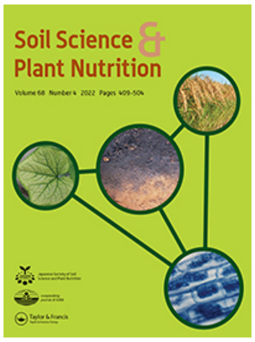

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ORIGINAL ARTICLE

Nitrous oxide and carbon dioxide emissions from two soils amended with different manure composts in aerobic incubation tests

Thanuja Deepani Panangala Liyanage[a], Morihiro Maeda[a], Hiroaki Somura[a], Nguyen Thi Thu Thuong[a], Makito Mori[b] and Taku Fujiwara[c]

[a]Graduate School of Environmental and Life Science, Okayama University, Okayama, Japan; [b]Agriculture Unit, Research and Education Faculty, Kochi University, Nankoku, Kochi, Japan; [c]Graduate School of Engineering, Kyoto University, Kyoto, Japan

ABSTRACT

Identification of nitrous oxide (N_2O) and carbon dioxide (CO_2) emissions from soils amended with different types of compost is needed for appropriate use of manure in agriculture. This study aimed at investigating the interaction effects of compost type and soil properties and effects of moisture contents on N_2O and CO_2 emissions, with identification of relative abundances of functional ammonia-oxidizing genes. Laboratory tests were conducted using cattle manure compost (CC) or mixed compost (MC) (cattle, poultry, and swine manure) amended Kochi (from a greenhouse) or Ushimado (from a paddy field) soils (3% by weight) with controls (no compost). Initial moisture contents were adjusted to 60% water-holding capacity (WHC) for Kochi soil and 70% WHC for both soils. The samples were aerobically incubated at 25°C. Emissions of N_2O and CO_2 and contents of ammonium N (NH_4^+-N) and nitrate N in soils were measured continuously until day 42. The abundances of ammonia-oxidizing bacteria (AOB) and archaea genes were estimated to evaluate nitrifying activities. Cumulative N_2O and CO_2 emissions were significantly higher ($p < 0.05$) in MC than those in CC treatments probably due to higher NH_4^+-N content and lower C/N ratio, which facilitated faster N mineralization and C decomposition. Emissions of N_2O and CO_2 were higher in compost-amended Kochi soil (70% WHC) with high total C and N, mineral N, and clay contents than those in less fertile Ushimado soil. Interestingly, interactions of compost type and soil properties on N_2O emissions were significant ($p < 0.05$) only in Kochi soil because the addition of decomposition resistant CC increased N_2O emissions only from this soil with high C and N contents. Higher soil moisture contents increased N_2O and CO_2 emissions significantly ($p < 0.05$) in Kochi soil. Emissions of N_2O until day 15 were mainly due to activities of AOB *amoA* genes ($R^2 = 0.91$). This study suggests that N_2O emissions are increased by high NH_4^+-N contents and a low C/N ratio in compost and high total C and N, mineral N, and clay contents in soil. The application of compost with less decomposable C increases N_2O emissions only from nutrient-rich soil.

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Aerobic incubation; carbon dioxide; compost; nitrous oxide; WHC

1. Introduction

Nitrous oxide (N_2O) is one of the longest-lived greenhouse gases with a global warming potential 298 times higher than that of carbon dioxide (CO_2) on a per mass basis over 100-year period (Signor and Cerri 2013). Emissions of N_2O have increased by 30% over the past four decades to 7.3 tera-grams of nitrogen (N) per year, of which 87% resulted from agricultural sources (Tian et al. 2020).

Microbial transformations of mineral N contribute to the production of N_2O in terrestrial ecosystems through nitrification and denitrification (Davidson et al. 1998; Deng et al. 2016). Nitrification is the aerobic oxidation of ammonium (NH_4^+) to nitrate (NO_3^-), which is primarily regulated by functional genes of autotrophic ammonia-oxidizing bacteria (AOB *amoA*), ammonia-oxidizing archaea (AOA *amoA*), and nitrite-oxidizing bacteria (Parton et al. 2001; Yin et al. 2019). Denitrification is a stepwise reduction of NO_3^- to N_2, generating intermediate products of NO_2^-, NO, and N_2O under anaerobic conditions and controlled by a wide range of heterotrophic microorganisms (Otte et al. 2019).

Production of N_2O is a result of complex interactions among factors such as soil moisture, temperature, decomposable organic C, contents and forms of mineral N, and relative abundances of enzymes of nitrification and denitrification (Signor and Cerri 2013; Hoang and Maeda 2018b; Meinhardt et al. 2018). Additionally, more intrinsic soil properties including pH, drainage capacity, and soil texture affect N_2O emissions (Boeckx, Beheydt, and Cleemput 2005; Cuhel et al. 2010).

Organic amendments are found to increase N_2O emissions from arable soils by increasing the microbial availability of N and carbon (C) and therefore accelerate nitrification and denitrification processes (Kim et al. 2019). Among different organic amendments, application of livestock manure to agricultural fields has been practiced for a long time to improve soil fertility and to increase soil organic C (SOC) content (Das et al. 2017; Rayne and Aula 2020). Zhou et al. (2017) estimated that livestock manure application largely increased soil N_2O emissions by 33% compared to synthetic N fertilizer. Thus, animal manure-amended agricultural soils are considered to be important sources of N_2O emissions.

CONTACT Morihiro Maeda ✉ mun@cc.okayama-u.ac.jp Graduate School of Environmental and Life Science, Okayama University, 3-1-1 Tsushima-Naka, Kita-Ku, Okayama 700-8530, Japan

Among different forms of processed manure, compost is preferred by many organic vegetable growers due to its potential benefits over raw manure. Those benefits include the stability of total C, slower release of nutrients, less transmission of pathogenic fungi, lower acidification potential by continuous application, lower risk of burning seedling roots by high levels of NH_4^+-N and salts in fresh manure, and reduced volume, which facilitates transportation (Diacono and Montemurro 2010; Brust 2019). A few studies have mainly focused on composted manure applications on N_2O emissions, while many have examined the effects of raw manure applications (Velthof, Kuikman, and Oenema 2003; Pelster et al. 2012; Thorman et al. 2020). Velthof, Kuikman, and Oenema (2003) found that high N_2O emissions were associated with liquid pig manure, which contained high contents of mineral N and easily decomposable C. Pelster et al. (2012) observed higher N_2O emissions from poultry manure than those from liquid cattle manure and liquid swine manure, likely because of high C content. Similarly, Thorman et al. (2020) reported higher N_2O emissions from poultry manure with high organic C and total N contents than those from slurry and farmyard manure of pig and cattle. The properties of raw manure can be largely altered by composting, resulting in increased pH and NO_3^--N contents, decreased total C and NH_4^+-N contents and C/N ratio. Moreover, labile C forms can be consumed during composting and result in recalcitrant C-rich materials. These property changes of manure during composting processes altered C and N dynamics in soil and therefore affected N_2O emissions (Li et al. 2017). Previous studies revealed that compost with readily available C and N resulted in higher N_2O emissions than those with low available C and N (Zhu et al. 2014). Furthermore, higher dissolved organic C in immature compost could increase N_2O emissions. No differences in N_2O emissions were found between fresh cattle manure and composted one although there were large differences in NH_4^+-N contents (Li et al. 2017). Masunga et al. (2016) suggested that different properties of compost induced different N mineralization rates and therefore might have effects on N_2O emissions. Effects of total C and N, and mineral N contents and C/N ratio in compost with different decomposition rates on N_2O emissions are still uncertain.

Emissions of N_2O from compost-amended soils can be further affected by soil properties such as total C content, N contents and their forms, pH, and soil texture (Zhu et al. 2020). According to Bouwman, Boumans, and Batjes (2002), N_2O emissions from inundated rice fields during a growing season were generally lower than those from upland fields because N_2O was further consumed by denitrifiers due to high soil water content, impeded drainage, shallow groundwater, and soil compaction. On the other hand, Xing and Zhu (1997) reported comparatively higher mean N_2O emissions from rice paddy fields (39.5 μg N m^{-2} h^{-1}) than those from upland fields (30.6 μg N m^{-2} h^{-1}) in China owing to flooded conditions and combined application of organic manure and inorganic N fertilizer, which would have created favorable anaerobic conditions for N_2O emissions. In a meta-quantitative analysis, Akiyama, Yan, and Yagi (2006) also documented that annual background N_2O emissions were higher in poorly drained paddy soils (1.40 kg N ha^{-1} $year^{-1}$) than those in well-drained upland soils (0.36 kg N ha^{-1} $year^{-1}$) in Japan due to anaerobic conditions in rice paddy fields and pointed out that large uncertainties remain in their estimations because of limited data availability. Thus, reasons for different N_2O emissions from different types of soil are still unclear. Interaction effects between soils with different properties and organic amendments have been studied by several researchers using fresh livestock manure under laboratory or field conditions (Chiyoka et al. 2011; Zhu et al. 2020). Chiyoka et al. (2011) observed more N_2O emissions from pelletized cattle manure than those from non-pelletized manure in a soil with higher N and C contents, which did not occur in the other soil with lower N and C contents. However, interactions of compost type and soil properties on N_2O emissions have not been yet studied to the best of our knowledge.

