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Mechanisms of lime-induced N_2O mitigation in acidic soils: A meta-analysis of microbial activity and substrate dynamics

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ABSTRACT

Previous studies reported a reduction in N_2O emissions following lime application. However, the mechanisms underlying N_2O reduction under different soil acidifications are not clear and require further investigation. As a result, it is imperative to gain insights into how lime application affects N_2O emissions and associated microbial activities under varying soil acidification and other factors. Only studies obtained from the agroecosystems were considered for the current meta-analysis. Accordingly, this meta-analysis was conducted with 684, 141, 149, and 94 paired observations for the response variables of N_2O emissions, archaeal *amoA* gene abundance, bacterial *amoA* gene abundance, and *nosZ* gene abundance, respectively, obtained from 39 peer-reviewed studies. The current meta-analysis findings indicated that the lime application reduced soil N_2O emissions by 46.63 % and raised soil pH by 27.63 % across all paired observations compared to control. Overall, lime application also increased the abundance of bacterial *amoA* and *nosZ* genes by 101.17 % and 49.63 %, respectively, while decreasing the abundance of archaeal *amoA* by 6.39 %. Our structural equation modeling (SEM) suggested that the differences in the reduction of N_2O emission magnitudes under different lime rates are due to differences in the degree of soil pH manipulation. Lime application rate was identified as the primary factor influencing the response of soil N_2O emissions to lime, followed by soil pH. Our results from SEM indicated that the main drivers of the variable responses in soil N_2O emissions to lime application under different soil acidifications are the variable responses of N_2O-associated microbial activities and substrate availability. The greater reduction in N_2O emissions under neutral soil conditions, compared to acidic conditions, is primarily attributed to a pH-driven shift in microbial activity, evidenced by a larger increase in *nosZ* gene abundance and a decrease in bacterial *amoA* gene abundance.

Grain yields of wheat, rice, and maize increased by 9.42 %, 11.40 %, and 62.42 %, respectively, following lime application compared to the control. Based on our findings, we concluded that applying lime to acidic soils is a suitable option for reducing soil N_2O emissions by affecting the activity of associated microbial functional genes and substrate availability in agricultural ecosystems.

1. Introduction

The concentration of atmospheric greenhouse gases (GHG) has increased significantly over the last three decades (Ciais et al., 2014). Nitrous oxide (N_2O) is among the major greenhouse gases, having a long lifetime (about 114 years) and a high global warming potential (GWP) of

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265 times higher compared to CO_2 on a 100-year time scale (IPCC, 2013). It has been documented that agricultural ecosystems are the major anthropogenic source of N_2O, which accounts for over 60 % of the global emissions (Bhatia et al., 2010). Soil N_2O is mainly resulted from nitrification and denitrification processes (Zhu et al., 2013). N_2O production and emissions are regulated by several factors, like soil moisture (Khalil et al., 2004), structure and texture (Skiba et al., 1998), nitrogen fertilization, and soil pH (Shaaban et al., 2020). Soil pH, as a measure of soil acidification, is the major factor regulating N_2O emission, directly affecting the microflora responsible for N transformation.

Nitrification, the main pathway responsible for N_2O emissions, is also driven by nitrifying bacteria, which have multiple functional genes. In the nitrification process, ammonia oxidation is the first and rate-limiting step, which is enforced by ammonia oxidizing archaea (AOA) or ammonia oxidizing bacteria (AOB), which carry the *amoA* gene encoding ammonia monooxygenase (Leininger et al., 2006; Pester et al., 2012). Soil pH affects nitrification primarily by altering substrate availability, with higher pH potentially enhancing substrate availability to ammonia mono-oxygenase (AMO) (Boer and Kowalchuk, 2001; Zhao et al., 2018). An increase in soil pH enhances nitrification rates, whereas acidification tends to reduce them in arable soils (Cheng et al., 2013; Jiang et al., 2015). The optimum pH for nitrification typically ranges from 7.0 to 7.5, as the activity of most nitrifiers is optimal within this range but inhibited at pH 5 (Le et al., 2019). However, nitrification can still occur in acidic soil due to the presence of acidophilic nitrifier strains (Jiang et al., 2015).

