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Review Paper

Effect of fertilization on soil microorganisms in paddy rice systems – A meta-analysis

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ABSTRACT

Soil microorganisms are considered a sensitive indicator of soil health and quality. In cropping systems, soil microorganisms are strongly affected by crop management, including the application of fertilizers. While studies in natural ecosystems have generally found that increased nitrogen (N) inputs decrease microbial biomass, microorganisms in soils under upland crops often benefit from mineral fertilizer input. Paddy rice soils, being flooded for part of the season, are dominated by different carbon (C) and N cycle processes and microbial communities than soils under upland crops. The objective of this study was to explore the effect of fertilizer on soil microorganisms in paddy rice systems in a meta-analysis of the peer-reviewed literature. Across all studies (n = 55), the addition of mineral fertilizer significantly increased microbial biomass carbon content (MBC) by 26% in paddy rice soils. Mineral fertilizer applications also increased soil organic carbon content (SOC) by 13%. The higher crop productivity with fertilization likely led to higher organic C inputs, which in turn increased SOC and MBC contents. The time of sampling within a season (pre-plant rice, in-season rice, post-harvest rice, or post-harvest rotational crop) did not significantly affect the response of MBC to mineral fertilizer. The positive effect of mineral fertilizer on MBC content did not differ between cropping systems with continuous rice and systems where paddy rice was grown in rotation with other crops. However, compared with upland cropping systems, the increase in the microbial biomass due to mineral fertilizer application is more pronounced in rice cropping systems, even when rice is grown in rotation with an upland crop. Differences in climate and soil oxygen availability likely explain the stronger response of soil microorganisms to mineral fertilizer input in paddy rice systems. Our analysis suggests that fertilization does not consistently select for specific microbial groups (e.g. gram positive or negative bacteria, fungi, actinomycetes) in paddy rice systems; however, it affects microbial community composition through changes in soil properties. How specific groups of microorganisms respond to mineral fertilization likely depends on environmental factors. Overall, our results suggest that in paddy rice systems the application of inorganic fertilizers increases SOC and MBC contents, both of which are important indicators of soil health.

1. Introduction

Soil microorganisms play an important role in soil biochemical processes, such as decomposition of organic material, nutrient cycling, and biotransformation of organic pollutants (Schimel, 1995; Thiele-Bruhn et al., 2012). The soil microbial community is therefore an important component of a healthy soil. Even though the soil microbial biomass constitutes only a small portion of soil organic matter, roughly 0.5–6.0%, (Insam, 1990; Shibahara and Inubushi, 1997), it is considered a sensitive indicator of soil health and quality (Doran and Zeiss, 2000). This is due to the fact that the microbial biomass responds more dynamically to management practices than the total soil organic carbon content (SOC) and may show the effect of management on soil health long before such effects can be detected by measuring total SOC (Powlson et al.,

Abbreviations: CI, confidence interval; CV, coefficient of variation; FYM, farm yard manure; K, potassium; N, nitrogen; NPK, mineral nitrogen, phosphorus and potassium fertilizer; P, phosphorus; PLFA, phospholipid fatty acid; RR, response ratio; MBC, soil microbial biomass carbon; SOC, soil organic carbon.

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1987).

In cropping systems, soil microorganisms are strongly affected by crop management, including the application of fertilizers. In a meta-analysis based on more than 100 datasets from long-term trials with annual upland crops from around the world, Geisseler and Scow (2014) found that mineral fertilizer increased microbial biomass carbon contents (MBC) compared with an unfertilized control by an average of 15.1%. This result contrasts to forest and grassland ecosystems where MBC is generally reduced by increased N input (Liu and Greaver, 2010; Geisseler et al., 2016). In upland cropping systems, mineral fertilization also increased SOC content relative to the unfertilized control (Geisseler and Scow, 2014). A close correlation between MBC and SOC suggested that SOC was a major factor contributing to the overall increase in MBC content with mineral fertilization. The analysis did not include data from lowland (paddy) rice systems. However, rice is one of the most important crops globally, being grown on about 160 million ha worldwide, and more than 90% of global rice production is harvested from irrigated or rainfed lowland rice fields (IRRI, 2013).

Compared with natural ecosystems, rice systems share many similarities with upland cropping systems, such as low plant diversity, periods of no plant cover, tillage or crop harvest. However, rice systems differ fundamentally from upland cropping systems in terms of tillage operations and water management. Two unique management practices of lowland rice systems are puddling and flooding. Puddling, which is a very common practice in rice systems in Asia, refers to the repeated tillage of submerged soil before rice is transplanted. By breaking down soil aggregates, reducing macroporosity and dispersing clay particles, puddling greatly restricts water percolation (Chauhan et al., 2012). Flooding creates anoxic conditions in most of the soil. In contrast, aerobic conditions prevail when soils are drained. Thus both puddling and flooding have considerable effects on physical and chemical soil properties, creating a temporally highly variable environment for soil organisms (Banerjee et al., 2006). Furthermore, many paddy rice systems are very intensive with two or even three crops grown each year and nitrogen (N) application rates may in rare cases even be as high as 500 kg ha^{-1} per crop (Che et al., 2015). To prevent losses through denitrification, N fertilizer is applied as ammonium or urea. Lack of oxygen prevents nitrification in most of the soil, resulting in prolonged periods of high ammonium concentrations after fertilizer applications under flooded conditions. High N application rates can thus lead to temporarily very high osmotic potentials and potentially toxic concentrations of ammoniacal N (Eno et al., 1955; Omar and Ismail, 1999). Rice field soil thus provides a unique environment for soil microorganisms and their response to fertilizer input may differ between rice systems and upland cropping systems.