Organic soil amendments increase soil CO_2 emissions (Grave et al. 2015). Ray et al. (2020) found that higher cumulative CO_2 emissions occurred from soils amended with chicken manure than those from soils amended with dairy manure. Chiyoka et al. (2011) observed rapid increases in the population of heterotrophic microorganisms and CO_2 emissions from manure-amended soils at initial stages of organic C decomposition. According to Hoang and Maeda (2018b), CO_2 emissions from chicken compost-amended soils were much higher than those of commercial compost and non-amended soil. Grave et al. (2015) reported that CO_2 emissions from soils amended with swine manure compost were lower than those from urea or raw manure. In contrast, some C fractions resistant to decomposition derived from compost can be sequestered for a long time or hydrophobic humic substances originating from compost delay the decomposition of organic C (Termorshuizen et al. 2004; Paustian et al. 2016). Thus, CO_2 emissions from soils are dependent on different compost types and reasons for different CO_2 emissions were not well identified.

Therefore, the gap in knowledge should be filled by assessments of N_2O and CO_2 emissions from different combinations of manure compost and soils with different properties. Laboratory level experiments are mandatory to form the basis for appropriate field practices of compost management to mitigate N_2O emissions such as selection, timing, and application methods (Thorman et al. 2020). The objective of this study was to investigate the effects and interactions of compost type (decomposition resistant or susceptible) and soil properties (total C and N, mineral N, and clay contents) on N_2O and CO_2 emissions under aerobic conditions. Moreover, we studied the effects of soil moisture content on N_2O and CO_2 emissions to determine additional interactive factors because soil moisture content would affect microbial activities in compost and soil. To identify the major microbial regulators of nitrification, we analyzed the relative abundances of functional genes of ammonia oxidation (AOB *amoA* and AOA *amoA*) in the incubated soil.

2. Materials and methods

2.1. Soil sampling and preparation

Two types of soil were used for laboratory incubation experiments under aerobic conditions. Kochi soil was collected from a greenhouse planted with vegetables at the Faculty of

Agriculture and Marine Science, Kochi University, Japan, in April 2019. Prior to the soil sampling, bark compost had been applied to the field at 18 kg m^{-2} in the last five years. Ushimado soil was collected from a paddy field in Ushimado, Okayama Prefecture, Japan, in April 2016. Kochi and Ushimado soils belong to Eutric Fluvisols and Dystric Gleysols soil groups (FAO), respectively. The two soils were totally contrasting in inherent properties, where Kochi soil initially contained higher total C and N, and mineral N (ammonium N: NH_4^+-N and nitrate N: NO_3^--N) contents compared to Ushimado soil (Table 1). Additionally, EC and cation exchange capacity (CEC) of the Kochi soil were higher than Ushimado soil. Kochi soil was sandy clay loam in texture, while Ushimado soil was sandy loam. Kochi soil contained a higher content of clay with compared to Ushimado soil (Table 1). These two soils were chosen to reflect effects of different properties of soil (total C and N, mineral N, and clay contents) on N_2O and CO_2 emissions after being amended with manure compost. The soil samples were air dried, passed through a 2-mm sieve, and stored until the experiments.

Two types of livestock manure compost: cattle manure compost (CC) and mixed compost (MC) were used as organic amendments. The CC, produced at the Research Institute for Livestock Science, Okayama Prefectural Agriculture, Forestry and Fisheries Research Center, was supplemented with sawdust. The MC was a mixture of manure from cattle, swine, and poultry and produced at the Tetta Town Composting Center, Okayama. Sawdust, rice husk, and bark were added as additives to MC in the composting process. The total N and mineral N contents were higher and total C content was slightly lower in MC than those in CC (Table 2). Higher C/N ratio and lower N content of CC than those of MC indicated that CC was more resistant to N mineralization and C decomposition. The CC represented a more stable form of manure compost and MC was more susceptible for easy decomposition and mineralization. To differentiate the effects of differences among manure compost types (total N and mineral N content, C/N ratio) on N_2O and CO_2 emissions, these two types of manure compost were used in the present study. Both CC and MC were air dried and ground into fine powders to assure uniform distribution in soil.

Table 1. Physiochemical properties of the two types of soil.

Property	Kochi soil	Ushimado soil
Total N (g N kg^{-1})	3.9	1.4
Total C (g C kg^{-1})	62.6	14.7
C/N ratio	15.9	10.2
CEC[†] ($cmol_c$ kg^{-1})	28.3	7.5
NH_4^+-N[‡] (mg N kg^{-1})	109.5	9.5
NO_3^--N[§] (mg N kg^{-1})	463.7	19.2
pH	5.5	8.5
EC[¶] (dS m^{-1})	0.8	0.1
Texture	Sandy clay loam	Sandy loam
Sand (%)	72	74
Silt (%)	1	12
Clay (%)	27	14

[†]Cation exchange capacity, [‡]Ammonium nitrogen, [§]Nitrate nitrogen, [¶]Electrical Conductivity

Table 2. Specific properties of cattle manure compost and mixed compost.

Property	Cattle manure compost	Mixed compost
Total N (g N kg^{-1})	16.3	26.0
Total C (g C kg^{-1})	301.6	273.3
C/N ratio	18.5	10.5
NH_4^+-N (mg N kg^{-1})	30.5	893.2
NO_3^--N (mg N kg^{-1})	18.1	58.6
pH	9.4	9.2
EC (dS m^{-1})	7.6	7.5

Total C and N in the original soil and compost samples were measured by the dry combustion method with a CN coder (MT-700, Yanaco, Japan). The CEC of soil was measured by the Schollenberger method at pH 7 (Gumbara, Darmawan, and Sumawinata 2019). The soil texture was determined by the sieve and pipette method (Kettler, Doran, and Gilbert 2001).

2.2. Treatments preparation

Kochi soil was uniformly mixed with two compost types separately at 3% (by weight) considering a common manure application rate (approximately 30 t/ha) in agricultural soils. Initial moisture contents of the treatments were adjusted to 60% (equivalent to water-filled pore space (WFPS) 61% for Kochi soil) or 70% (equivalent to WFPS 72% for Kochi soil and 46% for Ushimado soil) water-holding capacity (WHC) to assure aerobic conditions. Levels of WHC in compost-amended samples were adjusted according to water absorbed by compost particles. In general, the common optimal water content for nitrification ranges from 60% to 75% WHC (Mizota, Yamaguchi, and Noborio 2006). The initial WHC levels were maintained throughout the incubation period by adding water to compensate the loss by evaporation. The treatments at 60% or 70% WHC were noted as K-0_{60} (Control; no compost-amended Kochi soil), K-CC_{60} (Kochi soil + CC), and K-MC_{60} (Kochi soil + MC) or K-0_{70} (Control; no compost-amended Kochi soil), K-CC_{70} (Kochi soil + CC), and K-MC_{70} (Kochi soil + MC), respectively. Ushimado soil was amended with CC or MC at the same application rate and adjusted to 70% WHC. The treatments were denoted as U-0_{70} (Control; no compost-amended Ushimado soil), U-CC_{70} (Ushimado soil + CC), and U-MC_{70} (Ushimado soil + MC).

2.3. Laboratory incubation experiments

The soil samples (9 treatments with duplicates for each sampling date) were contained in 100-mL glass incubation bottles, and they were covered with a polyethylene film (0.02 mm thickness) to ensure minimal evaporation while maintaining gas exchange. The bottles were incubated at 25°C for 42 days to achieve complete nitrification. Emissions of N_2O and CO_2 were measured on days 0 (incubation start date), 3, 7, 15, 21, 28, and 42 during the incubation period.

2.4. Gas sampling and emission measurement

The incubation bottles were flushed with atmospheric air at 50 mL s^{-1} with a mini-pump (MP-2 N, Sibata/Code 8086–2, Japan) for 2 min to ensure the background air concentration.

