becomes more negative for deeper tillage (Fig. 4A). This matches up with tillage implement analysis as most of the shallow tillage is chisel tillage. As can be seen in Fig. 4A, disk tillage was done to a wide variety of depths with some at very shallow depths and some to as deep as 50–60 cm.

None of the remaining microbial properties differed based on tillage implement or tillage depth. Metabolic quotient was the only microbial property that was greater under tillage than no-till (Fig. 2). This indicates that the microbes are more active under tillage; it may be possible that the greater access to crop residues due to tillage may lead to an increase in microbial activity; however, this is likely to be a short-term effect and could not fully explain the results we found as only a small number of the observations were measured shortly after tillage. Timing of the sampling was tested as a moderator variable and was not significant so the more likely explanation is that there is greater activity per unit of microorganisms to compensate for the reduced size of the microbial community. It is possible that both explanations are partially responsible for this result, but we cannot tell from this data.

All of the enzyme activities were greater under no-till compared to tilled systems as has been previously reported (Gianfreda and Ruggiero, 2006; van Capelle et al., 2012). The degree to which each enzyme was reduced under tillage compared to no-till was very similar. The greater enzyme activity under no-till indicates there is also greater functional diversity. While outside the scope of this analysis, this may be due to more microbial diversity as well. As with microbial biomass, the greater enzyme activity and potentially microbial diversity under no-till is likely a result of favorable microclimate. Another important aspect is that with less frequent disturbance of the soil, fungal hyphae are less disturbed and fungi play an important role in the cycling of carbon and nitrogen and the enzymes measured (van Capelle et al., 2012).

4.2. Experimental procedure factors

A number of different experimental artifacts were evaluated as sources of variation, including study duration, sampling timing and depth. Surprisingly, sampling timing was not significant for any of the microbial properties. Others have reported that enzymes, in particular, can differ seasonally (Gianfreda and Ruggiero, 2006) so it was unexpected that sampling timing was not significant for any of the enzymes. This may be related to the manner in which the timing was recorded and analyzed. Each observation was categorized as one of three timing subgroups. The first subgroup was early timing—following tillage and either before or directly following planting of the main crop in the rotation. The second subgroup was during the growing season and the final subgroup was any time after harvest before tillage operations were completed. This categorization was chosen because of the difficulty of using dates or seasons because of the global scale of the data. Ideally, the timing would have been based on how many days or months following tillage, but this was the best compromise for data collection.

Study duration was significant for qCO_2 with long-term

experiments having similar microbial activity under no-till as tillage systems; in shorter studies, qCO_2 was greater in no-till than under tillage. Since many of these studies were started on previously cultivated soils, we cannot make any conclusions about how qCO_2 has changed from undisturbed systems. In fact, it is more likely that all of the soils were tilled prior to the initiation of the study. From this we can assume that the effect of tilling the soil on qCO_2 is unlikely to change over time and rather, it is the microbial activity under no-till that has changed over time. The results suggest that after 10 years of no-till the microbial activity has increased to be similar to the activity under tilled soils.

Sampling depth was significant for β-glucosidase with an increase in LRR at greater soil depths, which means that when sampled to greater depths, there was little difference between till and no-till while when sampled only to shallow depth, β-glu was greater for tillage compared to no-till. This is not too surprising since a common characteristics of no-till soils is stratification of nutrients and therefore microbial communities. Tillage mixes crop residues and nutrients into the soil as well as aerates the soil facilitating microbial growth at deeper depths than possible under no-till soils. For instance, if the depth of tillage in a soil were 30 cm, the LRR would be different depending on if β-glu were measured for only the top 20 cm or the top 30 cm. Microbial activity would be concentrated in the portion of the soil under no-till, but distributed down to at least the depth of 30 cm under tillage. Like we found, the LRR would be negative if measured at 20 cm, but if measured to the greater depth of 30 cm, the LRR would be closer to zero. This pattern is expected to be true for the other enzyme activities as well as microbial biomass, so it is somewhat surprising that sampling depth was not able to explain variation for the other microbial properties.

4.3. Environmental factors

Environmental factors that were assessed as possible sources of variation included climatic factors, such as temperature and precipitation and soil characteristics, such as soil organic carbon and soil texture. In sandier soils, qCO_2 was greater in tilled soils than no-till, but as the percent of fine particles increased, the closer the LRR became to zero. This indicates that with finer soil, microbial activity under no-till was similar to that of tillage. Finer particles, especially clay, play an important role in cation exchange capacity and water holding capacity; soils that have higher levels of those properties may lead to increases in microbial activity as there is more water and nutrients available for microbes under no-till so that qCO_2 is similar to that under tillage.

The LRRs for dehydrogenase were more negative with greater annual precipitation, while under drier conditions the LRRs were close to zero. Under dry conditions, there was little difference between till and no-till, perhaps as microbial activity was suppressed under both systems as soil moisture was scarce. When plenty of precipitation was available, DHA under no-till was greater than that under tillage. This results is somewhat surprising as it is under dry conditions, when no-till soils retain more moisture due to the residue mulch on the surface that we might expect to see greater microbial activity under no-till soils compared to tilled soils. This may be a function of using the mean annual precipitation, which does not necessarily the soil moisture at the time of sampling, nor the amount of precipitation received in the particular year of sampling.

4.4. Microbial property variability

Despite the significant test for heterogeneity for each, it was not possible to explain the source of variation using moderator variables for three of the microbial properties—MBN, FDA, and urease. This illustrates some of the difficulty in evaluating the effect of tillage (and other management practices) on microbial properties. These measurements are highly variable and even using the meta-analysis approach, it was difficult to determine the sources of that variability. It is possible that other moderator variables that were not provided in the articles could be important and unfortunately will be difficult to assess. Another possibility is that there is not a clear source of variability and the measurements themselves are just highly variable.

