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Cover cropping enhances soil microbial biomass and affects microbial community structure: A *meta*-analysis

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ABSTRACT

Cover crops have been increasingly grown for improving soil health and crop production and minimizing environmental impact compared to no cover crop. Systematic documentation of cover cropping effects on soil microbial abundance and community structure, however, is scarce. A *meta*-analysis including data from 81 available studies was conducted to elucidate the effect of "cover crop" *versus* "no cover crop" on soil microbial community abundance and structure. Microbial biomass C and N (MBC and MBN) and total phospholipid-derived fatty acids (PLFA) were taken as proxies for soil microbial abundance, and total fungi, total bacteria, gram-positive and -negative bacteria, actinomycete, and arbuscular mycorrhizal fungi (AMF) for microbial community structure. Compared to no cover crop, cover crop overall enhanced PLFA, MBC, and MBN by 24, 40, and 51%, respectively. Soil total bacteria and total fungi, and the groups in them increased by 7–31% with cove crop compared to no cover crop. Fungi were affected more by cover crop than bacteria as indicated by the greater fungi/bacteria ratio. In depth categorical *meta*-analyses revealed that the legume and nonlegume cover crop mixture reduced MBC, PLFA, and actinomycete compared to legume or nonlegume cover crop alone. Legume cover crop enhanced actinomycete in comparison to nonlegume or the cover crop mixture. Incorporation of cover crop residue into the soil increased PLFA, total bacteria, AMF root colonization, and spore density, but decreased gram-positive and -negative bacteria and AMF compared to residue placed at the surface or removed from the soil. Microbial parameters due to cover crop compared to no cover crop were related to soil properties and annual precipitation. Medium-textured soils showed greater response of cover crop on PLFA, total bacteria and fungi, and actinomycete than fine- or coarse-textured soils. We conclude that cover crops enhance soil microbial community biomass and affected community structure compared to no cover crop and the responses of microbial parameters to cover crop varied with soil and climatic conditions. Cover crops can enhance biological soil health by enhancing microbial community abundance compared to no cover crop.

1. Introduction

Cover cropping, a conservation practice to reduce soil erosion, has been widely adopted by producers to increase soil organic matter (Poeplau and Don, 2015) enhance nitrogen (N) cycling (Sainju et al., 2003), improve soil structure (Blanco-Canqui et al., 2011), and reduce pest infection and N leaching compared to no cover crop (Lupwayi et al., 2012; Daryanto et al., 2018). The improvement in soil and environmental quality with cover crop compared to no cover crop was primarily due to the addition of above- and belowground residue in the soil. As decomposition of crop residue is controlled by soil biota, information on the effects of cover crop on soil microbial biomass, community structure and diversity is needed to understand their relationship on nutrient cycling, C sequestration, and soil health (Frasier et al., 2016).

Cover crop species and management of residue affect microbial

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abundance and community structure due to difference in quality and quantity of residue returned to the soil (Martinez-Garcia et al., 2018). Generally, legume cover crops supply more N from biological N fixation to succeeding crops than nonlegume or no cover crop (Gabriel et al., 2012). In contrast, nonlegume cover crops can be more effective in enhancing soil organic matter and reducing N leaching due to their greater biomass production (Sainju et al., 2002, 2003). Sainju et al. (2007) reported that nonlegume cover crops increased microbial biomass C (MBC) compared to legume cover crops due to higher biomass yield and C content, but legume and mixed (legume + nonlegume) cover crops increased soil respiration compared to nonlegume cover crops. However, Wang et al. (2007) found that cover cropping with cowpea (*Vigna unguiculata* L.) had a similar MBC compared to that with sorghum sudangrass (*Sorghum bicolor*. L., *var. sudanense*). Others (Lehman et al., 2015; Sainju et al., 2003) found that legume cover crops increased MBN compared to no cover crop. The addition of high-quality residue from cover crops, such residue with high N content or low C/N ratio, favors bacterial dominance, whereas low-quality residue favors fungal growth (Bossuyt et al., 2001; Millar et al., 2004; Kramer et al., 2012). Both fungal and bacterial populations increased with nonlegume compared to legume or no cover crop (Patkowska et al., 2016). Cover crop residue management practices, such as residue incorporation into the soil surface placement, or removal from the soil also had significant impact on soil microbial diversity (Nevins et al., 2018).

Microbial community abundance and structure are highly regulated by soil properties, such as pH, C/N ratio, aeration (Drury et al., 1991; Fierer and Jackson, 2006; Peregrina et al., 2014; Yang et al., 2017), and soil temperature and water content (Kong and Six, 2012; Muhammad et al., 2019). Brennan and Acosta-Martinez (2017) found that cover crops increased MBC compared to no cover crop in sandy and loamy soils. Njeru et al. (2014); Njeru et al. (2015) reported that cover cropping improved arbuscular-mycorrhizal fungi (AMF) colonization compared to no cover cropping under organic maize (*Zea mays* L.) production in Italy. Reed-Jones et al. (2016) found that the effect of cover crop on some bacteria varied with soil temperature and water content. In order to synthesize the existing knowledge about the effect of cover crop on microbial community structure and abundance and identify driving factors for observed differences, a systematic study to assess the overall impact of cover crop on microbial parameters is needed.

Meta-analysis is a useful tool to pool together the data from various regions with different soil and climatic conditions and management practices using effect size from individual studies (Hungate et al., 2009; Borenstein et al., 2011). In this study, a *meta*-analysis based on the data available in the literature was conducted to synthesize the overall effect of cover cropping, cover crop species, and residue management practices on soil microbial community abundance and structure under different soil and climatic conditions. Soil microbial community abundance was assessed via MBC, microbial biomass nitrogen (MBN), and phospholipid-derived fatty acids (PLFA), and community structure via PLFA patterns as bacteria, fungi, actinomycetes, and AMF. We hypothesized that (1) cover cropping would have an overall positive effect on soil microbial community abundance and structure compared to no cover cropping, (2) such effect will vary with cover crop species and residue management practice, and (3) soil and climatic conditions of various regions will alter the effect of cover crop on soil microbial biomass and community abundance.