Then the bottles were sealed with butyl rubber septa tightened with aluminum caps for two hours before gas collection. Head space gas samples were injected to a gas chromatograph (GC-8A, Shimadzu, Japan) equipped with electron capture and thermal conductivity detectors to measure N_2O and CO_2 concentrations (Hoang and Maeda 2018b), respectively. The gas concentration was determined with respect to a calibration done using two standard gas samples separately for N_2O (0.298 and 1.512 ppm) and CO_2 (350 and 2190 ppm). Gas emissions were calculated using the following equation:

$$\begin{aligned} &N_2O \text{ or } CO_2 \text{ emissions } (\mu g \text{ N or C } kg^{-1} h^{-1}) \\ &= \rho \times C \times (V_g + V_L \times \alpha) \times 273/(W \times (273 + T))/t \end{aligned}$$

where ρ (kg m^{-3}) is the density of N_2O (1.25) or CO_2 (0.5357), C (ppm) is the concentration of N_2O or CO_2, V_g (m^3) is the volume of the headspace, V_L (m^3) is the volume of the liquid phase, α is the Bunsen absorption coefficients for N_2O (0.539) or CO_2 (0.614) at 25°C, W (kg) is the oven-dried weight of soil, T is temperature at determination (25°C), and t (h) is sealing duration. The air concentrations were eliminated from the measured concentrations of N_2O and CO_2.

2.5. DNA extraction and quantification of relative abundances of AOB amoA and AOA amoA genes

The functional genes, *amoA* of AOB and AOA, were analyzed to evaluate the cumulative effect of microbial growth on N_2O emissions. According to the results of N_2O emissions, the samples on day 15 of incubation (70% WHC) were used for the DNA and functional gene analysis.

2.5.1. DNA extraction from soil

DNA was extracted from 0.4 g of moist soil (the samples for DNA analysis were separately incubated in triplicates from those for gas measurements, and single samples of air-dried Kochi and Ushimado soils were analyzed for reference) using FastDNA Spin Kit for Soil (MP Biomedicals, USA). Eluted DNA (80 µL) was purified with DNA Clean and Concentrator^{TM}-25 (Zymo Research, USA) and used for quantification of DNA concentration and in quantitative PCR experiments. DNA was quantified using a Nanodrop Spectrophotometer (Thermo Scientific NanoDrop One).

2.5.2. Quantification of relative abundances of AOB and AOA amoA genes

Quantification of AOB and AOA *amoA* was done using a Step One Plus Real-Time PCR system (Applied Biosystems, System version 2.2.3), according to the method described by Morimoto et al. (2011). Data of qPCR tests were obtained from soil DNA samples, which were subjected to duplicate independent amplifications. Information on primer sets and thermo-cycling qPCR reaction conditions is shown in Table 3. The primer pair amoA-1F and amoA-2R was used for quantification of AOB. The reaction mixture (20 µL) contained 10 µL of KAPA SYBR FAST qPCR Master Mix, 0.8 µL of each primer, 0.2 µL of bovine serum albumin, 1 µL of hundredfold-diluted soil DNA, and 7.2 µL of autoclaved ultra-pure water. For quantification of AOA, the primer pair amoA-19F and crenamoA-616r was used. The PCR reaction mixture was the same as that for AOB except the amounts of 2 µL of each primer and 4.8 µL of sterilized water. The standard curves for quantification of AOB and AOA were generated from ten-fold serial dilutions of *Nitrosomonas europaea* NBRC 14298 and crenarchaeal amoA (Morimoto et al. 2011), respectively. PCR efficiencies and coefficients of determination (R^2) of the standard curves were 122% and R^2 = 0.98 for AOB and 90% and R^2 = 0.99 for AOA.

Table 3. Primer sets and thermo-cycling conditions used for quantitative PCR reactions.

Target gene	Primer set	Thermo-cycling conditions
AOB *amoA*	amoA-1F amoA-2R	Enzyme activation: 95°C, 2 min. Denaturation: (94°C, 30 s) × 40 Annealing: (54°C, 30 s) × 40 Extension: (72°C, 30 s) × 40
AOA *amoA*	amoA-19F crenamoA-616r	Enzyme activation: 95°C, 2 min Denaturation: (94°C, 30 s) × 40 Annealing: (55°C, 30 s) × 40 Extension: (72°C, 60 s) × 40

2.6. Mineral N, pH, and EC of incubated soil

A part of the soil sample in each bottle incubated for gas emission measurements was immediately extracted for mineral N measurement, and the other part was used for pH and EC determinations. The samples (1:10) and original compost samples (1:100) were extracted with 2 *M* KCl by shaking at 175 rpm for 1 hour, then used to measure NH_4^+-N and NO_3^--N using a continuous flow analyzer (QuAAtro 2-HR, Bltec, Japan). The pH and EC of samples were measured at a 1:10 solid:water ratio using a pH/Ion meter (F-23, Horiba, Japan) and a conductivity meter (DS-14, Horiba, Japan) after shaking at 175 rpm for 1 minute (Hoang and Maeda 2018a).

2.7. Data analysis

Cumulative N_2O and CO_2 emissions were calculated using trapezoidal integration of N_2O and CO_2 emission curves plotted against time. Two-way analysis of variance (ANOVA) was performed on cumulative N_2O and CO_2 emissions over 42 days from Kochi and Ushimado soils at 70% WHC (compost type × soil properties) and from Kochi soil at 60% and 70% WHC (compost type × Moisture content). Statistically significant differences in cumulative N_2O and CO_2 emissions were examined using Tukey's test in R software ($p < 0.05$, R Core Team 2019) separately for Kochi and Ushimado soils at 70% WHC and for Kochi soil at 60% and 70% WHC.

3. Results

3.1. Emissions of N_2O from compost-amended soils

In the K-MC_{60} treatment, N_2O emissions peaked on day 3, while they peaked on day 7 in the K-MC_{70} treatment, which was 4 times larger (Figure 1(a,b)). Both K-0_{60} and K-CC_{60} treatments showed continuously decreasing N_2O emissions with time

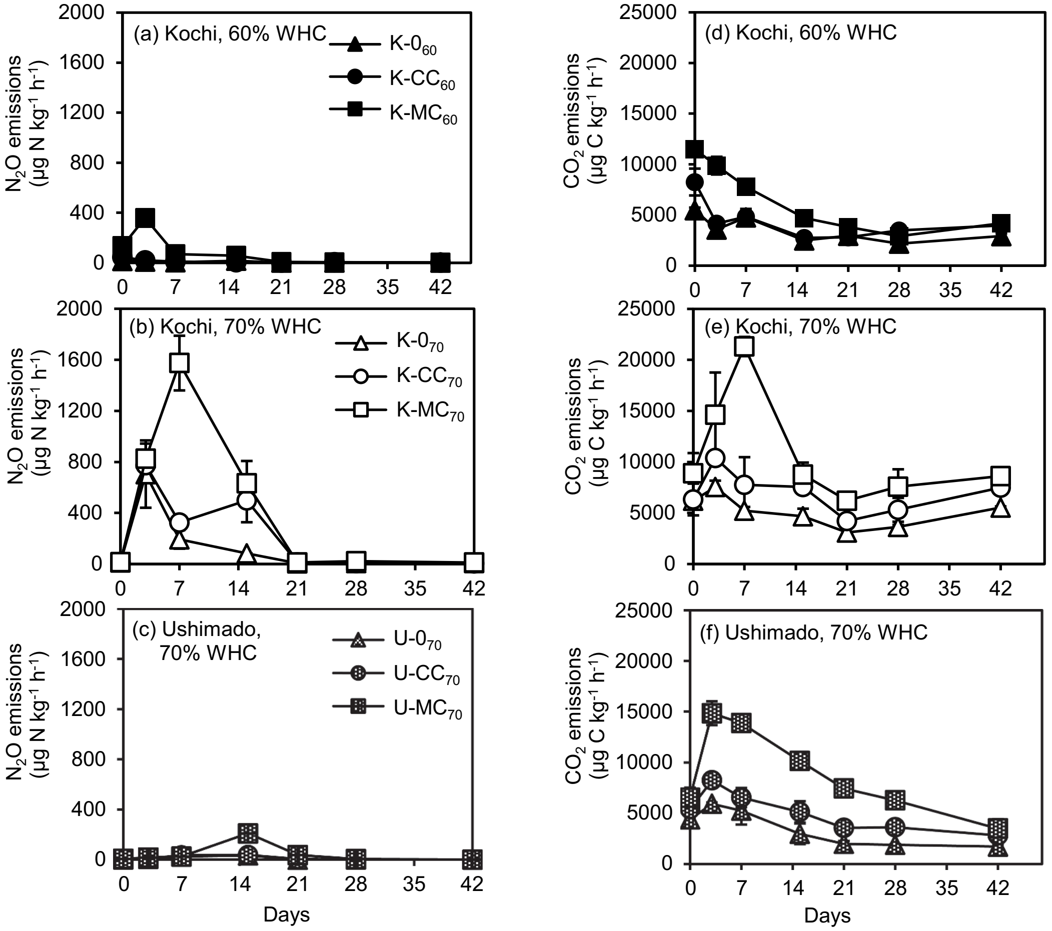

Figure 1. Variation of N_2O and CO_2 emissions from Kochi soil treatments at 60% WHC (a, d), 70% WHC (b, e), and Ushimado soil treatments at 70% WHC (c, f). Error bars indicate ± standard deviations. K-0_{60} or K-0_{70}: no compost-, K-CC_{60} or K-CC_{70}: cattle manure compost-, and K-MC_{60} or K-MC_{70}: mixed compost-amended Kochi soil at 60% or 70% WHC. U-0_{70}: no compost-, U-CC_{70}: cattle manure compost-, and U-MC_{70}: mixed compost-amended Ushimado soil at 70% WHC.