To explore the effect of fertilizer on soil microorganisms in paddy rice systems, we carried out a meta-analysis of the peer-reviewed literature. The results shall be compared with those from an earlier study in upland crops. Despite the differences between upland and paddy rice systems, we hypothesize that mineral fertilizer in paddy rice systems has a positive effect on the soil microbial biomass as well as on SOC content, as is generally the case in upland systems. Furthermore, we expect that mineral fertilizers lead to changes in the microbial community composition.

2. Material and methods

We investigated the effects of fertilization on soil microorganisms in paddy rice systems by meta-analysis. In a first step we searched the online database Web of Science for peer-reviewed papers using the topics 'rice', 'nitrogen', 'microbial' and 'fertili*'. The articles which met these criteria were then screened for data on microbial biomass. Articles cited in review papers and in the discussion of other articles were also included in our search. The following criteria were applied to select appropriate studies: (i) the data were from field trials with rice cropping systems in paddy soils and (ii) the study reported microbial biomass both from an unfertilized control and a treatment with mineral N addition either alone or in combination with other nutrients. The literature search was concluded in July 2017.

Meta-analysis requires that datasets are independent. To meet this requirement, we only included values from the topsoil when data from several soil layers were reported. When several studies reported data from the same trial, the study with the most complete dataset, including standard deviation and information about other soil properties, such as pH or SOC content, was preferred. When studies measured microbial biomass repeatedly over time or included treatments with different application rates, the datasets were considered dependent and the average response and a composite standard deviation (Borenstein et al., 2009) were calculated and used for the meta-analysis. However, for the analysis of trial duration, time of sampling and N application rate, results from individual sampling times and treatments were included as separate datasets. Meta-analyses were also performed on a subset of studies with both mineral and organic fertilizer treatments and a different subset comparing straw removal with straw retention.

2.1. Data analysis

The natural log of the response ratio (RR) was used as effect size in the meta-analysis (Hedges et al., 1999):

$$\ln(RR) = \ln\left(\frac{X_{+N}}{X_{-N}}\right) \quad (1)$$

where X_{-N} and X_{+N} are the means of the target variable in the control and fertilized treatment, respectively. The meta-analysis was performed using the program MetaWin (Rosenberg et al., 2000). MetaWin was also used for meta-regression analyses to investigate the effects of trial duration, N application rate and latitude. Effects of fertilization expressed in percent were calculated as (RR - 1) × 100%.

Meta-analysis requires a variability estimate for each dataset. Approximately two thirds of the studies reported a measure of variability for MBC content that could be used to calculate the standard deviation, while half the studies reported a measure of variability for SOC content and pH. The missing standard deviations were calculated using the average coefficient of variation (CV) of the datasets where the standard deviation was reported for that soil property.

Effects of fertilization on microbial community composition were assessed using different approaches, namely colony forming units, phospholipid fatty acid (PLFA), direct count, ester-linked fatty acid methyl esters, and selective inhibition. Only a small number of datasets measured the effects of N input on microbial community composition. Due to the small number and the fact that only few datasets included standard deviations, a meaningful meta-analysis was not possible. Instead, we calculated the standard deviation and 95% confidence interval (95% CI) of the RR considering individual datasets as experimental units. This approach results in a smaller error term compared with a meta-analysis and thus is more likely to result in significant differences.

Total PLFA was converted to MBC using a conversion factor of 5.8 μg C $nmol^{-1}$ PLFA (Joergensen and Emmerling, 2006). When organic matter was reported, we multiplied it by 0.58 (Stevenson and Cole, 1999) to calculate SOC content. These conversions were only relevant for data shown in Fig. 4 and had no effect on the response ratio used for the meta-analysis.

3. Results

A total of 55 trials met our search criteria and were included in the meta-analysis. Most studies were located in China (n = 26) and India (n = 21), reflecting the dominance of these two countries, which together produced roughly half of the global rice harvest in 2010 (IRRI, 2013). Trials from Japan (n = 5), Korea (n = 1), Pakistan (n = 1) and Taiwan (n = 1) completed the dataset (Fig. 1). The duration of the trials between establishment and sampling ranged from 10 weeks to 58 years, while the annual N application rate in the fertilized treatments ranged between 40 and 830 kg N ha^{-1}. 84% of the studies determined MBC by chloroform fumigation extraction with the remainder using either the chloroform fumigation incubation method or PLFA. Sampling depth averaged 16 cm and ranged from 5 to 30 cm. An overview of the trials can be found in Table S1, supplemental data.