2. Materials and methods

2.1. Data collection

To quantify the effect of cover crop on soil microbial community abundance and structure, a search on these parameters was carried out in peer review journals from 1990 to 2019 in Web of Science and Google Scholar. Keywords included PLFA, MBC, MBN, bacteria, fungi, and AMF as affected by cover crop, green manure or catch crop. About 169 publications were collected and screened using the following criteria for further data collection:

i. Experiments should be conducted in the field and data for legume, nonlegume, and/or mixed cover crops should be compared with no cover crop (fallow) in a region with similar soil and climatic conditions. Studies with no control treatment (or fallow) were discarded.
ii. Data comparing the effect of legume, nonlegume, and/or mixed (legume + nonlegume + oilseed crops) cover crops on soil microbial properties were selected.
iii. Treatments should be replicated at least three times and mean values shown with standard deviation (SD) or standard error (SE).
iv. Where different rates of fertilization were applied to crops following cover crops, only treatments with the recommended fertilizer rates based on the regions were selected. If different fertilizer types were used to supply nutrients, mean values of nutrients among fertilizer types were calculated and used for the study.

Based on these criteria, about 1824 pairwise observations from 81 publications were finally included for *meta*-analysis. These studies encompassed over 21 countries (Fig. 1). The annual mean air temperature and annual precipitation of the experimental sites were recorded for each study. The pH, initial organic C (SOCi), and texture of the surface soil were also recorded. In cases where the information was not found in the publications, an online search engine (https://www.whatsmygps.com) was used to determine the latitude and longitude of experimental sites and the data for soil properties and climatic conditions. The geographical information of experimental sites, soil properties and climatic conditions for each study were summarized in Appendix A.

During the *meta*-analysis, different cover crops in rotations with succeeding crops from a site were handled as individual comparison. Data for PLFA, MBC, MBN, total bacteria, total fungi, gram positive and negative bacteria, actinomycetes, AMF, AMF root colonization and spore density were extracted from the respective literature. A software of GetData graph digitizer 2.26 (http://getdata-graph-digitizer.com/index.php) was used to extract the data from the figures. If SEs were reported with means, the following equation was used to calculate the SD.

$$SD = SE \times \sqrt{n} \quad (1)$$

Where n is the number of replicates.

We extracted 134, 329, and 149 paired observations (cover crop *vs.* no cover crop) from the literature for PLFA, MBC, and MBN, respectively, to compare the response of microbial community abundance to cover crops. About 111, 272, and 130 pairwise observations of total bacteria, total fungi, and fungi/bacteria ratio, respectively, were collected for the microbial community structure analysis. About 127, 122, and 184 paired observations for gram-positive, gram-negative bacteria, and actinomycete, respectively, were collected for bacteria groups, and 78, 159, and 29 in AMF, AMF root colonization and AMF spore density, respectively, for soil fungi groups.

2.2. Variance estimators and weighting function

One of the challenges in conducting a systematic analysis is reporting the complete outcome of variance estimators and weighting functions (Furukawa et al., 2006; Wiebe et al., 2006). In this analysis, we estimated the effect size and related inferences using the weighting method (Hungate et al., 2009), based on the inverse of pooled variance (Van Groenigen et al., 2011). In studies where no variances were reported, the coefficient of variation (CV) was calculated using the following equation.

$$CV = \frac{SD_M}{M_m} \times 100 \quad (2)$$

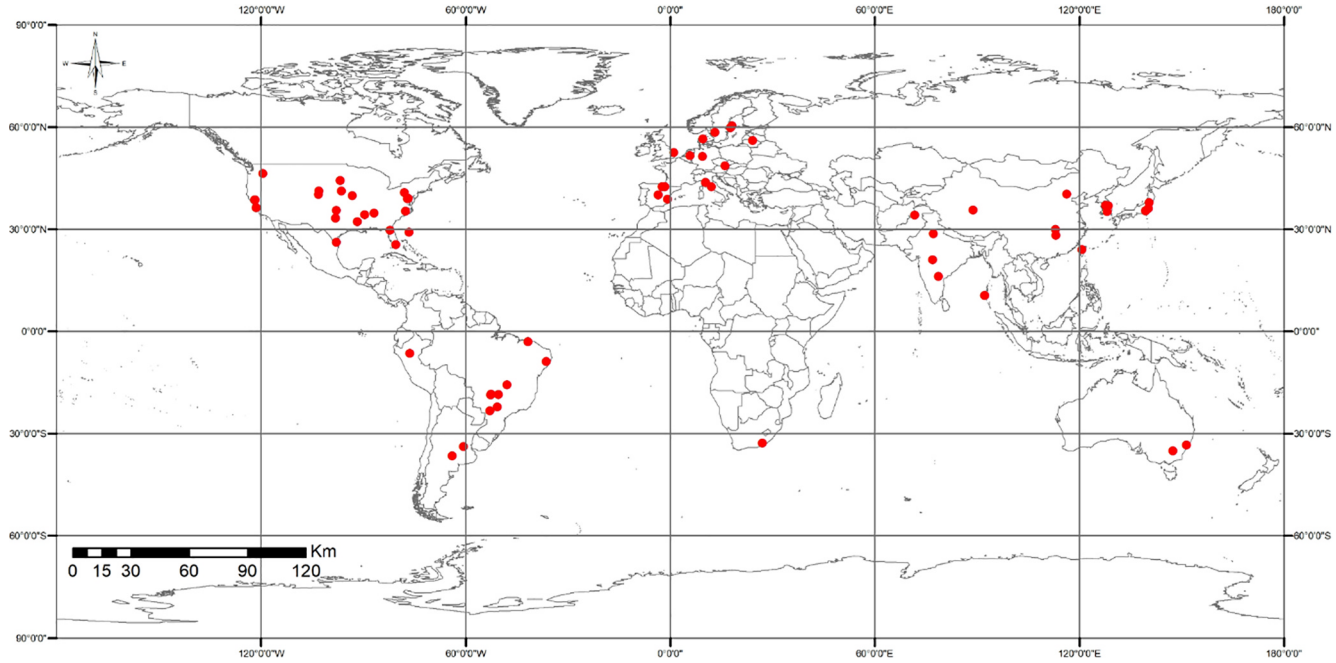

Fig. 1. Distribution of 81 experimental sites around the world where data were collected for the *meta*-analysis.