(Figure 1(a)). At 70% WHC, N_2O emissions of K-0_{70} and K-CC_{70} treatments peaked on day 3 (Figure 1(b)). Those peak emissions of N_2O were 50 (K-0_{70}) and 17 (K-CC_{70}) times higher than those at 60% WHC. The emissions of N_2O from all MC treatments (K-MC_{60}, K-MC_{70}, and U-MC_{70}) were higher for the first 21 days than those from no compost- and CC-amended soils (Figure 1 (a–c)). In Ushimado soil, all peak emissions occurred on day 15, and N_2O emissions were extremely low after day 21 irrespective of compost types (Figure 1(c)).

Compost additions increased cumulative N_2O emissions to different degrees by the type. The additions of MC significantly increased cumulative N_2O emissions ($p < 0.05$) in Kochi and Ushimado soils at 70% WHC (Figure 2(a)) and Kochi soil at 60% WHC (Figure 3(a)) than the respective controls. Kochi soil with MC had significantly higher cumulative N_2O emissions ($p < 0.05$) than those with CC at both 60% and 70% WHC levels (Figure 3(a)). In Kochi soil at 70% WHC, CC addition significantly increased cumulative N_2O emissions ($p < 0.05$) than the respective control, while at 60% WHC, the increment was insignificant ($p > 0.05$, Figure 3(a)). No compost- and CC-amended Ushimado soil had similar N_2O emissions, while MC-amended Ushimado soil had significantly higher cumulative N_2O emissions ($p < 0.05$, Figure 2(a)). All Ushimado soil treatments had significantly lower cumulative N_2O emissions ($p < 0.05$) than those in the respective treatments of Kochi soil at the same WHC (70% WHC, Figure 2(a)).

3.2. *Emissions of CO_2 from compost-amended soils*

The peak emission of CO_2 in the K-MC_{70} treatment was approximately double than that in the K-MC_{60} treatment (Figure 1(d,e)). The peak increments of K-0_{70} and K-CC_{70} treatments were almost 1.3 times higher than those at 60% WHC (Figure 1(d,e)). Initial peak CO_2 emissions from Kochi soil (60% WHC) decreased toward day 28, then increased slightly to day 42 (Figure 1(d)). In the K-MC_{70} treatment, CO_2 emissions peaked on day 7, and both K-0_{70} and K-CC_{70} treatments showed earlier peak emissions on day 3 (Figure 1(e)). Thereafter, emissions of CO_2 (70% WHC) decreased toward day 21, then increased again slightly (Figure 1 (e)), which was similar to those of 60% WHC (Figure 1(d)). All Ushimado soil treatments showed peak N_2O emissions on day 3 and, then decreased continuously during the rest of the period (Figure 1(f)).

Both types of compost additions significantly increased cumulative CO_2 emissions than the respective controls of two soils at 70% WHC ($p < 0.05$, Figure 2(b)). The

ANOVA of cumulative N_2O and CO_2 emissions to compost type and soil properties			
Factor	***p* value**	**Factor**	***p* value**
Compost type	3.3×10^{-6}	Compost type	1.8×10^{-6}
Soil properties	9.7×10^{-8}	Soil properties	1.0×10^{-4}
Compost type × Soil properties	1.5×10^{-5}	Compost type × Soil properties	0.8

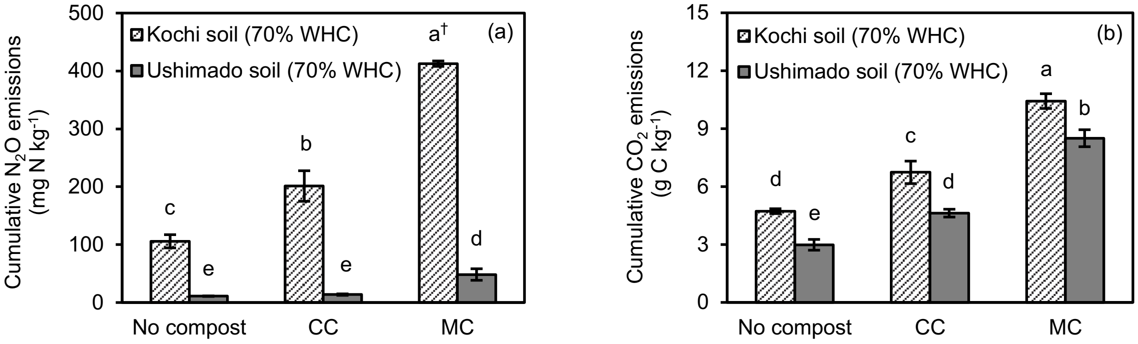

Figure 2. Two-way analysis of variance (ANOVA) results and cumulative N_2O (a) and CO_2 (b) emissions from no compost-, cattle manure compost (CC)-, and mixed compost (MC)-amended Kochi and Ushimado soils at 70% WHC during 42 days of incubation. Error bars indicate ± standard deviations. †Means with the same letters are not significantly different at $p > 0.05$ by Tukey's test.

ANOVA of cumulative N_2O and CO_2 emissions to moisture content and compost type			
Factor	***p* value**	**Factor**	***p* value**
Moisture content	9.9×10^{-8}	Moisture content	2.1×10^{-6}
Compost type	1.9×10^{-6}	Compost type	9.3×10^{-6}
Moisture content × Compost type	1.7×10^{-5}	Moisture content × Compost type	8.1×10^{-4}

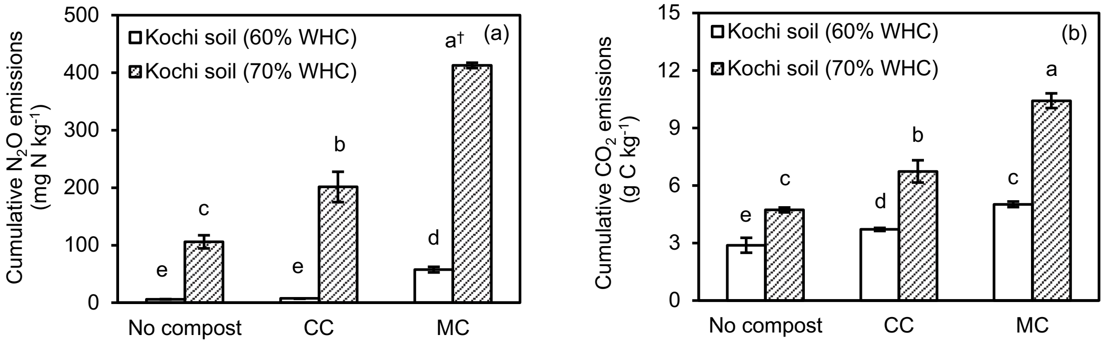

Figure 3. Two-way analysis of variance (ANOVA) results and cumulative N_2O (a) and CO_2 (b) emissions from no compost-, cattle manure compost (CC)-, and mixed compost (MC)-amended Kochi soil at 60% and 70% WHC during 42 days of incubation. Error bars indicate ± standard deviations. †Means with the same letters are not significantly different at $p > 0.05$ by Tukey's test.

significantly highest cumulative CO_2 emissions ($p < 0.05$) were in MC treatments compared with those in CC treatments of Kochi (both 60% and 70% WHC, Figure 3(b)) and Ushimado (Figure 2(b)) soils. Kochi soil treatments at 70% WHC had significantly higher cumulative CO_2 emissions than the respective treatments at 60% WHC (Figure 3(b)).