The denitrification pathway is primary responsible for N_2O production in the soil (Simek et al., 2002). Denitrification processes are driven by denitrifying bacteria, which possess multiple functional genes. *nirK*, *nirS*, and *nosZ* are the main marker genes involved in denitrification processes. Nitrite reductase genes *nirK* and *nirS* are responsible for the reduction of NO_2^- to NO, which is considered the rate-limiting step in denitrification (Braker et al., 2000; Kuypers et al., 2018). N_2O reductase is encoded by the *nosZ* gene. Soil pH affects the denitrification process by affecting the soil denitrifying community (Jones et al., 2014). Generally, the highest denitrification rates are found at near-neutral soil pH conditions (Simek and Cooper, 2002), even if some adaptation to natural soil pH can be observed. Several previous research reports indicated that the maximum denitrification process occurs at pH values between 7.0 and 8.2 (Simek and Cooper, 2002). The synthesis and functionality of the N_2O reductase enzyme and transcription of the *nosZ* gene are inhibited in acidic soil (Bergaust et al., 2010).

Liming is a common mitigation strategy for soil acidification (Goulding, 2016; Holland et al., 2018). Lime has been demonstrated to influence N_2O emissions through a variety of mechanisms, including changes in N_2O-associated microbial activity, which is mainly induced by changes in soil pH (Page et al., 2009; Holland et al., 2018). There is considerable controversy regarding whether liming would be a mitigation technique to minimize N_2O emissions under acidic arable soils (Higgins et al., 2013; Qu et al., 2014; Senbayram et al., 2019). Our understanding of the impacts of lime on climate change mitigation and greenhouse gas emissions through biological drivers is increasing (Wang et al., 2021; Zhang et al., 2022). These biological processes, influenced by varying thresholds of soil acidity and substrate availability, contribute to the variable response in N_2O emissions following liming. A comprehensive study evaluating the integrated effects of these factors on N_2O emissions in agroecosystems is still lacking. Integration of these factors offers new insights into the complex interactions between soil acidity, microbial activity, substrate dynamics, and N_2O emissions. The current study provides an integrated assessment of microbial activity and substrate dynamics under varying levels of soil acidity, shedding new light on their collective impact on N_2O emissions in agroecosystems.

For the current meta-analysis work, we compiled all the available data from each study that quantified the effects of lime on N_2O emissions and associated MFGs in agricultural ecosystems and then quantitatively evaluated these responses under various soil acidification and other environmental conditions. This work aimed to address the following questions: (1) N_2O-associated microbial activities and substrate concentration under different soil acidification and links to N_2O emissions (2) What is the mechanisms responsible for reduction of N_2O emissions following lime application under different soil and environmental conditions (3) Relative influence of soil factors affecting N_2O emissions (4) What is the relationship of N_2O emissions and associated MFGs with the other factors? This meta-analysis provides a detailed insights into how lime application reduces N_2O emissions and affects the associated MFGs across different soil and environmental conditions in agricultural ecosystems.

2. Materials and methods

2.1. Data collection

Studies were obtained by performing a comprehensive, systematic literature search for relevant articles in: "Google Scholar (Google, Mountain View, CA, USA), Science Direct (https://www.sciencedirect.com), Scopus (https://www.scopus.com/search/form.uri?display,=basic#basic) and the China Knowledge Resource Integrated Database (http://www.cnki.net/)" which was done in February 2023.The literature was searched with the following keywords in various combinations: Lime application, N_2O emissions, and functional genes. The Boolean operators 'AND' and 'OR' were used to combine two separate searches and with alternative search terms. The search terms considered consisted of the following lists: "Google Scholar" database: "lime OR lime application OR lime amendment AND N_2O emission AND functional genes OR archaeal *amoA* OR bacterial *amoA* OR *nirS* OR *nirK* OR *nosZ*". The sets of criteria used for the papers included in the meta-analysis include: (1) only papers published in English and Chinese; (2) only journal articles; (3) only experiments conducted under agricultural ecosystem; (4) studies having lime amendment and control each having mean, standard deviation (SD), standard error (SE) or could be calculated and at least three independent replicates; (5) control and lime amended treatments should be subject to the same management practices; (6) studies with clearly described methods of lime application; (7) studies concurrently reporting effects of lime on N_2O emissions and at least one of microbial functional genes (archaeal *amoA*, bacterial *amoA*, *nirS*, *nirK*, and *nosZ*). Additionally, we considered each year, each location, each liming material, and each lime rate as individual observations for experiments with multiyear, multilocation, liming materials, and liming rates, respectively, when studied in the same paper. We took soil data from the top soil, when soil data from different soil layers was provided. Experiments with multiple points data from the same experimental unit, we limited our analysis to the latest time point.

The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) approach was used for the screening of the obtained literature (Liberati et al., 2009, Fig. S1). The rejected studies are compiled in an exclusion database with reasons for the rejection. Citations were imported into Zotero software. Finally, the current meta-analysis was done with a total of 684, 141, 149, and 94 paired observations for the response variables of N_2O emissions, abundance of the archaeal *amoA* gene, abundance of the bacterial *amoA* gene, and abundance of the *nosZ* gene, respectively (Fig. 3a) which were found from 39 peer-reviewed journal papers. The details and relevant information obtained from each selected article are presented in the supplementary materials (Table S1).