3.1. Overall effects

Across all studies, the addition of mineral fertilizer significantly increased MBC contents by 26.4%, with the response ratio ranging from 0.84 to 1.89 (Fig. 2). Only 5 out of the 55 studies reported a negative effect of mineral fertilization on MBC. Neither the duration of the trial (Fig. 3), nor the annual N application rate, which ranged from 40 to more than 800 kg ha^{-1} (Fig. S1, supplemental data), had an effect on the response of the microbial biomass to mineral fertilizer. Including only studies where the microbial biomass was determined by chloroform fumigation extraction (n = 46), MBC content increased significantly by 24% with fertilization.

Mineral fertilizer applications significantly increased SOC contents by 13% compared to the unamended control (n = 46; Table 1). The proportion of SOC found in the microbial biomass (MBC/SOC ratio) was also increased in fertilized soil, from an average of 27.7 g kg^{-1} in the control to 30.5 g kg^{-1} (Fig. 4). Mineral fertilizer had no significant effect on soil pH (n = 27; Table 1).

The yield response of rice to fertilizer applications was stronger than that of SOC and MBC. On average yield of fertilized rice exceeded that of unfertilized rice by 90% (n = 22; Fig. S2, supplemental data). However, three datasets with yield RR of more than 3 had a strong effect on the overall average. Excluding these three values, the yield RR was 1.58. The yield response was most pronounced in treatments with the combined application of N, phosphorus (P) and potassium (K), as compared with treatments where only N was applied. The correlation between the RR for yield and MBC was weak.

3.2. Factors affecting the microbial response

The time of sampling had only a small, non-significant effect on the response of MBC content to mineral fertilizer. In about half of the studies, soil samples were taken after the rice harvest. In these studies, mineral fertilization resulted in a 22% increase in MBC content (Fig. 2). In studies where the samples were taken during the rice growing season or after the harvest of the rotational crop, which in most cases was wheat, the positive effect of mineral fertilizer was more pronounced, resulting in an increase in MBC content of 32 and 30%, respectively. Only four studies determined the effect of mineral fertilizer in samples collected before rice was

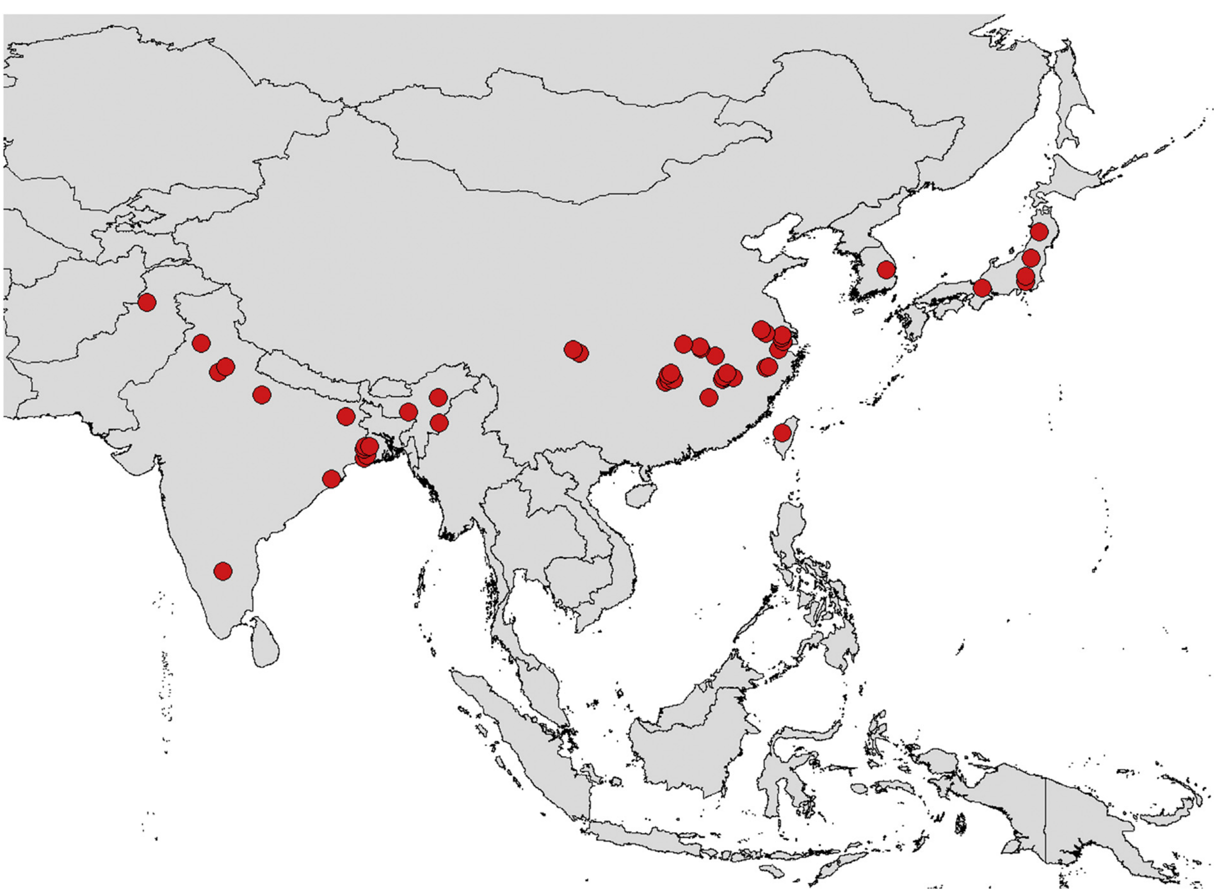

Fig. 1. Location of the trials included in the meta-analysis.