3.3. ANOVA results of cumulative N_2O and CO_2 emissions from compost-amended soils

According to the ANOVA (Figure 2), the main effects of compost type or soil properties on cumulative N_2O and CO_2 emissions were statistically significant ($p < 0.05$). However, the interactions of compost type and soil properties on N_2O emissions from both Kochi and Ushimado soils were significant ($p < 0.05$, Figure 2). On the other hand, the interactions of compost type and soil properties on cumulative CO_2 emissions were statistically insignificant ($p > 0.05$, Figure 2). The main effects of moisture content and the interactions of moisture content and compost type on cumulative N_2O and CO_2 emissions from Kochi soil at 60% and 70% WHC were significant ($p < 0.05$, Figure 3)

3.4. Changes in NO_3^--N and NH_4^+-N contents

In Kochi soil treatments at 60% WHC, NO_3^--N content on day 0 decreased toward day 3, then increased until day 21 (Figure 4(a)). The values had only slightly fluctuated thereafter until day 42 (600–800 mg N kg^{-1}, Figure 4(a)). At 70% WHC, NO_3^--N content decreased until day 3 or 7, then increased toward day 21 or 28 (Figure 4(b)). The values had flattened thereafter on day 42 (620–900 mg N kg^{-1}, Figure 4(b)). Ushimado soil also showed the same trend as Kochi soil in initial reduction and later increment of NO_3^--N content, although the values were much lower than those in Kochi soil (Figure 4(c)).

At 60% and 70% WHC, NH_4^+-N content of Kochi soil treatments increased until day 3 and 7, respectively, then decreased with time to day 42 (Figure 4(d,e)). The maximum NH_4^+-N contents at 60% and 70% WHC were 218–303 mg N kg^{-1} on day 3 and 270–380 mg N kg^{-1} on day 7, respectively. Ushimado soil also showed a similar trend of NH_4^+-N variation although the values were lower than those in Kochi soil (maximum NH_4^+-N content: 40–75 mg N kg^{-1}, Figure 4(f)).

Total mineral N content of Kochi soil (60% WHC) on day 42 (680–850 mg N kg^{-1}) was in a range similar to that on day 0 (700–800 mg N kg^{-1}, Figure 4(g)), indicating no clear immobilization. At 70% WHC, the same behaviors were observed in both K-0_{70} and K-CC_{70} treatments, while the total mineral N content showed a remarkable reduction in the K-MC_{70} treatment (Figure 4(h)). This might be due to the high rate of NO_3^--N reduction in the K-MC_{70} treatment until day 7. Total mineral N contents in Ushimado soil treatments showed slight fluctuations, but the values were lower than those in Kochi soil treatments (Figure 4(i)).

3.5. Changes in pH and EC

At 60% WHC, Kochi soil showed a pH increment on day 3, and it then decreased slightly with time (Figure 5(a)). Similarly, EC values increased slightly on day 7 and gradually increased to the end of experiments (Figure 5(d)). At 70% WHC, pH increased slightly in the first week and, then decreased slightly with fluctuations (Figure 5(b)). The increments and reductions were not as prominent as those at 60% WHC. At 70% WHC, EC of Kochi soil decreased on day 3 or 7, then increased with slight fluctuations (Figure 5(e)). In Ushimado soil treatments, pH (7–8.5, Figure 5(c)) was comparatively higher than those in Kochi soil treatments at 70% WHC (5–7.7, Figure 5(b)) during the entire incubation period, while EC values were considerably lower than those in Kochi soil treatments, which did not change over the experimental period (Figure 5(e,f)). Among all treatments, the lowest pH and EC values were observed in controls.

3.6. Relative abundances of functional genes of AOB and AOA (amoA)

The AOB genes of original soil samples increased during the incubation in both Kochi and Ushimado soils (Table 4). The AOB gene copy numbers in Kochi soil were significantly higher ($p < 0.05$) than those in Ushimado soil (Table 4). Both CC and MC additions to Kochi soil significantly increased ($p < 0.05$) the AOB gene count with compared to the control. A higher number of AOB gene copies were observed in the K-MC_{70} treatment than those in the K-CC_{70} treatment, while this difference was not statistically significant. In Ushimado soil, no significant differences in AOB gene counts were detected between treatments.

During incubation, AOA gene copy numbers of original soil samples decreased in both soils. In Kochi soil, the highest AOA gene copy numbers were observed in the K-CC_{70} treatment, although it was not significantly different from MC treatments on day 15 (Table 4). In Ushimado soil, the lowest AOA gene count was seen in the U-CC_{70} treatment. The ratio of AOB/AOA was in the range of 549–881 in Kochi soil and 43–90 in Ushimado soil.

The linear relationship between AOB gene copy numbers and cumulative N_2O emissions until day 15 was positively and significantly correlated ($R^2 = 0.91$, $p < 0.05$, Figure 6). In contrast, the relationship between AOA gene copy numbers and cumulative N_2O emissions was only weakly correlated ($R^2 = 0.03$). This indicated that N_2O emissions were very much related to the activities of AOB genes.

4. Discussion

4.1. Main effects of compost type and soil properties on N_2O and CO_2 emissions

In our study (Figure 1), higher emissions of N_2O and CO_2 in compost-amended treatments were observed than those in no compost-amended controls at initial stages of the incubation. After the peaks N_2O and CO_2 emissions showed decreasing trends. Initial peak emissions of N_2O and CO_2 can be explained by the provision of more decomposable organic C and N in compost, which are substrates for microbial growth and activities (Signor and Cerri 2013). Similar to our observations, peak emissions of N_2O occurred after the application of manure and plant residues to soil under adequate moisture and available N conditions (Badagliacca et al. 2017; Cao et al. 2019). Rahman (2013) observed enhanced CO_2 emissions from soil amended with organic amendments containing high amounts of labile C. Reductions in N_2O and CO_2 emissions thereafter were possibly due to the consumption of decomposable N and C substrates with time.

ANOVA results showed that the main effects of compost type on cumulative N_2O and CO_2 emissions were statistically significant ($p < 0.05$, Figure 2). The addition of MC significantly increased N_2O and CO_2 emissions ($p < 0.05$) from Kochi soil (at both 60% and 70% WHC, Figure 3) and Ushimado soil (at 70% WHC, Figure 2) than that of CC. Relatively higher NH_4^+-N content in the original MC compared with CC (Table 2) and NH_4^+-N derived from mineralization during the early stages of incubation (Figure 4(d–f)) may have resulted in higher emissions of N_2O. Kim et al. (2019) explored a significantly positive relationship between daily N_2O emissions and soil NH_4^+-N contents. Hence, it was clear that high NH_4^+-N content derived from compost was a key factor promoting N_2O emissions.

The lower C/N ratio of MC (Table 2) would have increased N_2O and CO_2 emissions because organic amendments with a small C/N ratio stimulate N mineralization, resulting in increased NH_4^+-N contents (Signor and Cerri 2013), which can be nitrified. Toma and Hatano (2007) observed high N_2O emissions from soils treated with low C/N ratio amendments because of faster N mineralization. Velthof, Kuikman, and Oenema (2003) reported that cattle manure with a comparatively high C/N ratio is less decomposable than other common livestock manure types.