Where SD_M and M_m are SD and mean, respectively. When SD was missing, it was calculated as:

$$SD_{missing} = \frac{CV \times M}{100} \tag{3}$$

Where CV is coefficient of variance, and M is the mean.

2.3. Data analysis

The effect of cover crop on microbial variables was calculated using the response ratio (RR) as the effect size which is calculated as the natural log of ratio of treatments with and without cover crop (Hedges et al., 1999) as follows:

$$RR = Ln\left(\frac{X_{cc}}{X_{ncc}}\right) = Ln(X_{cc}) - Ln(X_{ncc}) \tag{4}$$

Where X_{cc} and X_{ncc} are arithmetic mean of the microbial variables in cover crop (CC) and no cover crop treatments (NCC), respectively. The natural log ratio confirms that changes in the numerator and denominator are affected equally. If the distributions of X_{cc} and X_{ncc} are normal and X_{ncc} is unlikely to be negative, the RR will be approximately normally distributed, with a mean equal to the true log response ratio (Gurevitch, 1993). Furthermore, the error variance of the RR (V_{LnRR}) for each study was calculated using the following equation (Hedges et al., 1999).

$$V_{LnRR} = \frac{S_{cc}^2}{n_{cc}X_{cc}^2} + \frac{S_{ncc}^2}{n_{ncc}X_{ncc}^2} \tag{5}$$

Where S_{cc} and S_{ncc} are SD, n_{cc} and n_{ncc} are number of replications, and X_{cc} and X_{ncc} are means for cover crop and no cover crop treatments, respectively.

The random effect model with 95% confidence interval using the reciprocal of the variance (V) and the weight (W) for each RR was calculated as (Borenstein et al., 2011):

$$W = 1/V \tag{6}$$

The overall mean response ratio (RR_{E++}) for individual cover crop treatment was calculated as:

$$RR_{E++} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{m} W_{ij}RR_{ij}}{\sum_{i=1}^{n}\sum_{j=1}^{m} W_{ij}} \tag{7}$$

Where "n" and "m" are the number of treatments and comparisons for each microbial variable, respectively. The standard error of RR_{E++} was calculated as:

$$SE(RR_{E++}) = \sqrt{\frac{1}{\sum_{i=1}^{n}\sum_{j=1}^{m} W_{ij}}} \tag{8}$$

To analyze the effect of cover crop on microbial variables, random model MetaWin 2.1 (Sinaure Associate Inc., Sunderland, USA) was used to compute the mean effect size at bias-based bootstrap 95% confidence intervals (CIs). The effect of cover crop was considered significant if the 95% CIs did not overlap the vertical zero line.

The effect of cover crop species and residue management was also examined on soil microbial community abundance and structure. Oilseed cover crops were treated as nonlegumes. Residue management practices included incorporation into the soil (Incorporated), placement at the soil surface (Surface), and removal from the soil (Removal). The random effect models allow comparisons among both studies and groups. Statistical results reported the total heterogeneity of RR (95% CIs) among studies (Q_T), between studies (Q_B) and within studies (Q_W) (Hedges and Olkin, 1985). We also calculated the I-square index by dividing the difference between variance and its degrees of freedom (n − 1) by total variance itself (Huedo-Medina et al., 2006). Greater I^2 values than 25% or 50% indicate a significant amount of heterogeneity. Data heterogeneities for target variables were summarized in Table S1 in the Supplementary information. To determine how cover crop affect soil microbial variables due to changes in soil and climatic conditions, regression analysis of RR to soil pH, SOCi and C/N ratio as well as annual mean air temperature and precipitation were conducted using the Origin 2018 software based on single observation (OriginLab Corporation, USA). The publication bias was tested with Rosenthal's fail-safe number using MetaWin 2.1 (Table S2). Greater fail-safe number than 5n + 10, where n is the observations' number, indicates no publication bias (Rosenthal, 1991; Dieleman and Janssens, 2011).