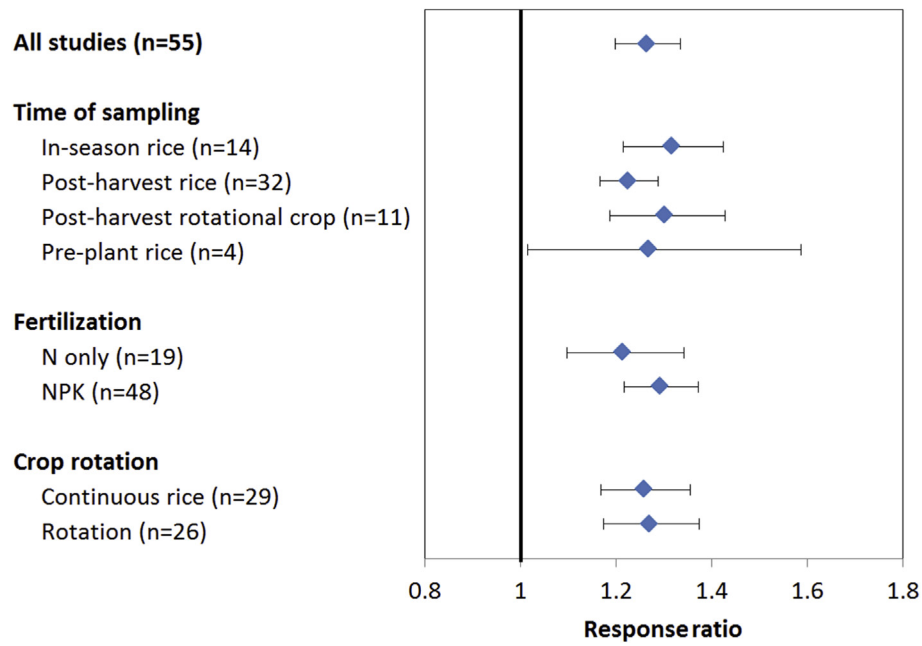

Fig. 2. Effect of mineral fertilizer on the soil microbial biomass in paddy rice systems and differences in the response to fertilizer when studies are grouped based on time of sampling, nutrients applied and crop rotation.

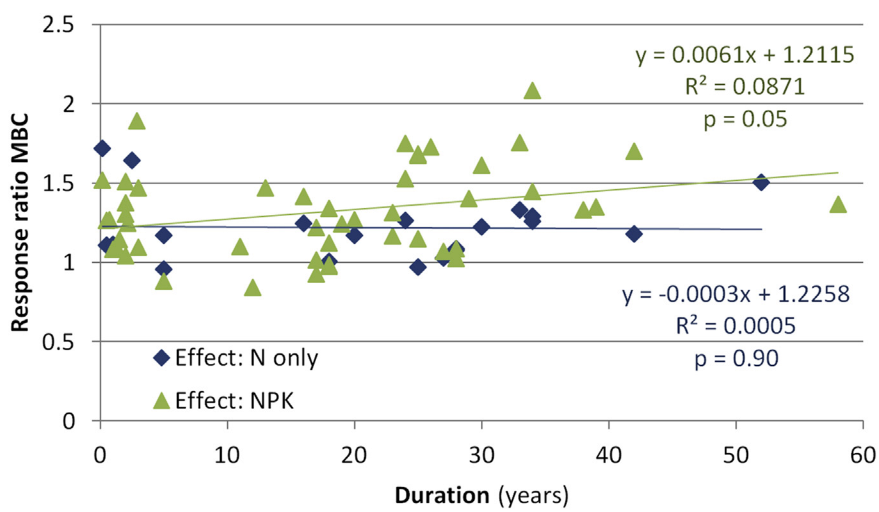

Fig. 3. Response of the soil microbial biomass to N input as affected by duration of study and nutrients applied.

Table 1
Effect of fertilization on soil pH and soil organic carbon. The meta-analysis was done for all studies reporting data and for two subsets of studies. One subset included studies with both mineral and organic fertilizer treatments and the second subset included studies with mineral fertilizer applications and treatments with and without straw removal (n = number of studies; NPK = mineral nitrogen, phosphorus and potassium fertilizer; FYM = farm yard manure; RR = response ratio).

Soil Property	n	RR	95% CI		
pH					
All studies	27	0.988	0.972	to	1.004
Soil organic carbon					
All studies	46	1.134	1.094	to	1.175
Mineral N (N or NPK)	15	1.155	1.022	to	1.306
Organic N (FYM or compost)	15	1.305	1.155	to	1.475
Mineral N straw removed	16	1.143	1.077	to	1.213
Mineral N straw retained	16	1.129	1.062	to	1.199

planted. Microbial biomass was increased by 27% in these studies.