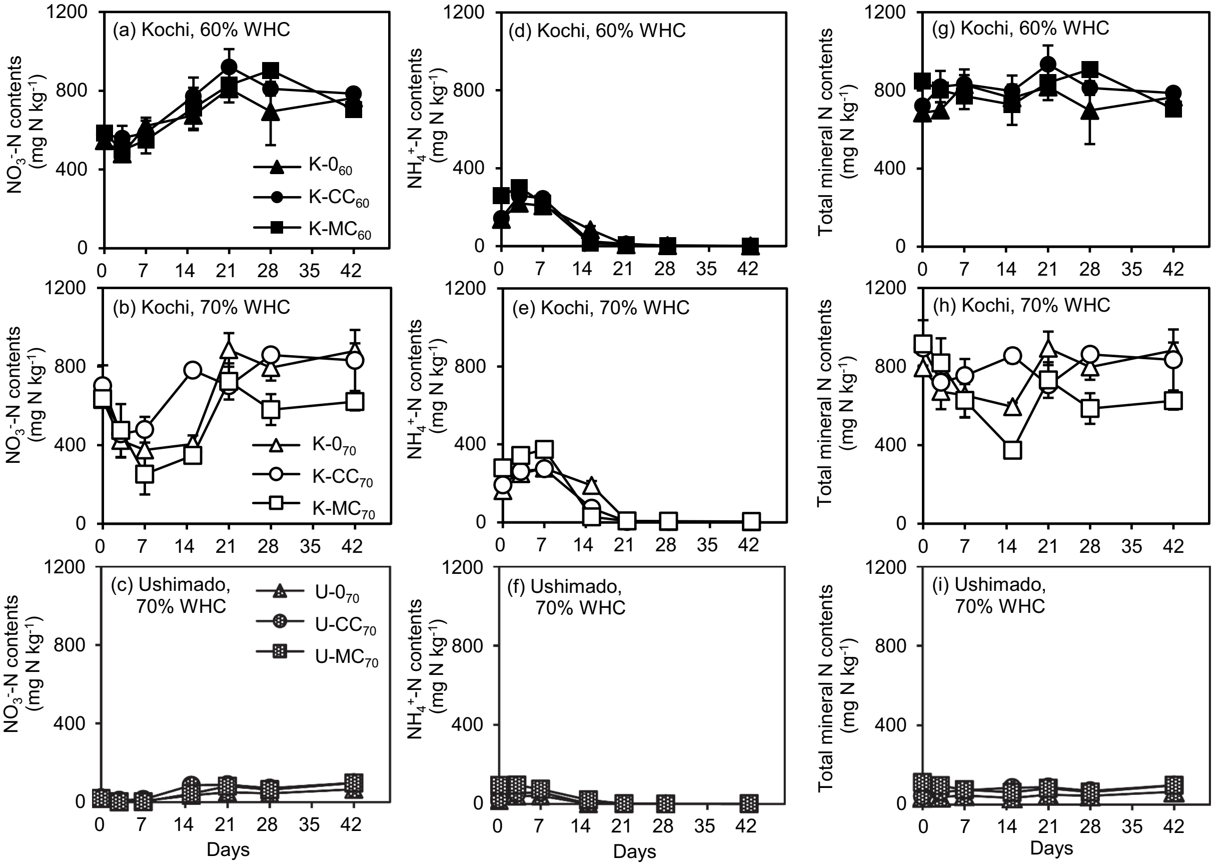

Figure 4. Variation of NO_3^--N, NH_4^+-N, and total mineral N contents of Kochi soil treatments at 60% WHC (a, d, and g, respectively), 70% WHC (b, e, and h, respectively), and Ushimado soil treatments at 70% WHC (c, f, and i, respectively). Error bars indicate ± standard deviations. K–0_{60} or K–0_{70}: no compost–, K–CC_{60} or K–CC_{70}: cattle manure compost–, and K–MC_{60} or K–MC_{70}: mixed compost–amended Kochi soil at 60% or 70% WHC. U–0_{70}: no compost–, U–CC_{70}: cattle manure compost–, and U–MC_{70}: mixed compost–amended Ushimado soil at 70% WHC.

Mohammed-Nour et al. (2021) also documented low cumulative CO_2 emission from composted cattle manure with a high C/N ratio. Thus, the higher C/N ratio of CC would have slowed N mineralization and C decomposition, therefore resulting in less N_2O and CO_2 emissions compared with those in MC (Figure 2). Our results suggested that MC with high NH_4^+-N content and low C/N ratio enhanced N_2O and CO_2 emissions than CC with low NH_4^+-N content and high C/N ratio under aerobic conditions.

The main effects of soil properties on N_2O and CO_2 emissions were statistically significant by ANOVA ($p < 0.05$, Figure 2). Ushimado soil had lower cumulative N_2O emissions than those in Kochi soil at 70% WHC (Figure 2(a)). Ushimado soil was characterized by lower contents of total C and N, mineral N, and clay than those in Kochi soil (Table 1). Similar to our results, Feng et al. (2003) observed lower N_2O emissions in mineral soils with low total C contents during nitrification under aerobic conditions. Badagliacca et al. (2017) also reported that total N_2O emissions from Cambisol with higher SOC content were higher than Haploxerert with lower SOC content. Mazzarino et al. (1991) and Zhu (1997) found that N mineralization was limited with low total N contents in soil. In addition, low mineral N contents in Ushimado soil (Table 1) would have suppressed nitrification because the process is affected by the availability of NH_4^+-N to the populations of nitrifying microorganisms (Sahrawat 2008). Chiyoka et al. (2011) reported that N_2O emissions from soil depend on other factors such as soil texture and aeration. They observed higher N_2O emissions occurred in a soil with high clay and total C contents, which favored the formation of anaerobic micro-sites to promote denitrification at aerobic conditions. Hence, the lower contents of total C and N, mineral N, and clay in Ushimado soil (Table 1) might have resulted in lower cumulative N_2O emissions (Figure 2(a)) than those in Kochi soil (70% WHC) with high contents of C, N, and clay, which could promote both nitrification and denitrification. The lower total C content in Ushimado soil (Table 1) possibly resulted in lower cumulative CO_2 emissions than those in Kochi soil (70% WHC, Figure 2(b)). Silva et al. (2008) found that different characteristics between soils had profound effects on C and N dynamics in soil amended with mineral fertilizers. In our study, we found that a soil with higher total C and N, mineral N, and clay contents increased N_2O and CO_2 emissions than a soil with lower C, N, and clay contents at the same moisture content.

4.2. Interactions of soil and compost amendments

In addition to the main effects of compost type or soil properties, their interactions on N_2O emissions were significant by ANOVA ($p < 0.05$, Figure 2). According to our results, the addi-

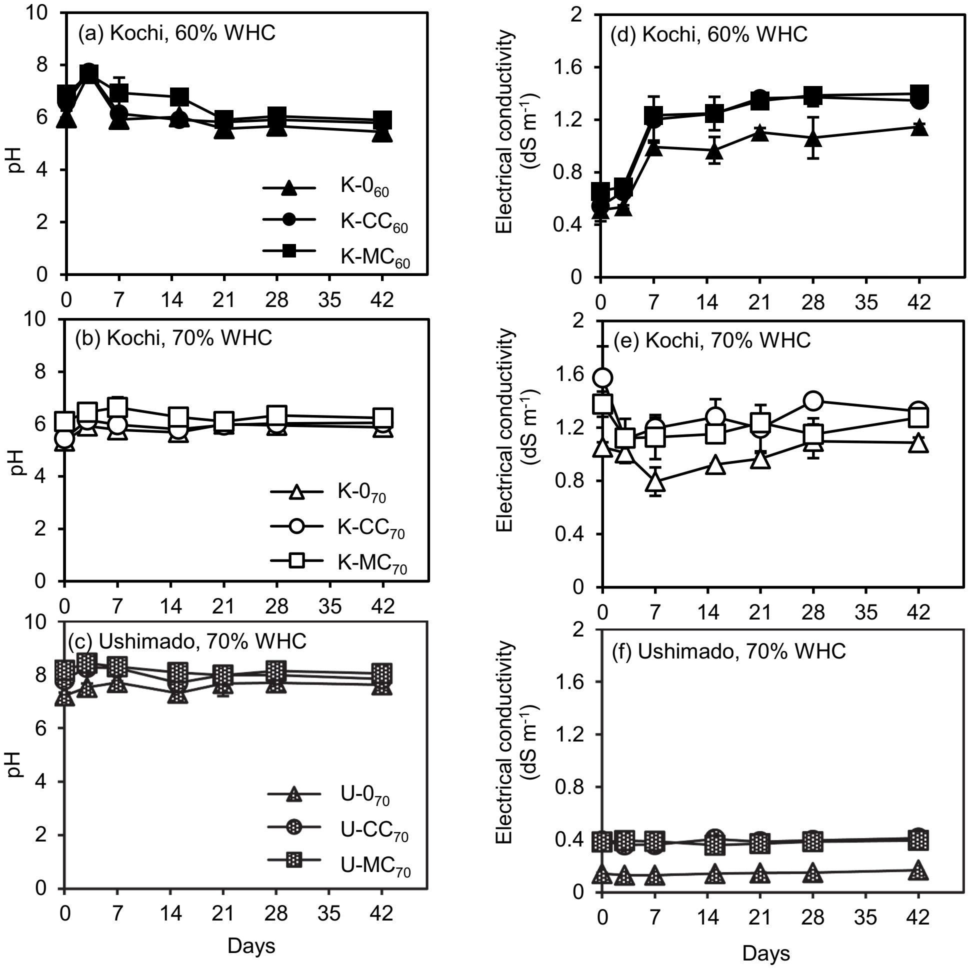

Figure 5. Variation of pH and electrical conductivity of Kochi soil treatments at 60% WHC (a, d), 70% WHC (b, e), and Ushimado soil treatments at 70% WHC (c, f). Error bars indicate ± standard deviations. K-0_{60} or K-0_{70}: no compost-, K-CC_{60} or K-CC_{70}: cattle manure compost-, and K-MC_{60} or K-MC_{70}: mixed compost-amended Kochi soil at 60% or 70% WHC. U-0_{70}: no compost-, U-CC_{70}: cattle manure compost-, and U-MC_{70}: mixed compost-amended Ushimado soil at 70% WHC.