5. Conclusions

Meta-analysis allows us to draw conclusions from a much larger source of data to determine how microbial properties respond to tillage compared to no-tillage and to determine how other sources of variation may impact those results. Our analysis compile the results of more than 60 experiments from across the globe for seven different microbial properties. Based on the results of this meta-analysis, microbial biomass and enzyme activities, in general, are greater under no-till than under tillage. There are some exceptions to this; one of the most important is that microbial biomass was not diminished under chisel tillage. Classifying chisel tillage as conservation tillage is in fact accurate from the perspective of the size of the microbial community as it was similar to no-till. Unfortunately, there were no difference among tillage implements for other microbial properties, indicating that for other microbial properties, chisel tillage reduced enzyme activities and microbial biomass nitrogen similarly to other tillage practices. Metabolic quotient was, in general, greater under no-till than tillage; however, for long-term experiments qCO_2 was similar for till and no-till, perhaps indicating an increase in microbial activity under no-till after at least 10 years without soil disturbance. Environmental conditions, such as precipitation and soil texture can also impact the effect of tillage on microbial properties.

Ultimately, evaluating microbial properties is often difficult due to the high variability within the measurements due to a number of factors including seasonal differences and environmental differences. In this analysis, we attempted to test for those sources of variability, but they were surprisingly not as important to the variability as expected. This means that there are other causes for the variability that we were not able to assess. Further use of the meta-analysis approach in soil biology is needed to help to fill in those gaps, especially as these measures are increasingly utilized to assess soil quality and health.

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Appendix

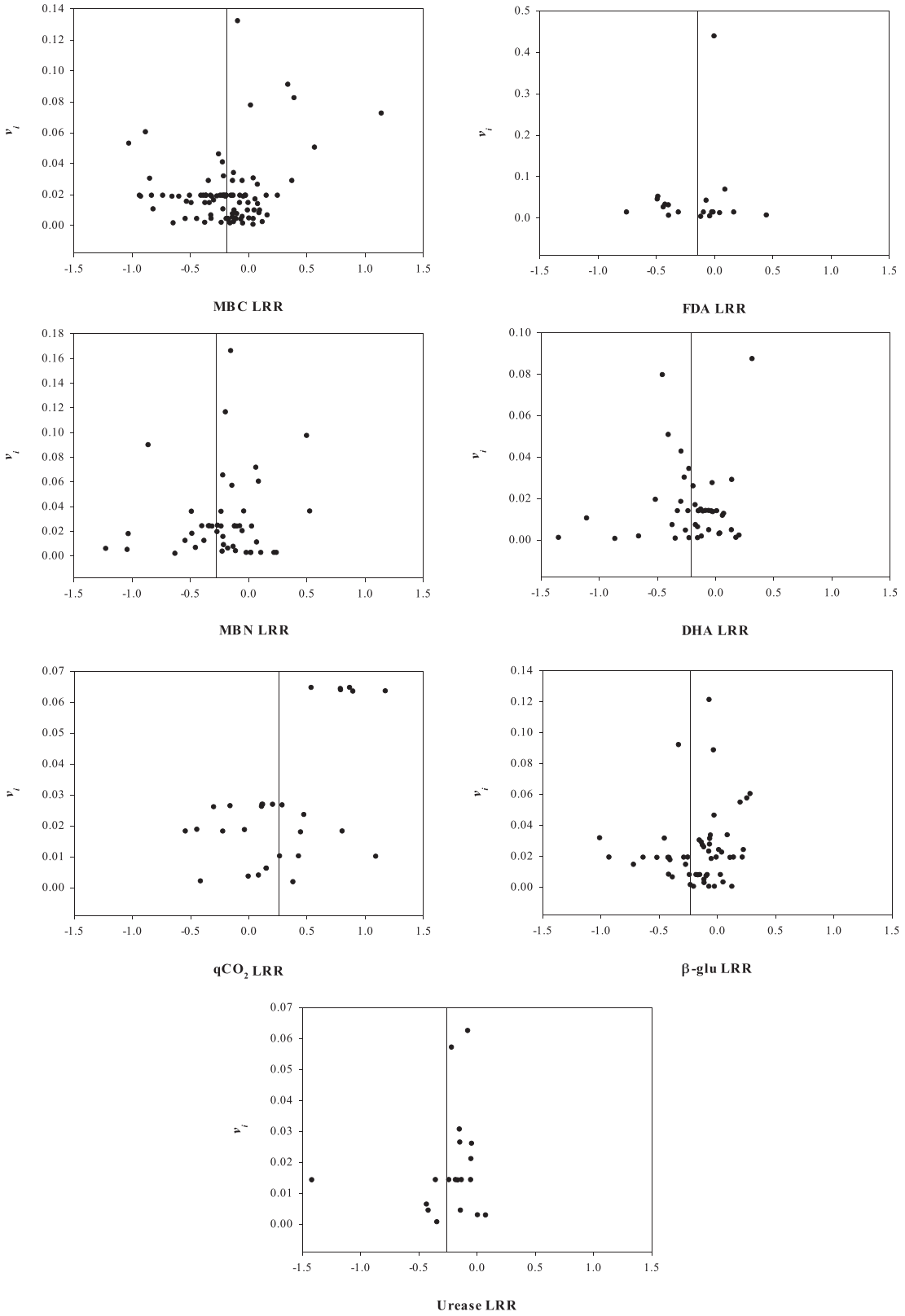

Fig. A.1. Funnel plots for microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), fluorescein diacetate (FDA), dehydrogenase (DHA), β-glucosidase (β-glu), and urease. Each graph has the variance of the observation (v_i) plotted against the natural logarithm of the response ratio (LRR); the vertical line is the weighted mean effect size.

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