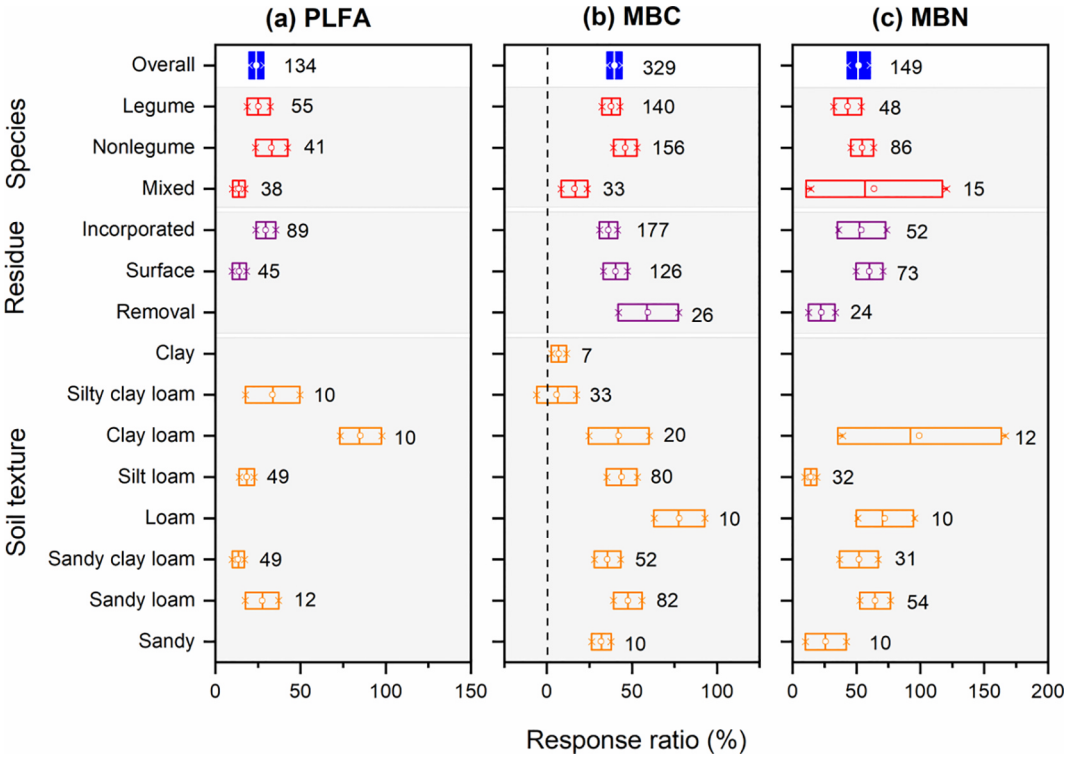

Fig. 2. Mean response ratio of cover crops compared to no cover crop and bootstrapped 95% confidence intervals (horizontal box) for total phospholipid-derived fatty acid (PLFA) and microbial biomass C and N (MBC and MBN) affected by cover crop species, residue management practices and soil textures. The vertical line (RR = 0) indicates no difference between cover cropping and no cover cropping systems. Numbers following the box indicate the number of observations for comparison.

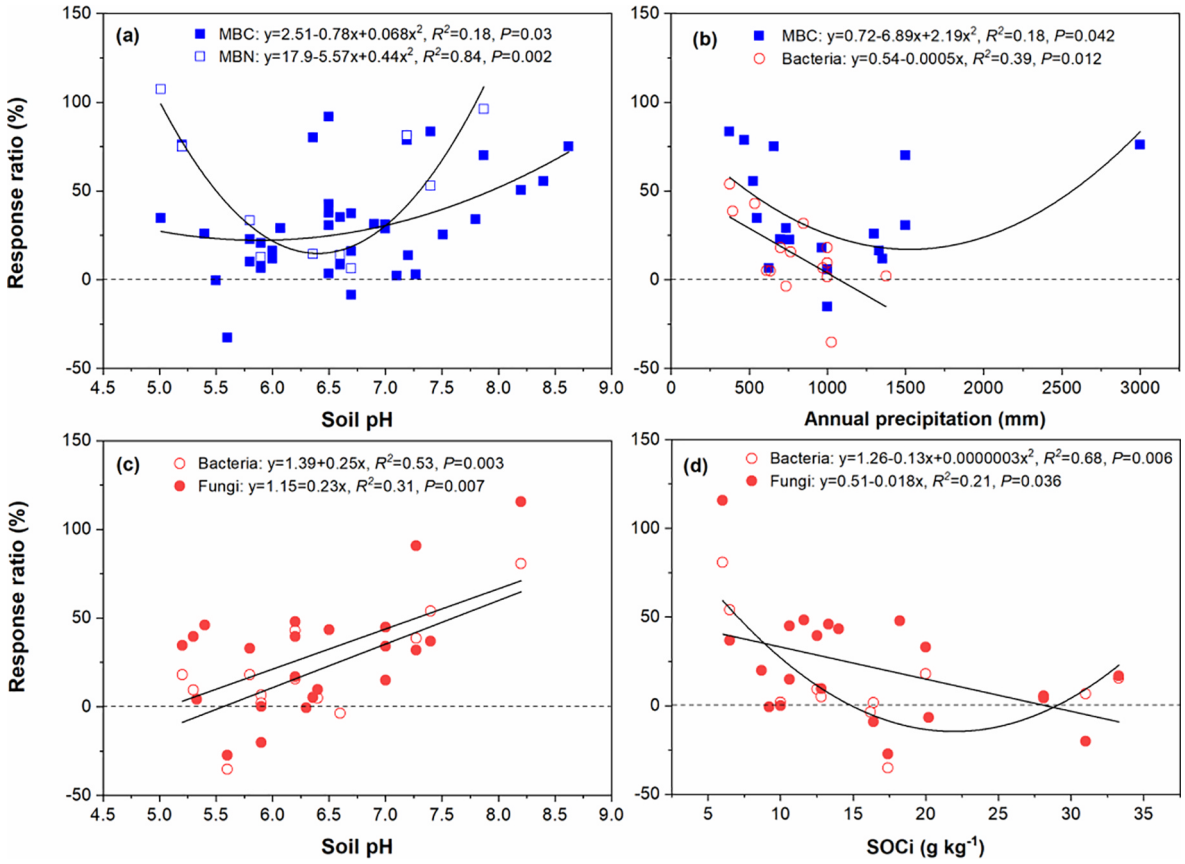

Fig. 3. Relationships between the response ratio of cover crop compared to no cover crop and soil pH, initial organic C (SOCi), and annual precipitation. The horizontal dash line (RR = 0) indicates no difference between cover cropping and no cover cropping systems.

3. Results

3.1. Data heterogeneity and publication bias

Our *meta*-analysis involving 1824 pairwise comparisons from 81 studies extending 21 countries showed that observations for MBC, MBN, and PLFA were different and data for most microbial variables exhibited a high heterogeneity among cover crop species, residue management practices, and soil textures, as characterized with great values of Q_T and I^2 (Table S1). The great fail-safe numbers for all target variables indicate no publication bias (Table S2). These suggest that the data quality met the standard for *meta*-analysis.