The application of mineral N alone increased MBC content by 21% (n = 19), while a combination of N, P and K led to a 29% increase in MBC (n = 48; Fig. 2). Even though the effect was not significant, the response of MBC tended to increase over the years in trials where N was applied in combination with P and K, while trial duration had no effect on MBC content when N was the only nutrient applied (Fig. 3).

The positive effect of mineral fertilizer on MBC content was similar for cropping systems with continuous rice and systems where paddy rice was grown in rotation with upland crops (Fig. 2). However, whether rice is grown continuously or in rotation with other crops is often determined by climatic factors, especially temperature and water availability. Therefore, the effects observed (or their absence) are not solely be attributed to crop rotation. All trials with a crop rotation (n = 26) grew at least two crops per year,

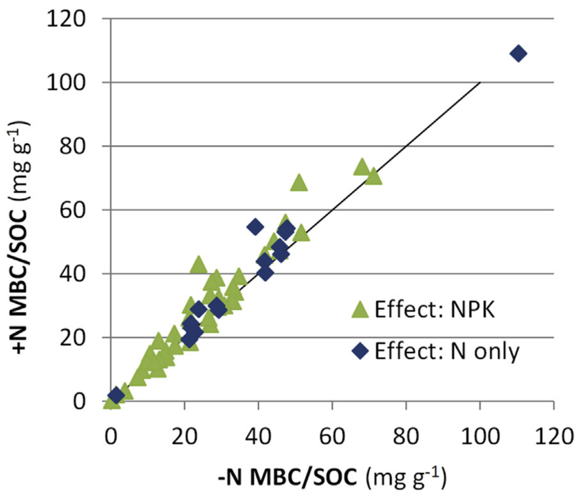

Fig. 4. Microbial biomass carbon (MBC) to soil organic carbon (SOC) ratio in unfertilized soils (-N) plotted against the MBC/SOC ratio in soils fertilized with mineral fertilizer (+N). The diagonal line is the equality line.

while only 14 of the 29 studies with continuous rice grew two crops per year. In the continuous rice studies with two crops per year, the application of mineral fertilizer increased MBC content by 17.5% with the 95% confidence interval of the RR ranging from 1.06 to 1.29. In contrast, when rice was grown in rotation with other crops, the MBC response to mineral fertilizer was 27.0%. Therefore, in systems with two or more crops per year, MBC tended to respond more strongly to mineral fertilizer in rotations with multiple crops than in continuous rice systems.

3.3. Organic versus mineral fertilizer, straw management

The effects of mineral fertilizer on MBC and SOC contents are small when compared with the effect of organic fertilizers. A subset of 16 trials included a mineral fertilizer treatment and a treatment with only organic fertilizer applications (farm yard manure [FYM] or compost). While mineral fertilizer increased MBC content by 29% in these studies relative to the unfertilized control, organic fertilization led to an increase of 61% (Fig. 5). The difference of both treatments compared with the control was significant, as was the difference between the two treatments when analyzed as a paired comparison. Soil organic carbon contents also increased much more with organic fertilizer (31%) than with mineral fertilizer (16%) in these studies (Table 1). The MBC/SOC ratio was 19.6 mg kg^{-1} in the control. It increased slightly to 21.0 mg kg^{-1} with mineral fertilization, while it increased to 24.5 mg kg^{-1} in the treatments with organic fertilizer. Only the increase with organic fertilizer was statistically significant. In contrast, organic fertilizer resulted in an 89% yield increase, while yield increased by 109% with the addition of mineral fertilizer (n = 5). The weaker yield response to organic fertilizers is likely due to the fact that the total amount of N added with FYM and compost was equal to and in some cases lower than the amount of N added in the corresponding treatment with mineral fertilizer. As only part of the N in organic fertilizers is available to the following crop, available N concentrations may have been lower in treatments with organic fertilizers compared with the corresponding treatments with mineral fertilizer.

A subset of 17 trials included mineral fertilization treatments with and without straw removal. When straw was removed, MBC contents increased by 28% compared with the unfertilized control (Fig. 5). When straw was retained, this increase was 49%. As with organic fertilizers, retaining straw significantly increased MBC contents compared with treatments where straw was removed when analyzed as a paired comparison. However, the yield and the increase in SOC content were lower when straw was retained than when it was removed (Table 1). When straw was removed, the MBC/SOC ratio increased by 13% compared with the unfertilized control (from 29.0 to 32.8 mg kg^{-1}) while it increased by 5% when straw was retained (from 32.8 to 34.3 mg kg^{-1}). The increase was statistically significant only in the case of straw removal. The comparison between these two treatments is somewhat complicated by the fact that in some trials, the mineral fertilization rate was reduced when straw was retained.