Additionally, from the selected study, categorical variables were collected to investigate the responses of N_2O emissions and associated MFGs to the lime application. These variables were: (1) experimental conditions (field, incubation, laboratory); (2) climatic zones (tropical, sub-tropical, temperate); (3) soil texture (coarse, medium, fine); (4) pH (very acidic: < 5.5, acidic: 5.5–6.5, neutral: 6.5–7.5) (Gao et al., 2019); (5) water filled pore spaces (< 60, at 60, 60–90, ≥ 90 %); (6) type of liming materials (calcium carbonate, dolomite, calcium hydroxide, calcium oxide); (7) lime application rates (1–3,3–6, >6 t ha^{-1}); (8) nitrogen application rates (<150, 150–250, >250 kg ha^{-1}); (9) soil organic carbon (<15, 15–30, >30 g C kg^{-1}); (10) straw management (with straw addition, without straw). The other auxiliary variables, like location (latitude and longitude), were also extracted and used to map the global distribution of the selected studies. Regarding the experimental location, GPS coordinates were used, or, if not reported, they were estimated using GPS-coordinates.net. In studies with no reported climate zones, the IPCC climate zones of the experimental sites were determined from the world map of the IPCC climate zones and geographic coordinates. Precipitation and temperature data were also used as additional information for the confirmation of the determined climate zones We also extracted the data on crop yield from the selected studies (in t ha^{-1}).

The majority of numerical data included in the current meta-analysis were obtained from the text and tables, or, if found in the figure, extracted from the original papers with the WebPlotDigitizer 4.5 (Rohatgi, 2021). The standard error (SE) values were converted to standard deviation (SD) values for those studies with no SD value. SD was computed as follows:

$$SD = SE \times \sqrt{n} \tag{1}$$

N represents the number of replicates. Papers having mean and a confidence interval (CI) value, the standard deviation is calculated as:

$$SD = (CI_u - CI_l)\sqrt{\frac{n}{2Z_{\alpha/2}}} \tag{2}$$

CI_u and CI_l represents the upper and lower limits of CI, and $Z\,a/2$ is Z score of a given level of significance and it is equal to 1.96 when $\alpha = 0.05$ and 1.645 when $\alpha = 0.10$. For studies with no above values, we contacted key authors, and if not assigned, the value of 1/10 of the means was used to get standard deviations (Luo et al., 2006).

Soil textural classes were classified into coarse, medium, and fine-textured soils as per the classification of the (Soil Survey Staff, 2003). Unit conversion was performed when required, such as: “soil pH 1:2.5 KCl, 1:2.5 H_2O, or 1:5 $CaCl_2$ to 1:5 H_2O (Minasny et al., 2011; Kabała et al., 2016) “before conducting meta-analysis.

$$pH_{H2O1:5} = -1.95 + 11.58 \times \ln(pH_{1:2.5K}) \tag{3}$$

$$pH_{H2O1:5} = 0.14 + 0.99 \times (pH_{1:2.5W}) \tag{4}$$

$$pH_{H2O1:5} = 0.67 + 1.01 \times pH_{1:5Ca} - 0.116 \times \ln(EC_{1:5W}) \tag{5}$$

The soil water content reported in soil water holding capacity (WHC) is changed to water-filled pore space (WFPS). The percentage of soil volume occupied by the pores spaces is called porosity (S_t). Soil pore spaces are filled with either air (F_a, air-filled porosity) or water (WFPS). WFPS was determined from gravimetric soil water content as described by Lan et al. (2013).

$$WFPS = \left(\frac{St - Fa}{St}\right) \tag{6}$$

The total porosity of the soil (S_t) was computed with the following formula from soil particle density and bulk density:

$$S_t = \left(1 - \frac{Db}{Dp}\right) \tag{7}$$

The air-filled porosity (F_a) based on the bulk density and gravimetric moisture content (Θ_W) at any moisture content was determined using the equation:

$$F_a = \left(\frac{\Theta w^{*} Db}{Db}\right) \tag{8}$$

2.2. Meta-analysis

To determine the magnitude of the treatment effect, the effect size for each measured variable of interest was calculated (Osenberg et al., 1999). The response ratio was employed as the measure of the effect size (the natural log of the ratio of the mean value of the lime applied treatment to that of the control) and was calculated for each treatment in each trial, which was used as an index to describe the effects of lime application on soil N_2O emissions and associated microbial functional genes (Hedges et al., 1999; Luo et al., 2006):