3.2. Effect of cover crop on soil microbial community abundance

Cover crop overall increased PLFA, MBC, and MBN by 24, 40, and 51%, respectively, compared to no cover crop ($P \leq 0.05$, Fig. 2). The categorical *meta*-analyses revealed that PLFA and MBC increased with legume and nonlegume compared to mixed cover crops ($P \leq 0.05$). The response for MBN, however, was inconsistent among cover crop species (Table S1). The RRs of PLFA, MBC and MBN was also affected by cover crop residue management practices. Incorporation of cover crop residue into the soil increased PLFA compared to surface placement ($P \leq 0.05$). Removal of cover crop residue reduced MBN compared to residue incorporation or surface placement.

The RR of cover crop on soil microbial parameters also varied in relation to soil texture (Fig. 1a). The RR of PLFA was greater in clay loam than other soil textures, although only 10 observations were available ($P \leq 0.05$). The RR of MBC was lower in clay and silty clay loam but greater in loam when compared with other soil textures. Similarly, the MBN with cover crops was lower in silt loam than other textures except of sandy soil.

The RR of PLFA due to cover crop was not related to soil properties and climatic condition, while the RRs of MBC and MBN related nonlinearly to soil pH (Fig. 3a). The RRs of MBC and MBN declined as soil pH increased to 6.5, after which they increased with further increase in pH. About 18% of variability in RR of MBC and 83% in RR of MBN were explained by soil pH. Similarly, the RR of MBC was nonlinearly related to annual precipitation, with minimum response occurring at 1500 mm (Fig. 3b). About 18% of variability in RR of MBC was explained by annual precipitation.

3.3. Effect of cover crop on soil total bacteria, total fungi, and the fungi/bacteria ratio

Cover crops increased total bacteria by 15% and total fungi by 19% compared to no cover crops ($P \leq 0.05$, Fig. 4a and b). Increases for total bacteria and fungi for legume cover crops were 23 and 16% and for nonlegume cover crops were 10 and 26%, respectively. Such differences, however, were not significant for mixed cover crops. The RR of cover crop for fungi/bacteria ratio was positive for all cover crop species (Fig. 4c). Incorporation of cover crop residue into the soil increased total bacteria compared to surface placement of the residue or removal from the soil ($P \leq 0.05$), but residue management has no effect on RR of cover crop on total fungi, although all residue management practices showed positive effect. Residue incorporation enhanced the fungi/bacteria ratio compared to residue removal.

The RRs of cover crop on total bacteria, fungi and the fungi/bacteria ratio varied with soil textures (Fig. 4). Cover crops enhanced soil bacteria growth compared to no cover crop in most textures, except for clay loam and silty clay loam, where the RR was not significant ($P > 0.05$). The RR of bacteria was greater in sandy clay loam than silt loam and sandy loam soils. Similarly, cover crop increased total fungi in most soil textures, except sandy loam and clay. Cover crop increased the fungi/bacteria ratio compared to no cover crop and the RR of the fungi/bacteria ratio was greater in silty clay loam than clay loam and silt loam ($P \leq 0.05$). Cover crop reduced the fungi/bacteria ratio in sandy clay loam soils ($P \leq 0.05$), and had a non-significant effect in sandy loam. The RR of cover crop for total fungi and bacteria increased linearly with soil pH, explaining 31 and 53% of the variability, respectively (Fig. 3b). With increases in SOCi, the RR of cover crop decreased linearly for total fungi, but RR was related nonlinearly with SOCi for total bacteria (Fig. 3d). The RR of cover crop for total bacteria minimized at 20 mg kg^{-1} SOCi. The RR of cover crop for total bacteria decreased linearly with increased annual precipitation (Fig. 3b), explaining 39% of the variability.

3.4. Effect of cover crop on soil gram-positive and -negative bacteria and actinomycete

Cover crop overall increased soil gram-positive and -negative bacteria and actinomycete by 17, 11, and 23%, respectively, compared to no cover crop ($P \leq 0.05$, Fig. 5). The categorical *meta*-analyses showed that the effects of cover crops on the groups of gram-positive and -negative bacteria were not dependent on cover crop type or residue management practices, while the RR of actinomycete was greater with legume than nonlegume or mixed and with nonlegume than mixed cover crops. Mixture of legume and nonlegume cover crops had a neutral effect on actinomycete. Cover crop residue management practices did not affect the RR of actinomycete to cover crops. The RR of cover crop for actinomycete was significantly higher in sandy clay loam followed by clay loam than silt loam and sandy loam soils ($P \leq 0.05$). The RRs of gram-positive and gram-negative bacteria and actinomycete were not correlated to soil pH, SOCi or annual precipitation and air temperature (Data not shown).

3.5. Effect of cover crop on arbuscular mycorrhizal fungi

Compared to no cover crops, cover crops overall increased AMF, AMF root colonization and AMF spore density by 26%, 13, and 47% ($P \leq 0.05$, Fig. 6), respectively. The categorial analysis showed that the effects of cover crops on AMF and AMF root colonization and spore density were not dependent with cover crop types but varied with residue management practices. Surface-placed residue increased AMF compared to incorporated residue. In contrast, incorporated residue increased AMF root colonization and spore density compared to surface placed residue or residue removal. No significant correlations to soil pH, SOCi or annual precipitation and air temperature were found for AMF, AMF root colonization or AMF spore density (Data not shown).

4. Discussion

4.1. Soil microbial community abundance and structure

The positive effect of cover crop on microbial parameters compared to no cover crop clearly confirmed our first hypothesis that cover crop enhanced soil microbial community abundance and structure. The increases in PLFA, MBC and MBN with cover crops were probably due to enhanced C and N inputs from above- and below-ground cover crops residue (Chavarría et al., 2016; Schmidt et al., 2019). These inputs probably increase substrate availability for soil microbes, stimulating their growth and biomass. Considering the importance of soil microbes in maintaining soil health (Lehman et al., 2015), our findings suggest that cover crops can enhance biological soil health by stimulating soil microbial community abundance compared to no cover crop.