3.4. Microbial community

The biomass of bacteria, actinomycetes and fungi tended to increase with fertilization, with the increase being more pronounced with manure and compost than with mineral fertilizer (Table 2). The response, however, varied considerably. Only the increase in fungi in treatments with mineral fertilizer application and the increase in actionmycete biomass in treatments with manure and compost were significant. However, due to the low number of datasets reporting standard deviations, the statistical analysis was done considering individual datasets as experimental units. This approach is more likely to result in significant differences than a meta-analysis. Overall, the fungal to bacterial ratio changed little

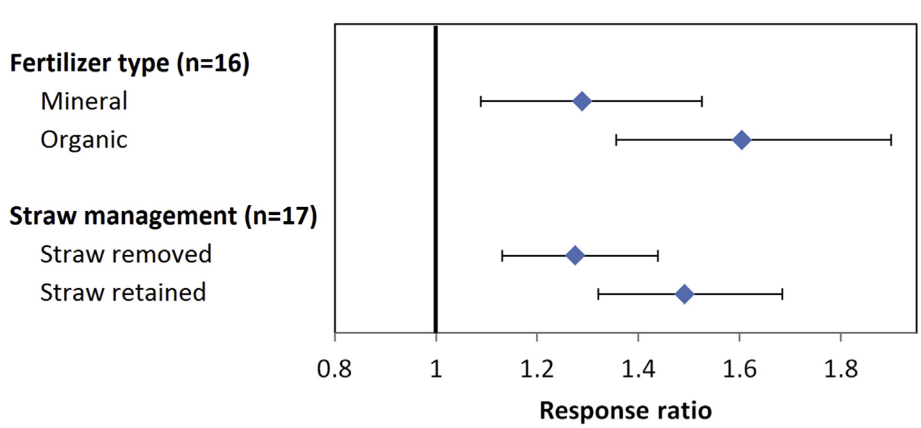

Fig. 5. Effect of mineral and organic fertilizer as well as straw management on the soil microbial biomass in paddy rice systems. Only studies with both fertilizer types or both straw treatments were included in this comparison. Both straw treatments were fertilized with mineral fertilizer; however, in some trials, the fertilizer application rate was reduced when the straw was retained.

Table 2
Effect of fertilization on microbial community composition in paddy rice systems. The values are means and standard deviation (n = number of studies; SD = Standard deviation; CI = confidence interval; SOC = Soil organic carbon; Actin = Actinomycetes; G+ = Gram positive bacteria; G- = Gram negative bacteria).

Statistic	Number of observations and response ratios (RR)						
	SOC	Total biomass	Bact (B)	Actin	Fungi (F)	F/B	G+/G-
Mineral (N or NPK)							
n	17	10	19	9	19	19	6
Average RR	1.18	1.50	1.76	1.91	1.70	1.04	1.19
SD	0.22	1.08	1.69	1.77	1.44	0.24	0.43
CI 95%	±0.11	±0.67	±0.76	±1.16	±0.65	±0.11	±0.34
Range	0.98–1.84	0.8–4.47	0.80–7.90	0.89–6.50	0.65–6.91	0.67–1.72	0.92–2.04
Organic (manure or compost)							
n	8	7	9	4	9	9	4
Average RR	1.47	2.77	2.63	2.95	2.17	1.00	1.06
SD	0.46	3.33	2.91	1.98	2.03	0.51	0.15
CI 95%	±0.32	±2.47	±1.9	±1.94	±1.33	±0.34	±0.14
Range	1.06–2.48	0.76–10.2	0.74–10.2	1.48–5.87	0.77–7.41	0.37–2.22	0.90–1.23

with the application of mineral or organic fertilizers, while the ratio of Gram positive to Gram negative bacteria tended to increase. However, these effects were not significant. The lack of significant effects of fertilizer on the microbial community despite the relatively large RR is mainly due to the small sample number and the large variability among studies. This large variability, in turn, is partly caused by the fact that different methods were used (direct count, counts of colony forming units, and fatty acid analysis). However, even within the same analytical method, the variability among studies was large (data not shown).

4. Discussion

4.1. Overall effects

Paddy soils fertilized with mineral fertilizer support a larger microbial biomass than unfertilized soils. Mineral fertilizer also led to higher yields and increased SOC contents. The higher crop production likely increased residue inputs, as well as root biomass and root exudates (Liu et al., 2016; Wang et al., 2016; Ge et al., 2017). This in turn increased SOC and MBC contents. The weak correlation between the RR yield and MBC does not invalidate this hypothesis, as crop management, which differed strongly among studies, may affect the relationship between crop productivity and MBC. Our observed increase in SOC content due to fertilization of 191 mg C kg soil^{-1} year^{-1} across all studies is somewhat higher than the results of a meta-analysis of paddy topsoil in fertilization trials from China (Tian et al., 2015), where SOC content increased by an average of 140 mg kg^{-1} year^{-1} (n = 163).

Positive effects of N on MBC content have also been observed in upland cropping systems, while MBC contents in forest and grassland ecosystems is generally reduced by increased N input (Liu and Greaver, 2010; Geisseler et al., 2016). In grassland ecosystems, this is likely due to the fact that N inputs gradually reduce grassland plant species richness which leads to a decrease in MBC (De Schrijver et al., 2011; Geisseler et al., 2016). The decrease in MBC content in N enriched treatments in forests and other ecosystems has been attributed to increasing osmotic pressure, soil acidity, aluminum toxicity (Liu and Greaver, 2010), inhibition of ligninase activity, and condensation of organic compounds with N-containing compounds (Treseder, 2008). With soil microorganisms being more sensitive indicators of soil health than SOC, the presence of toxic or adverse effects should result in a decrease in the MBC/SOC ratio. However, the MBC/SOC ratio tended to increase across the paddy rice studies included in our analysis. Furthermore, across all studies the annual N application rate had no effect on the response of the microbial biomass to mineral fertilizer and pH dropped only slightly in the fertilized treatments. Therefore, while short-term negative effects cannot be excluded, our dataset does not suggest that fertilizer applications have lasting negative effects on the microbial biomass in paddy rice systems.