$$RR = \ln x_t / \ln X_c \tag{9}$$

X_t and X_c represent means in the treatment and control groups, respectively. The logarithm was chosen because it provided better statistical properties for the distribution of effect size and because the nominator and denominator had equal effects on the metrics. The effect sizes with a positive value indicate that lime application increased N_2O emissions and the associated MFGs.The variance (ʋ) of effect size, was calculated as follows:

$$\upsilon = \frac{SD_L^2}{N_L\,X_L^2} + \frac{SD_C^2}{N_C\,X_C^2} \tag{10}$$

SD_L and SD_C are standard deviations of the lime-applied groups and the control groups, respectively, and N_L and N_C are the sample size of lime-applied groups and control groups, respectively.

OpenMEE (Wallace et al., 2017) was used to generate the weighted response ratio (RR_{++}) and 95 % bootstrap confidence interval (CI) using the Hedges-Olkin random model. RR_{++} was considered significant if the 95 % confidence interval did not overlap zero. For each subgroup, the RR_{++} and 95 % CI were determined. The percent change was computed using the equation:

$$\text{Percentage Change } (\%) = \left(e^{RR++} - 1\right) \times 100\% \tag{11}$$

Between-group heterogeneity across all data for a given categorical variable was used to further analyze the lime application effects among different subgroupings within a category. Between-group heterogeneity analysis (QM) was applied to determine whether there is significance in each moderator variable (Koricheva et al., 2013). Meta-regression was used for the evaluation of between-group heterogeneity analysis, and according to this model, the variation within a group of studies is due to random variation, whereas the variation between groups is fixed.

A linear regression was done to evaluate the relationship between the effect sizes of the lime application on N_2O emissions and associated functional genes. All other graphs and figures are plotted using Origin (Pro), Version, 2024. To determine the relative influence of different predictor variables on N_2O emissions, Boosted Regression Tree (BRT) analysis was conducted with gbm package in R (R Core Team., 2021). The recommended parameter values: a learning rate (0.01), bag fraction (0.50), cross-validation (10), and a tree-complexity (5) were used to build the boosted trees (Elith et al., 2008). The map indicating the global distribution of the selected studies was made by ArcMap 10.8 (Fig. S2).

Rosenthal's fail-safe or file drawer number was calculated using OpenMEE, and if the mean effect showed a significant deviation from zero and studies were not dispersed symmetrically in a “funnel” pattern around the mean (i.e., showing publication bias) (Rothstein et al., 2005). The results of our meta-analysis indicated that all the Rosenthal's Failsafe numbers of all the target variables were larger than 5n + 10 (Table S2), indicating the results were robust with regard to publication bias (Toth and Pavia, 2007). The normality test was determined as per the procedure of Shapiro and Wilk (1965).

3. Results

3.1. Responses of N_2O emissions to lime applications under different moderating variables and soil acidification

Combined across all the paired observations, the findings of our meta-analysis indicated that lime significantly decreased cumulative soil N_2O emission by 46.63 % (Fig. 3a). The responses of soil N_2O emissions to lime application were significantly affected across the moderating variables of climatic zones ($p = 0.03$), soil textural categories ($p < 0.001$), type of liming materials ($p = 0.03$), and lime application rates ($p < 0.001$) (Fig. 1). More specifically, lime application decreased soil N_2O emissions by 31.75 % in soil without straw addition, by 29.32 %, and by 39.59 % at soil organic concentrations of <15 and > 30 g kg-1, respectively (Fig. 1 and Table 1). In addition, soil textural categories and the experimental settings had a substantial impact on the variations in N_2O emissions in response to lime application (Fig. 1 and Table 1). Lime application considerably reduced N_2O emissions in soils with medium and fine textures by 31.20 % and 66.95 %, respectively (Fig. 1 and Table 1). Liming of acidic soils resulted in a significant reduction in N_2O emissions relative to the control by 25.99 %, 58.23 %, and 50.09 % under field, laboratory, and incubation experimental settings, respectively (Fig. 1 and Table 1). Regarding soil WFPS, the smallest 1.19 % and non-significant reduction in soil N_2O emission was reported at a soil WFPS of 60 %. Soil N_2O emissions decreased by 43.67 % and 79.26 % at soil WFPS of <60 and 60–90, respectively (Fig. 1 and Table 1).

Moreover, the lime application across all the liming materials and lime application rates considerably and negatively affected the amount of soil N_2O emissions. Interestingly, the magnitude of the decrease in soil N_2O emissions at the higher lime application rates was the higher than those obtained with the other two levels of lime application. There was also a reduction in soil N_2O emissions by 17.72 % and 83.83 % in soils that received lime dosages of 1–3 and > 6 t ha^{-1}, respectively (Fig. 1 and Table 1).