Although cover crops enhanced the growth of total bacteria and fungi, the positive RR of the fungi/ bacteria ratio (Fig. 4c) suggests that fungi responded to cover crops more than bacteria. Greater fungi/bacteria ratio with than without cover crop has been reported by some researchers (Nakamoto et al., 2012; Martinez-Garcia et al., 2018; Schmidt et al., 2019). Sanz-Cobena et al. (2014) found that additional input from cover crop residues increased the growth of fungi more than

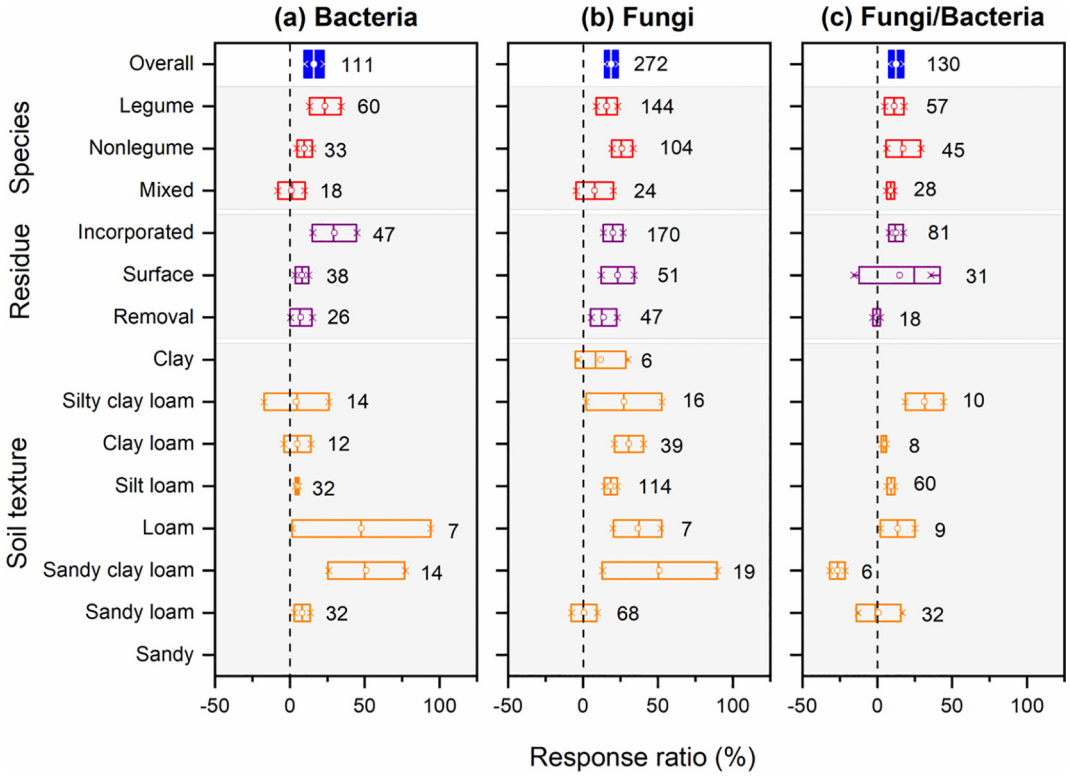

Fig. 4. Mean response ratio of cover crops compared to no cover crop and bootstrapped 95% confidence interval (horizontal box) for total bacteria, total fungi and the fungi/bacteria ratio affected by cover crop species, residue management practices and soil textures. The vertical line (RR = 0) indicates no difference between cover cropping and no cover cropping systems. Numbers following the box indicate the number of observations for comparison.