tion of easily decomposable MC significantly increased N_2O emissions than controls in Kochi soil at both 60% and 70% WHC ($p < 0.05$, Figure 3(a)). Although the addition of MC significantly increased N_2O emissions in Ushimado soil than the respective control sample, the increase was not the same as the extent of Kochi soil at the same WHC ($p < 0.05$, Figure 2(a)). At 70% WHC, the addition of decomposition resistant CC significantly increased N_2O emissions in Kochi soil than the respective control sample ($p < 0.05$), whereas the increase was not significant in Ushimado soil ($p > 0.05$, Figure 2(a)). This can be due to low decomposable C and N contents in Ushimado soil combined with low decomposability of CC. This reveals that after being amended with manure compost, N_2O emissions can be interactions between decomposability of compost and total C and N, and mineral N contents of soil. The addition of CC with less decomposable C to Kochi soil significantly increased N_2O emissions, while that to Ushimado soil did not significantly. Thus, the interactions between compost type and soil properties on N_2O emissions were significant (Figure 2). Chiyoka et al. (2011) showed that N_2O emissions significantly increased from pelletized cattle manure than those from non-pelletized cattle manure amended in Black Chernozem soil with high total N, mineral N and organic C contents, while those did not significantly increase in Dark-brown Chernozem soil with low N and C contents. Zhu et al. (2020) and Van der Weerden et al. (2011) found no differences in N_2O emissions in soils with contrasting properties amended with manures under field conditions. All these interactions have been reported in experiments that used fresh livestock manures. Interactions of compost type and soil properties were suggested for the first time in our study to the best of our knowledge, although the main effects of compost type and soil properties have been examined separately in previous studies as explained in the *section 4.1*. Therefore, this is a key finding, which emphasizes the novelty of the present study.

4.3. Effects of soil moisture

In the present study, the effects of moisture content were significant by ANOVA ($p < 0.05$, Figure 3), because N_2O (Figure 3(a)) and CO_2 (Figure 3(b)) emissions from all Kochi soil treatments were higher at 70% WHC than those from the respective treatments at 60% WHC. Klemedtsson, Svensson, and Rosswall (1988) reported that soil moisture content is a key factor controlling N_2O emissions because nitrification was increased with increasing moisture content of 60–90% WHC. The moisture content

Table 4. AOB and AOA *amoA* gene copy numbers in original soils and incubated soils on day 15.

Treatment	AOB *amoA* gene copy numbers (10^{11} copies g^{-1} dry soil)	AOA *amoA* gene copy numbers (10^{8} copies g^{-1} dry soil)	AOB/AOA ratio
Kochi soil	0.37	7.42	50
Ushimado soil	0.03	9.01	3
K-0_{70}	$0.79^{b†}$	1.44^{c}	549
K-CC_{70}	2.67^{a}	7.08^{a}	377
K-MC_{70}	3.62^{a}	4.11^{ab}	881
U-0_{70}	0.26^{c}	4.13^{ab}	63
U-CC_{70}	0.07^{c}	1.62^{c}	43
U-MC_{70}	0.42^{c}	4.68^{ab}	90

[†] Means with the same letters are not significantly different at $p > 0.05$ by Tukey's test. K-0_{70}: no compost-, K-CC_{70}: cattle manure compost-, and K-MC_{70}: mixed compost-amended Kochi soil at 70% WHC. U-0_{70}: no compost-, U-CC_{70}: cattle manure compost-, and U-MC_{70}: mixed compost-amended Ushimado soil at 70% WHC.

significantly affected the growth of ammonia oxidizers, and they were able to grow even under very wet soil conditions (Bustamante et al. 2012; Di et al. 2014). Flowers and O'Callaghan (1983) reported that nitrification rates increased with increasing moisture content in pig slurry-amended soil. At high moisture contents, the diffusional limitation of NH_4^+-N supply and adverse physiological effects associated with cell dehydration were minimized, resulting in high nitrifying microbial activities (Stark and Firestone 1995). Moreover, Congreves, Phan, and Farrell (2019) suggested that N_2O production from soil at WFPS of 53% to 78% can be attributed to denitrification as well. Hence, effects of moisture increment on N_2O emissions might be due to the stimulation of denitrifying microorganisms in addition to nitrification. In Kochi soil at 70% WHC, both nitrification and denitrification would have been accelerated than in those at 60% WHC, which were supported by more reductions in NO_3^--N content and increment in NH_4^+-N content in the first week (Figure 4(b,e)). Emissions of CO_2 are suppressed if soil moisture content is low because water is required for aerobic organic C respiration by microbes (Gritsch, Zimmermann, and Zechmeister-Boltenstern 2015; Sapkota et al. 2020). Dong, Cai, and Zhou (2014) also observed significantly increased CO_2 emissions when soil moisture content was boosted from air-dried conditions to 70% WHC.

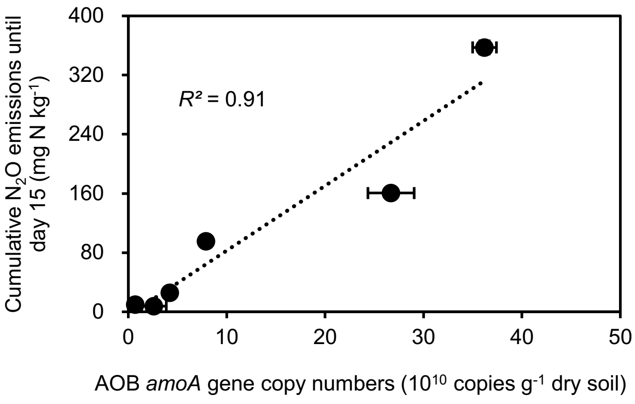

Figure 6. Relationship between cumulative N_2O emissions until day 15 and AOB *amoA* gene copy numbers.

Furthermore, the interactions between moisture content and compost type on N_2O emissions were significant by ANOVA ($p < 0.05$, Figure 3). The addition of MC in Kochi soil significantly increased N_2O emissions than the respective controls at both 60% and 70% WHC ($p < 0.05$). On the other hand, CC addition significantly increased N_2O emissions than the respective controls only at 70% WHC ($p < 0.05$), whereas it did not at 60% WHC ($p > 0.05$, Figure 3(a)) possibly because CC was more resistant to N mineralization at lower WHC.

4.4. Effects of NO_3^--N and NH_4^+-N contents on N_2O emissions

In our experiment, NO_3^--N contents in all treatments decreased from day 0 to 3 or 7 (Figure 4(a–c)). Okada et al. (2005) found that some microorganisms performed aerobic denitrification in the presence of O_2 by co-respiration of O_2 and NO_3^- (or NO_2^-). Hoang and Maeda (2018a) suggested the occurrence of both coupled nitrification-denitrification and nitrifier denitrification in high NH_4^+-N-amended soils. These specific pathways are possible sources of N_2O in the present study. The denitrification was presumably attributed to the addition of easily decomposable C as compost. Similarly, Velthof, Kuikman, and Oenema (2003) documented that volatile fatty acids in manure were metabolized within a few days after incorporation into soil by denitrification. This indicates that N_2O emissions in the first week of incubation were from nitrifier denitrification or denitrification. More reduction of NO_3^--N content in the K-MC_{70} treatment (383 mg N kg^{-1}) than that in the K-CC_{70} treatment (223 mg N kg^{-1}) from day 0 to 7 suggested prominent denitrification in Kochi soil after being amended with easily decomposable compost at 70% WHC (Figure 4(b)). This could be a reason for higher N_2O emissions occurred on day 7 in the K-MC_{70} treatment than those in the K-CC_{70} treatment (Figure 1(b)). On the other hand, NO_3^--N contents in soils amended with compost decreased during the latter incubation period (after day 21, Figure 4(a–c)), indicating that denitrification occurred throughout the experimental period, although N_2O emissions were very low after day 21 (Figure 1(a–c)). The latter incubation period conditions were probably suitable for further reduction of N_2O produced via denitrification to N_2.