The overall response of soil pH to lime application is summarized in Fig. 3b. Following lime application, soil pH was increased by 27.63 % (Fig. 3b). Under both soil acidity conditions, the effect size of lime application on soil N_2O emissions was significantly less than zero (Fig. 1), indicating that liming inhibited soil N_2O emissions compared to controls and that the inhibition effects were highly stimulated at neutral soil pH conditions. Soil N_2O emissions were considerably reduced by 56.26 % and 70.00 % under the acidic and neutral soil conditions, respectively (Fig. 1 and Table 1). The meta-analysis of these recent findings revealed that the neutral soil conditions had greater inhibitory effects on soil N_2O emissions.

3.2. Responses MFGs abundance to lime application under different moderating variables and soil acidification

There was no significant difference across most of the moderating variables except climatic conditions ($p = 0.0009$) (Fig. 2a) on soil AOA *amoA* abundance in response to lime application. The inhibitory responses in the abundance of the archaeal *amoA* gene in response to lime application were observed (Fig. 3a). Overall, the lime application reduced the abundance of archaeal *amoA* gene by 6.39 % (Fig. 3a). The AOA *amoA* abundance showed a significant negative response to lime application when the liming material used is dolomite and calcium hydroxide, under tropical climatic conditions, and at the lime application rate of >6 t ha^{-1}, with percentage decrease values of 23.05 %, 11.22 %, 79.61 %, and 22.66 % (Fig. 2a, Table 1), respectively.

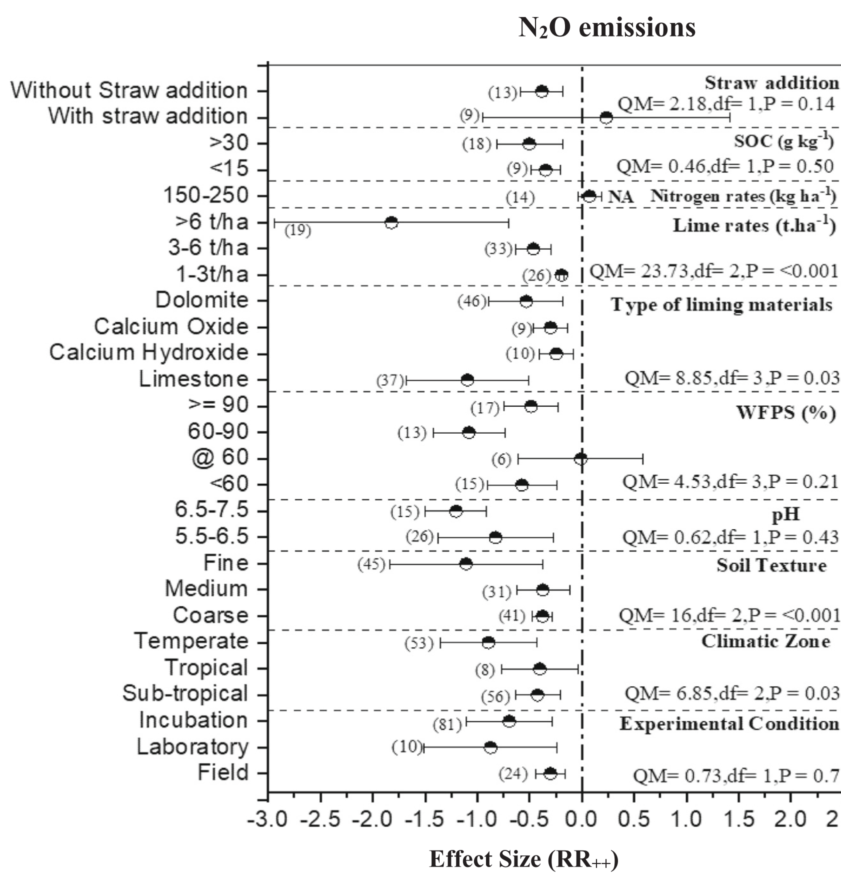

Fig. 1. The effect of lime application on soil N_2O emissions depends on different moderating variables and shown as weighted response ratio (RR_{++}). Mean effect size/ weighted response ratio and 95 % CIs are shown. Numbers in the brackets indicate number of paired observations; df, degree of freedom; QM, between group heterogeneity; NA, not applicable; SOC, soil organic carbon; WFPS, water filled pore spaces.

Table 1
Percentage changes of soil N_2O emissions and MFGs in response to a lime application under different categorical variables.