4.2. Effect of organic C input and sampling time

In our analysis, the increase in MBC content was much more pronounced with the addition of manure or compost and when straw was retained in the field. This indicates that soil microorganisms in paddy soils are C limited and that MBC content strongly depends on the availability of organic C, which serves as both the energy source for heterotrophic microorganisms and a building block of microbial biomass. However, the slightly stronger response of the microbial biomass to the combined application of mineral N, P and K as opposed to the application of N alone suggests that rice demand for P or K may exceed supply in fields when yield is increased with N fertilizer. A limited availability of P and K prevents the plants from achieving their full yield potential, which in turn affects input of organic C from the plants. This is supported by our finding that the positive effect of mineral N, P and K fertilizers on MBC tended to increase over time. In fact, in an analysis of long-term trials in Asia, including upland, mixed and lowland systems, Ladha et al. (2003) found that 94% of the trials had a negative K balance.

Studies taking multiple measurements during the season generally found that MBC content and its response to fertilization vary among sampling times. It was therefore unexpected that we did not find significant differences among sampling times in our analysis. However, the differences between specific sampling times are not consistent in the literature. While some studies found that the effect of fertilizer on MBC content was more pronounced post-harvest than in-season (Bhattacharyya et al., 2005; Liu et al., 2009), Kyaw et al. (2005) reported the opposite trend. Positive and negative trends were also observed between pre-plant and post-harvest samples (Hasebe et al., 1985; Kyaw et al., 2005; Liu et al., 2009). Even changes in MBC content during the rice growing season and the effect of fertilizers on MBC contents are not consistent across studies (Bhattacharyya et al., 2005; Zhang et al., 2009; Datta et al., 2013; Das and Adhya, 2014). Site specific factors, such as climate, soil properties and crop management seem to strongly influence the response of the microbial community to fertilizer input over time.

4.3. Comparison with upland cropping systems

Paddy rice soils tend to accumulate more SOC than soils under upland crops (Sahrawat, 2004; Kögel-Knabner et al., 2010; Sun et al., 2015). This is mainly caused by the limited availability of oxygen under flooded conditions, which slows down decomposition of organic inputs, especially lignin and other phenolic compounds (Olk and Senesi, 2000; Gao et al., 2016).

The increase in SOC content observed in response to mineral fertilizer in paddy systems was higher than the average increase observed by Geisseler et al. (2016) for upland systems. In paddy soil studies that lasted at least one year, SOC content increased by 191 mg C kg soil^{-1} year^{-1} relative to the unfertilized control (n = 45, average duration 18.4 years), compared with 83 mg C kg soil^{-1} year^{-1} (n = 126, average duration 32 years) in upland systems. However, in the comparison of two long-term trials at the Institute of Red Soil in Jiangxi Province, China, mineral fertilizer significantly increased SOC contents in the upland system, while no significant effect was observed in the paddy system (Sun et al., 2015). Fertilizer applications tend to result in smaller yield increases in paddy rice systems than in upland cropping systems. A comparison of long-term trials in China found that N, P, and K fertilization increased yield on average 2.6 fold in upland wheat-maize rotations, while the yield increase was only 1.8 and 1.7 fold in rice-wheat and continuous rice systems, respectively (Shang et al., 2014). Similarly, a comparison of two long-term trials located at the Institute of Red Soil in Jiangxi Province in China found that N and N, P, and K fertilizer increased paddy rice yield by 10 and 44%, respectively, while the maize yield in the adjacent upland trial increased by 95 and 414%, respectively (Yan et al., 2013). In both studies, the small increase in rice yield was mainly due to the much higher yield of unfertilized rice compared with unfertilized maize. Unfertilized rice is generally less N limited than upland crops because the higher soil organic matter content in paddy soils leads to an increased N mineralization potential, which can provide a significant part of the N available to rice plants (Sahrawat, 1983). Therefore, while the decreased decomposition rate may reduce N mineralization during the initial years after establishing paddy rice systems, N mineralization is increased in fields that have been under paddy rice production for a long time. Furthermore, flooded rice fields harbor N_2 fixing microorganisms. The contribution of N_2 fixation has been estimated to range between 10 and 80 kg N ha^{-1} crop^{-1} (App et al., 1986; Roger and Ladha, 1992; Bei et al., 2013). However, biological N fixation tends to be decreased when mineral fertilizer is applied (Roger and Ladha, 1992). A small effect of mineral fertilizer on yield not only results in a low N use efficiency, but likely leads to a small increase in organic inputs from the crops.