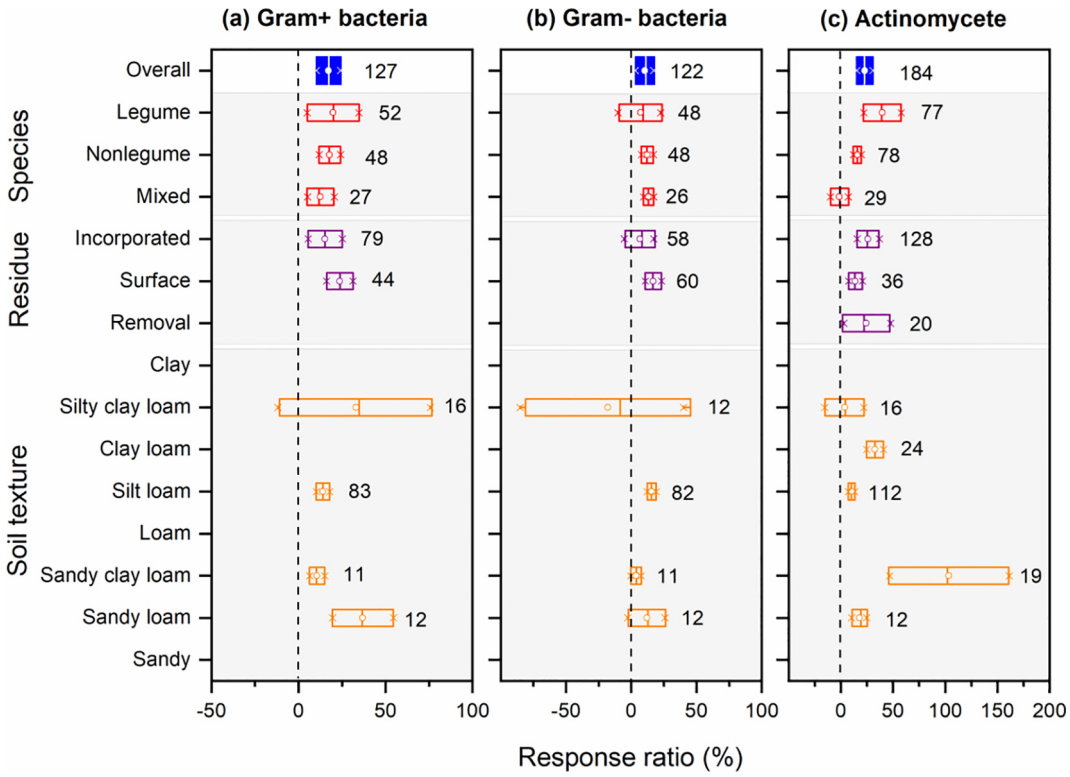

Fig. 5. Mean response ratio of cover crop compared to no cover crop for gram-positive (+) and negative (−) bacteria and actinomycete with bootstrapped 95% confidence intervals (horizontal box) affected by cover crop species, residue management practices and soil textures. The vertical line (RR = 0) indicates no difference between cover cropping and no cover cropping systems. Numbers following the box indicate the number of observations for comparison.

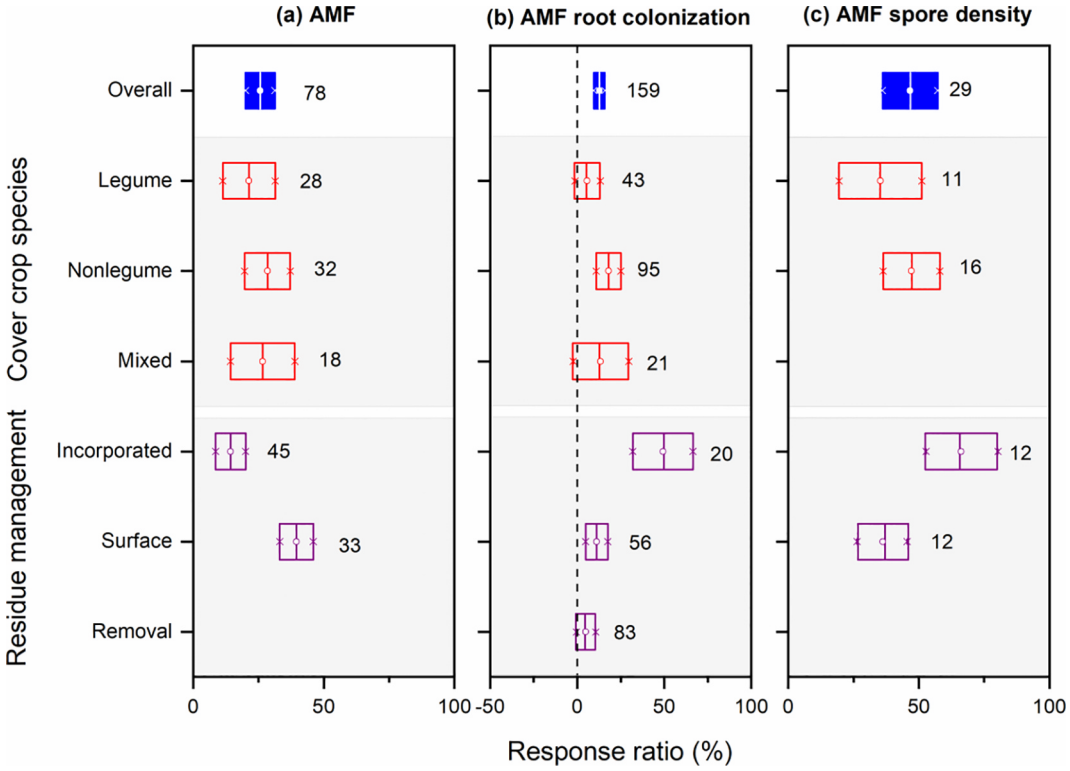

Fig. 6. Mean response ratio of cover crops compared to no cover crop for arbuscular mycorrhizal fungi (AMF), AMF root colonization and spore abundance and with bootstrapped 95% confidence intervals (horizontal box) affected by cover crop species and residue management practices. The vertical line (RR = 0) indicates no difference between cover cropping and no cover cropping systems. Numbers following the box indicate the number of observations for comparison.

bacteria, as soil fungi are more sensitive to cover crop than bacteria (Schmidt et al., 2019). Numerous researchers (Kabir and Koide, 2002; White and Weil, 2010; Lehman et al., 2012; Njeru et al., 2015; Brennan and Acosta-Martinez, 2017) have reported that cover crops enhanced AMF growth which increased P availability and abiotic stress tolerance, suppress the infection of pathogens, and promote crop yields compared to no cover crop. Benitez et al. (2016) found that stimulation of AMF by cover crop improved soil fertility and crop yield.

4.2. Impacts of cover crop species and residue management practice

The varying effect with legume, nonlegume and mixed cover crops on soil microbial community abundance and structure can be explained by the quality and quantity of cover crop residue returned to the soil (Frasier et al., 2016; Bacq-Labreuil et al., 2019). Nonlegume cover crops generally produce greater above and belowground biomass, increase C supply, and have higher C/N ratio than legume cover crops (Kuo et al., 1997; Sainju et al., 2007). In contrast, legume cover crops fix N from the atmosphere, increase N supply to succeeding crops due to higher residue N concentration, and have lower C/N ratio than nonlegume cover crops (Kuo et al., 1997; Sainju et al., 2003). Although not significant, the slightly greater PLFA, MBC, and MBN with nonlegume than legume cover crop (Fig. 2) suggests that increased C substrate availability from enhanced cover crop biomass input probably increased microbial abundance and communities with nonlegume cover crop. Several researchers (Sainju et al., 2003, 2007; Mbuthia et al., 2015; Muhammad et al., 2019) observed that nonlegume cover crops increased MBC and soil respiration, but legume cover crops increased MBN compared to no cover crop. The increased MBN with nonlegume than legume cover crop in this *meta*-analysis, however, was in disagreement with the results found by above researchers. In contrast, greater actinomycetes with legume than nonlegume cover crops (Fig. 5) suggests that these microorganisms thrive better in the N-rich environment. The reverse was true with fungi, which thrive better in the C-rich environment with nonlegume cover crops. The different responses of bacteria and fungi to legume and nonlegume cover crops have been well documented in the literature (Nakamoto et al., 2012; Frasier et al., 2016; Brennan and Acosta-Martinez, 2017). Fungi promote better in decomposing low quality residue, such as those of nonlegume cover crops, while bacteria favor decomposition of high-quality residue, such as from legume cover crops (Bossuyt et al., 2001; Frasier et al., 2016; Brennan and Acosta-Martinez, 2017). The AMF, AMF root colonization, and AMF spore density also enhanced slightly with nonlegume compared to legume cover crops (Fig. 6). Increased N input from legume cover crops can have a negative effect on AMF root colonization (Mbuthia et al., 2015).