N_2O emissions		Archaeal amoA gene abundance		Bacterial amoA gene abundance		nosZ gene abundance	
Variables	PC (%)	Variables	PC (%)	Variables	PC (%)	Variables	PC (%)
Field	−25.99	Sub-tropical	9.09	Coarse	159.61	Sub-tropical	104.62
Lab	−58.23	Tropical	−79.61	Medium	16.18	Tropical	−27.75
Incubation	−50.09	Coarse	3.87	<5.5	159.61	Coarse	2.63
Sub-tropical	−34.62	Medium	−5.73	5.5–6.5	25.48	Medium	60.64
Tropical	−33.17	<5.5	−7.60	6.5–7.5	−2.76	5.5–6.5	14.45
Temperate	−59.14	5.5–6.5	−17.30	Limestone	103.60	6.5–7.5	157.02
Coarse	−31.48	6.5–7.5	29.95	Calcium Hydroxide	−4.78	Limestone	−13.24
Medium	−31.2	Calcium Hydroxide	−11.22	Calcium Oxide	85.34	Dolomite	151.18
Fine	−66.95	Calcium Oxide	−15.55	1–3 t ha^{-1}	89.65	1–3 t ha^{-1}	62.74
pH (5.5–6.5)	−56.26	Dolomite	−23.05	3–6 t ha^{-1}	108.13	3–6 t ha^{-1}	44.63
pH (6.5–7.5)	−70.00	1–3 t ha^{-1}	5.34	>6 t ha^{-1}	−3.54		
WFPS <60 %	−43.67	3–6 t ha^{-1}	−5.64				
WFPS at 60 %	−1.19	>6 t ha^{-1}	−22.66				
WFPS 60–90 %	−79.26						
WFPS ≥ 90 %	−19.35						
Limestone	−66.51						
Calcium Hydroxide	−21.81						
Calcium Oxide	−25.92						
Dolomite	−41.32						
1–3 t ha^{-1} Lime	−17.72						
3–6 t ha^{-1} Lime	−37.19						
>6 t ha^{-1} Lime	−83.83						
150–250 kg N ha^{-1}	7.47						
<15 g.C. kg^{-1}	−29.32						
>30 g.C. kg^{-1}	−39.59						
With straw addition	26.11						
Without straw addition	−31.75						

Archaeal amoA gene abundance:
* PC indicates percentage Change
* <5.5, 5.5–6.5 and 6.5–7.5 are pH rates observed
* 1–3 t ha^{-1}, 3–6 t ha^{-1} and > 6 t $ha^{-1}$are lime rates
* MFGS indicates microbial functional genes

Bacterial amoA gene abundance:
* PC indicates percentage Change
* <5.5, 5.5–6.5 and 6.5–7.5 are pH rates observed
* 1–3 t ha^{-1}, 3–6 t ha^{-1} and > 6 t $ha^{-1}$are lime rates
* MFGS indicates microbial functional genes

nosZ gene abundance:
* PC indicates percentage Change 5.5–6.5 and 6.5–7.5 are pH rates observed
* 1–3 t ha^{-1} and 3–6 t ha^{-1} are lime rates
* MFGS indicates microbial functional genes

There was no significant difference across the majority of the moderating variables (Fig. 2b) on soil AOB *amoA* abundance in response to lime application, except soil pH ($p = 0.04$). AOB *amoA* response to the lime application differs from AOA *amoA*, and it was overall increased by 101.17 %, respectively (Fig. 3a). The highest and significant increase in AOB *amoA* abundance in response to lime application was detected at a lime application rate of 3–6 t ha^{-1}, with limestone liming materials and under the coarse textured soil, and with a percentage increase of 108.13 %, 103.60 %, and 159.61 % (Fig. 2b, Table 1), respectively.

Lime application had a notable effect on *nosZ* gene abundance and overall increased it by 49.63 % (Fig. 3a). Our meta-analysis results indicated that, except lime application rates and soil textural category, other moderating variables strongly influenced the response of *nosZ* gene abundance to lime applications (Fig. 2c). The greatest and significant increase in the activities of *nosZ* gene abundance in response to lime application was observed at lime application rates of 1–3 t ha^{-1}, with dolomitic lime material and medium-textured soil under the sub-tropical climate, with values of 62.74 %, 151.18 %, 60.64 %) and 104.62 % (Fig. 2c, Table 1), respectively. The other types of denitrifying genes, like *NirK* and *nirS*, are excluded from current study since the number of observations is not sufficient to be analyzed by the software package used in our meta-analysis work.