Compared with upland cropping systems, the increase in the microbial biomass is much more pronounced in rice cropping systems, even when rice is grown in rotation with an upland crop. In the present study, MBC content increased by 26.4% with fertilization, while in a previous meta-analysis focusing on upland cropping systems, we found that MBC content increased on average by 13.6% (Geisseler et al., 2016). Differences in climate and soil oxygen availability may explain the stronger response of soil microorganisms to N input in paddy soil. The paddy rice trials included in this analysis were all carried out within a latitude of 40°. In the dataset with upland systems, however, 80 trials were within 40°, while 70 trials were between a latitude of 40° and 60° (Geisseler et al., 2016; supplemental data). A regression analysis of the RR of MBC as a function of latitude showed that latitude has a small, insignificant effect on the response of soil microorganisms to mineral fertilizer in paddy rice systems and that the RR differed little between paddy and upland systems at latitudes where rice studies were conducted (Fig. 6). In contrast, the RR tended to decrease at latitudes beyond 40°, where only upland system trials were located. Therefore, the stronger response of paddy soil microbes to mineral fertilization seems to be mainly due to their location at lower latitudes. The analysis also revealed that the variability of the data is much larger in upland cropping systems compared with paddy rice systems.

Differences in oxygen availability for the decomposer community may be another reason why the response of the MBC content was not considerably smaller in paddy rice systems compared with upland systems. While yield trends suggest that fertilization likely results in a smaller increase in the total amount of residue input in paddy systems compared with upland cropping systems, N fertilizer reduces the C:N ratio of residues and reduces cell wall thickness (Nori et al., 2006). Under anaerobic conditions, the decomposition of cell wall components is reduced, while the degradation rate of leachable and easily hydroyzable compounds from residues has been found to be similar under aerobic and anaerobic conditions (Kristensen et al., 1995). Therefore, N fertilization increases the proportion of compounds in the residue that

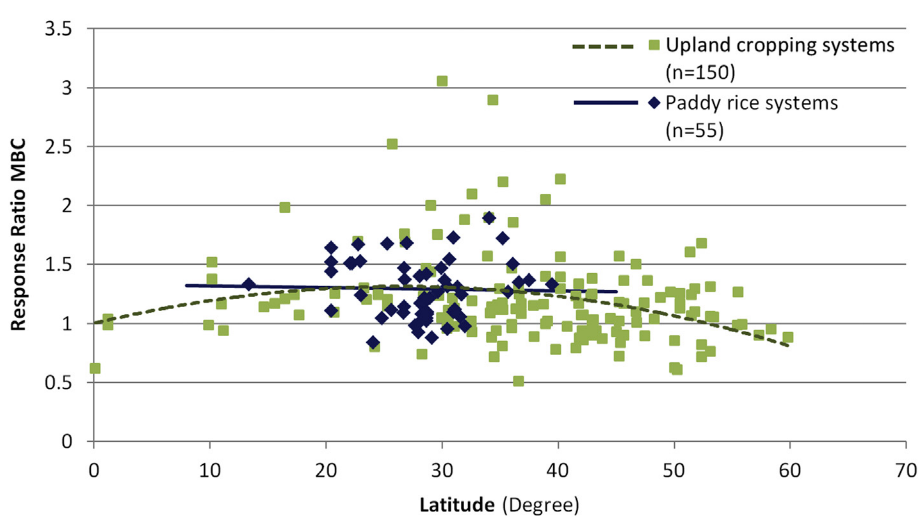

Fig. 6. Effect of latitude on the response of soil microbial biomass carbon (MBC) to mineral fertilizer in paddy rice systems (this study, supplementary data) and upland cropping systems (data from Geisseler et al., 2016; supplementary data).

are readily degraded under anaerobic conditions. Furthermore, when samples are taken from drained soils, some of the organic compounds not available under flooded conditions become available under aerobic conditions, boosting the microbial biomass.

4.4. Microbial community composition

Both bacteria and fungi benefitted from mineral fertilizers. Across all studies, the fungi to bacteria ratio increased by only 4% compared with the unfertilized control, a difference that was not significant. However, the number of studies reporting the effects of mineral N inputs on microbial community composition is small and the variability within the dataset large.

The absence of significant effects of mineral fertilizer on microbial community composition across studies is in contrast to many individual studies. However, in several studies, multivariate analyses revealed that the response of the microbial community composition to fertilization treatments was correlated with soil properties, such as SOC, total P and pH (Zhong and Cai, 2007; Ahn et al., 2012; Yuan et al., 2013; Dong et al., 2014; Zhao et al., 2014; Zhang et al., 2016). These results suggest that fertilization affects microbial community composition through changes in soil properties. The effect of fertilization on soil properties in turn highly depends on the initial soil characteristics, which may explain why the response of the microbial community is so variable and site-specific. Another factor affecting microbial communities is sampling season (Ahn et al., 2012; Zhao et al., 2014), highlighting the fact that soil microorganisms respond dynamically to changes in environmental conditions.

Overall, our analysis suggests that fertilization does not consistently select for specific microbial groups in lowland rice systems. However, the response of soil microorganisms to fertilizer applications depends strongly on environmental factors and may vary considerably among study sites. In contrast, the microbial biomass as a whole benefits from mineral fertilizer, most likely due to increased organic inputs from the crops. Across all studies, mineral fertilizer does not seem to have lasting negative effects on soil microorganisms.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.09.018.

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