The significantly lower PLFA and MBC with mixed cover crops than legume and nonlegume cover crops was a surprise (Fig. 2). Lower number of observations reported in the literature may have resulted in incomplete assessment of mixed cover crops on microbial parameters compared to legume and nonlegume cover crops. Several researchers (Sainju et al., 2007; Mukumbareza et al., 2016), however, reported that MBC and enzyme activities were greater with mixed than legume or nonlegume cover crops. Chavarría et al. (2016) found that cover crop enhanced PLFA compared to no cover crop.

Cover crop residue management affected soil microbial community abundance and structure probably by altering residue contact with soil microbes. Increased contact of cover crop residue with microbes may have enhanced C and N substrate availability, thereby enhancing PLFA, total bacteria, AMF root colonization and AMF spore density with residue incorporation into the soil compared to surface-placed residue or residue removal from the soil (Figs. 2, 4, and 6). Nevins et al. (2018) also found that incorporation of cover crop residue into the soil stimulated microbial growth, which improved soil fertility and crop yield (Brozovic et al., 2018). Surface placement of cover crop residue, however, promoted gram-positive and -negative bacteria and AMF (Figs. 5 and 6), probably due to reduced soil temperature and increased water content from the mulch effect of the surface residue (Karuku et al.,

2014).

4.3. Impacts of soil and climatic conditions

Soil and climatic conditions of various regions affected microbial community abundance and structure due to cover crop compared to no cover crop probably by altering soil water and nutrient availability and temperature that influenced cover crop residue decomposition. Increased PLFA with clay loam (Fig. 2), total bacteria with loam and sandy clay loam, fungi/bacteria ratio with silty clay loam (Fig. 4), and actinomycete with sandy clay loam (Fig. 5) indicate that medium-textured soils favored the growth of microorganisms probably by providing optimum soil aeration and water content. Medium-textured soils with 50% porosity filled equally by air and water are ideal for soil microbial growth (Moore and Bradley, 2018). While fine-textured soils enhance anaerobic condition and limit the growth of aerobic microorganisms, the reverse is true for the coarse-textured soil. Microbial activity and decomposition rates of organic materials are highly regulated by soil properties, such as soil texture, pH and the C/N ratio of the crop residue (Drury et al., 1991; Fierer et al., 2009; Peregrina, 2016). Generally, decomposition rates of crop residues are higher in coarse-textured soils and lower in in fine-textured soils (Drury, et al., 1991), which may lead to a greater microbial biomass in fine-textured soil (Brennan and Acosta-Martinez, 2017). While MBC and MBN were minimized at 6.5 pH (Fig. 3a), total bacteria and fungi increased with increased pH (Fig. 3c). Acidic and alkaline soil pH limit soil microbial growth (Chen et al., 2004; Pietri and Brookes, 2009; Yang et al., 2017). The coefficient of determination (R^2) for the relationship between RR of cover crop and soil pH was greater for MBN (0.84) than MBC (0.18) (Fig. 3a), indicating that N availability may play an important role in the decomposition of cover crop residues. Increased C substrate availability minimized fungi growth at 20 g kg^{-1} and increased SOCi decreased total bacteria or minimized gram-positive bacteria at 6.5 pH. The SOCi can have a variable effect on soil bacterial and fungal growth, as C provides energy source to microorganisms (Lekberg and Koide, 2005; Patkowska et al., 2016).

The significance of climatic factors in cover crop residue decomposition and microbial community abundance and structure have been well described in long-term field studies (Njeru et al., 2014; Higo et al., 2015a, 2015b; Reed-Jones et al., 2016). In this study, cover crops decreased MBC, bacteria and gram-positive bacteria with increasing annual precipitation up to 1500 mm (Fig. 3b). Reduced soil aeration due to enhanced soil water content as a result of increased precipitation probably decreased microbial growth due to cover crop compared to no cover crop.

5. Conclusions

The *meta*-analysis identified that cover crops overall increased soil microbial community abundance as characterized by increased PLFA, MBC, and MBN compared to no cover crop. Cover crops favored growth of fungi more than bacteria. Legume cover crops increased total bacteria and actinomycete, but decreased total fungi compared to non-legume cover crops. Mixed cover crops, however, had a negative impact on soil microbial community abundance compared to legume or non-legume cover crops. Cover crop residue incorporated into the soil increased PLFA, total bacteria, actinomycete, AMF root colonization, and spore density compared to residue placed at the soil surface or removed from the soil. The effect of cover crops on microbial variables was pronounced more in medium-textured soils, neutral soil pH, and moderate soil organic C. Increased precipitation, however, decreased microbial community abundance and structure due to cover crop compared to no cover crop. Although cover crop species and residue management have variable effect on microbial properties in various soil and climatic conditions, cover crops overall can enhance biological soil health by enhancing microbial community abundance compared to no cover crop.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2020.114696.

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