Interestingly, across very acidic and acidic soil pH conditions, the lime application considerably and negatively affected the abundance of AOA *amoA*, contrary to neutral soil pH, which showed an increasing pattern. Very acidic and acidic soil pH conditions led to a pronounced decrease in the gene abundance of AOA *amoA* by 7.60 % and 17.30 %, respectively (Fig. 2a and Table 1). The responses of the AOA *amoA* gene abundance to the lime application were increased by 29.95 % for the neutral soil pH category (Fig. 2a and d).

We found that, with the exception of the neutral soil pH, AOB *amoA* abundance indicated positive responses across the other soil pH classes in response to lime application, with the highest responses being observed at very acidic soil pH conditions (Fig. 2b and Table 1). Lime applied to soil increased the AOB *amoA* gene abundance, and it increased by 159.61 % and 25.48 % in the categories of highly acidic and acidic, respectively (Fig. 2b and Table 1). However, the effects showed the opposite trend at neutral soil pH conditions, which decreased the gene abundance by 2.76 % (Fig. 2b and d).

Moreover, our meta-analysis results indicated that the response of *nosZ* gene abundance to lime application was strongly influenced by soil pH (Fig. 2c). The positive effects of lime application on *nosZ* gene abundance were more pronounced at neutral than acidic soil pH (Fig. 2c). *NosZ* abundance increased noticeably by 157.02 % under neutral soil pH conditions (Fig. 2c and d). However, the increased value of *nosZ* gene abundance by 14.45 % at acidic soil pH is not significant (Fig. 2c and Table 1).

3.3. Overall effects of lime applications on selected soil properties and crop yield

Combined across all the paired observations, the findings of the current meta-analysis showed that lime application had a significant effect on selected soil chemical properties (Fig. 3b). Regarding inorganic N (NH_4^+ and NO_3^-), compared to control, lime application decreased soil NH_4^+ by 7.13 % and increased NO_3^- by 41.20 % (Fig. 3b). Crop yields of all selected crops were significantly increased following lime application (Fig. 3b). Wheat had the lowest percentage change in yield, while maize had the highest percentage change (estimated using Eq. (11); Fig. 3b), with percentage changes of 9.42 % and 62.42 %, respectively. Similarly, rice yield also positively responded to the lime application and increased with 11.4 % (Fig. 3b).

3.4. Relationship between N_2O emissions, archaeal amoA, bacterial amoA, and nosZ gene abundance with different variables and relative influence of predictors on N_2O emissions

Soil N_2O emission was not significantly and negatively correlated with pH rates ($r = -0.30$, $R^2 = 0.09$, $p = 0.17$), nitrogen fertilizer rates, and soil organic matter additions but positively correlated with water-filled pore spaces (Fig. 4a, Table S3). Compared with the other correlation values, soil N_2O emission is highly correlated with lime application rates ($r = -0.62$ and $R^2 = 0.38$, $p = 0.0000$) (Fig. 4b, Table S3). Except for archaeal *amoA* gene abundance, the genes abundance of