In the present study, the initial increment of NH_4^+-N was due to decomposition of total C (Figure 4(d–f)). Interestingly, N_2O emissions later than day 3 or 7 were synchronized with temporal reductions of NH_4^+-N contents (Figure 4(d,e)) and increases of NO_3^--N contents (Figure 4 (a,b)) in Kochi soil at both WHC levels. These results suggested that N_2O after the first week was mainly produced by nitrification. The decreased N_2O emissions after the third week can be attributed to less NH_4^+-N for nitrification and consumed easily decomposable C after day 21 (Figure 4(d–f)). Both NH_4^+-N and easily decomposable C were presumably limiting factors of N_2O emissions, because NH_4^+-N is the primary substrate of N_2O formation through nitrification (Hu et al. 2020), and available C stimulates growth and activities of nitrifying microorganisms (Bremner 1997).

The low NO_3^--N and NH_4^+-N contents in MC- and CC-amended Ushimado soil, which did not change considerably over the experimental period (Figure 4(c,f)) emphasize the need of studies with the presence of crops to identify the detrimental effects of low mineralization of N on fertility of Ushimado soil.

Temporal variation of NO_3^--N (Figure 4(a–c)) and NH_4^+-N (Figure 4(d–f)) contents and N_2O emissions (Figure 1(a–c)) clearly showed that initial denitrification and later nitrification resulted in higher N_2O emissions in MC- and CC-amended soils in the first three weeks of incubation. Many studies have observed high N_2O emissions immediately after organic manure application due to greater NH_4^+-N and NO_3^--N contents under field conditions. In an experiment by Kim et al. (2019), high N_2O emissions appeared six days after animal manure application due to higher inherent NH_4^+-N and NO_3^--N contents in manure. In addition, they found higher precipitation increased N_2O fluxes under field conditions. Nishiwaki, Mizoguchi, and Noborio (2015) observed that maximal N_2O fluxes occurred in a paddy soil amended with manure compost before rice planting due to increased NH_4^+-N contents derived from decomposition of compost. Generally, livestock compost is applied some weeks before transplanting (Adekiya and Agbede 2017; Ibukunoluwa 2015). Our results suggest that high emissions of N_2O continue for three weeks after compost application. This period should be further examined under field conditions in different regions.

4.5. Effects of pH and EC

In the present study, Kochi soil at both 60% and 70% WHC showed a pH increment during the first week, and then decreased slightly with time (Figure 5(a,b)). Khalil, Mary, and Renault (2004) mentioned that nitrification decreased soil pH values. Hence, the slight reductions of pH observed in Kochi soil at 60% and 70% WHC support the occurrence of nitrification. Nitrification hardly occurred below pH 4 and increased with soil pH over the range of 4.9–7.2 (Stams, Flameling, and Marnette 1990). Accordingly, the pH range in Kochi soil was favorable for nitrifying activities. Many neutrophilic denitrifying bacteria have an optimum pH ranging between 7.5 and 9.5 (Albina et al. 2019). Therefore, some denitrifiers may be activated at increased pH in the first week, resulting in a decrease of NO_3^--N, as explained in the *section 4.4*.

Ushimado soil had a high pH during the entire incubation period (Figure 5(c)) and showed lower N_2O emissions than those in Kochi soil at 70% WHC (Figure 2(a)). In general, if nitrification is the main process of N_2O production, high pH values stimulate N_2O emissions (Signor and Cerri 2013). On the other hand, our results agreed with Wang et al. (2018), who detected less N_2O emissions in alkaline soils (pH 8) than those in acid soils (pH 5). Kyveryga et al. (2004) found that nitrification rates increased with soil pH ranging between 6 and 8 in soils with high availability of NH_4^+-N contents. In Ushimado soil, nitrification was suppressed presumably by low NH_4^+-N content in soil (Table 1) and low mineralization of N in compost, resulting in low N_2O emissions (Figure 2(a)) as explained in *Section 4.1*.

In Kochi soil at both 60% and 70% WHC, EC values increased after day 3 or 7 to the end of experiments (Figure 5(d,e)). In Ushimado soil, EC values were considerably lower than those in Kochi soil treatments and did not change over the experimental period (Figure 5(f)). The temporal reductions of N_2O emissions (Figure 1(a,b)) were likely associated with decreased activities of nitrifiers at high EC levels in Kochi soil. A higher soil EC suppresses soil respiration because of the osmotic stress on microbial activities (Adviento-Borbe et al. 2006). Thapa et al. (2017) also reported that N mineralization rates and CO_2 emissions decreased with high soil EC levels. The lower EC in Ushimado soil (Figure 5(f)) is likely to have no impacts on temporal variation of N_2O emissions (Figure 1(c)).

4.6. Relative abundances and relation of nitrification genes to N_2O emissions

In the present study, AOB gene copy numbers in Kochi soil at 70% WHC were significantly ($p < 0.05$) higher than those in Ushimado soil (Table 4). Clear increases in AOB were detected in Kochi soil with MC because the growth of AOB may have been promoted by high initial NH_4^+-N contents. Application of manure compost has a great impact on nitrifying bacteria by providing the substrates for microbial activities. Manure application was found to significantly increase copy numbers of the AOB gene more than those in no manure-amended soils (Yin et al. 2019). Generally, AOB growth is favored by high NH_4^+-N in soil (Hayashi et al. 2016; Wang et al. 2016). Therefore, high N_2O emissions in Kochi soil at 70% WHC (Figure 2(a)) might be due to the activities of AOB genes in high abundance.

During the incubation, AOA gene copy numbers of original soil samples decreased in both types of soils. AOA in the original Ushimado soil was higher than the original Kochi soil (Table 4), because AOA were more adaptable to low NH_4^+-N contents (Morimoto et al. 2011). Similarly, low NH_4^+-N contents lead the growth of only AOA in particular under aerobic conditions (Hink, Nicol, and Prosser 2017; Hink et al. 2018).

In our study, the strong positive correlation between AOB and cumulative N_2O emissions suggested that N_2O emissions until day 15 were primarily driven by AOB (Figure 6). Stieglmeier et al. (2014) reported that AOB have more capacity to produce N_2O than AOA through a side reaction of ammonia oxidation because they have genes for homolog of hydroxylamine oxidoreductase that is responsible for N_2O formation. Moreover, AOB genes encoding a potential NO-reductase are involved in nitrifier denitrification that contributes to direct N_2O production in soils (Stieglmeier et al. 2014). Lourenco et al. (2018) also found that nitrifier denitrification by AOB could play a role in N_2O emissions from organic fertilizer-amended soils because they can actively grow under high NH_4^+-N concentrations, creating micro-oxic or anoxic conditions. These conditions could induce denitrification by nitrifiers or heterotrophic denitrifiers. In contrast, AOA does not respond to NH_4^+ oxidation and N_2O production in intensively managed agricultural soils (Huang et al. 2014). In our study, higher N_2O emissions (Figure 1(a–c)) and distinct NO_3^--N reduction (Figure 4(a–c)) during the first two weeks suggested the occurrence of denitrification. According to the temporal variation of NH_4^+-N (Figure 4(d–f)), N_2O emissions on day 15 were due to nitrification. These results suggested that cumulative N_2O emissions until day 15 can be primarily due to activities of AOB *amoA* functional genes. Similar findings were reported by Morimoto et al. (2011), suggesting the importance of AOB activities in N_2O emissions in agricultural soils. The results revealed that relative abundances of AOB and AOA are good indicators of N_2O emission potentials and are dependent on NH_4^+-N contents derived from both soil and compost.

5. Conclusions

We investigated effects and interactions of compost type and soil properties and effects of moisture content of soil on N_2O and CO_2 emissions. Two soils were collected from a greenhouse in Kochi and a paddy field in Ushimado to reflect effects of C, N, and clay contents on N_2O and CO_2 emissions. In addition, the relationships between relative abundances of ammonia oxidizing genes and N_2O emissions were analyzed. The lower C/N ratio and higher NH_4^+-N content in MC were key factors promoting N_2O and CO_2 emissions. Kochi soil with higher total C and N, mineral N, and clay contents had higher N_2O and CO_2 emissions than those in Ushimado soil at the same WHC. In addition to the main effects of compost type or soil properties, their interactions on N_2O emissions were significant. Namely, the addition of decomposition resistant CC to Kochi soil significantly increased N_2O emissions, while that to Ushimado soil did not significantly increase. Emissions of N_2O and CO_2 decreased temporally due to less NH_4^+-N and easily decomposable C. Moisture content was the key to increasing N_2O and CO_2 emissions from compost-amended Kochi soil at 70% WHC than those at 60% WHC. Cumulative N_2O emissions until day 15 were primarily due to AOB *amoA* functional gene activities. In conclusion, N_2O emissions can be increased by high NH_4^+-N contents and low C/N ratio in compost and high C, N, and clay contents in soil. The application of compost with less decomposable C increases N_2O emissions only from soil with high total C and N, mineral N, and clay contents, which is the interaction between compost and soil properties.

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Disclosure statement

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