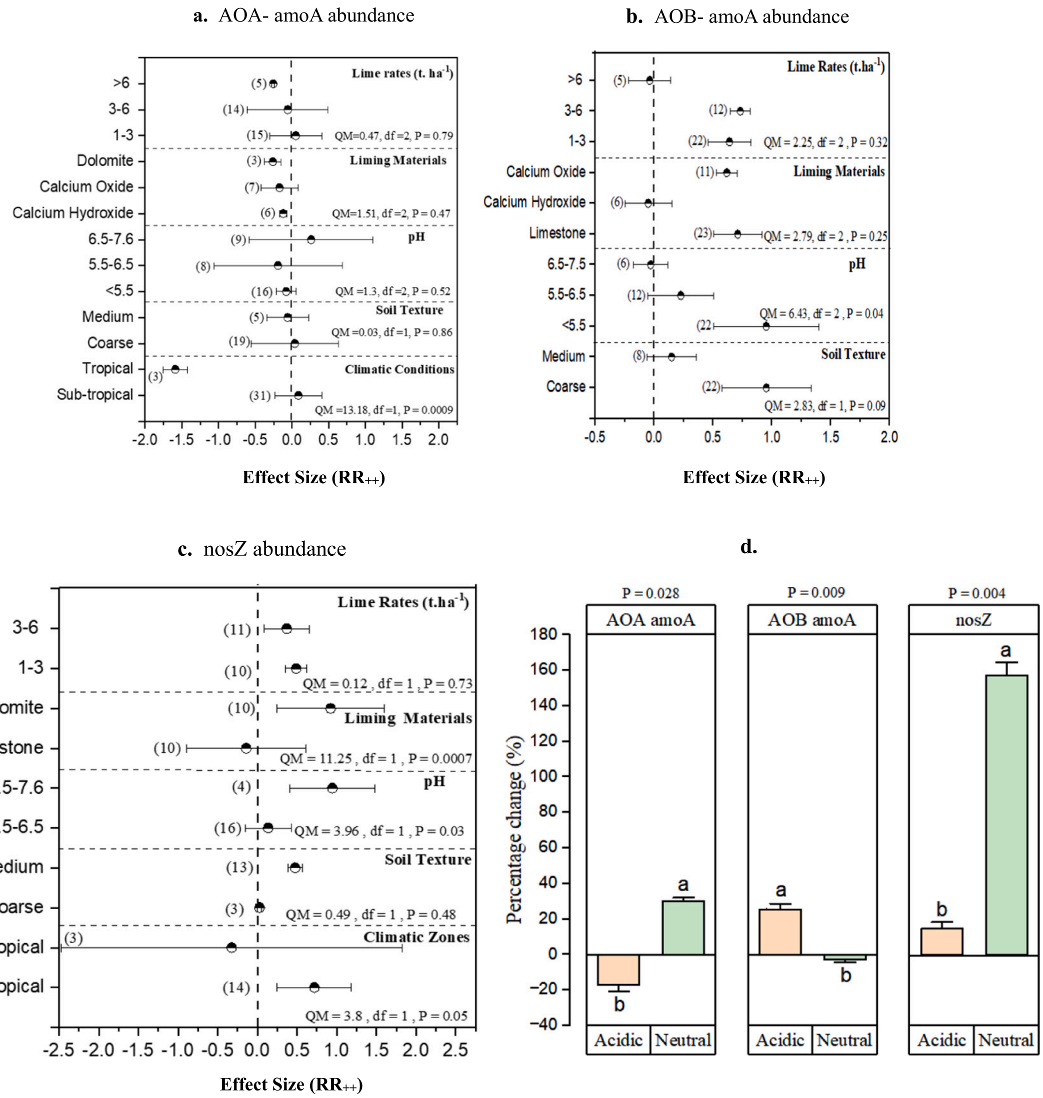

Fig. 2. Effects of lime application on archaeal amoA gene abundance (a) bacterial amoA gene abundance (b) nosZ gene (c) under different categorical variables as shown by weighted response ratio (RR_{++}) and percentage change in microbial functional genes under different soil acidification in response to lime application (d). Mean effect size/weighted response ratio and 95 % CIs are shown. Numbers in the brackets indicate number of the paired observations. Abbreviation: Abbreviation: AOA, ammonia oxidizing archaea; AOB, ammonia oxidizing bacteria; df, degree of freedom; QM, between group heterogeneity.

bacterial *amoA* and *nosZ* was positively correlated with soil pH and lime application rates (Table S3). The gene abundance of *nosZ* was highly correlated with soil pH, with a value of ($r = 0.54$, $p = 0.013$) (Table S3) compared to the other microbial functional genes. Among microbial functional genes, bacterial *amoA* was highly positively correlated with lime application rates ($r = 0.36$, $p = 0.02$, Table S3). Fitted line regression indicated that AOA *amoA* gene abundance had a nonsignificant a negative relationship with soil acidification, ($r = -0.53$ and $R^2 = 0.28$, $p = 0.18$) at acidic and ($r = -0.35$ and $R^2 = 0.12$, $p = 0.36$) neutral soil conditions, respectively (Fig. 4c). AOB *amoA* gene abundance showed a contrasting response to soil acidification ($r = 0.48$ and $R^2 = 0.23$, $p = 0.12$) at acidic and ($r = -0.45$ and $R^2 = 0.20$, $p = 0.27$) at neutral soil conditions, respectively (Fig. 4d). Positive relation of *nosZ* gene abundance was observed with soil acidification, ($r = 0.12$ and $R^2 = 0.01$, $p = 0.8$) at acidic and ($r = 0.82$ and $R^2 = 0.66$, $p = 0.002$) neutral soil conditions, respectively (Fig. 4e).

4. Discussion

4.1. Variation in soil N_2O emissions in response to lime application under different conditions and soil acidification

Liming is one of the most important and effective management practices to mitigate soil acidification because it neutralizes excess hydrogen ions in the soil solution (Pagani and Mallarino, 2012). Lime application rates being a dominant factor affecting the responses of soil N_2O to lime application, two categories of soil acidity conditions were observed from current meta-analysis (Fig. 5a and b). These differences in acidity conditions could be the result of the difference in the degree of pH manipulation resulting from various lime application rates. Surprisingly, in line with this statement, the order of the effectiveness of lime application in reducing soil N_2O emissions follows the order >6 t ha^{-1} > 3–6 t ha^{-1} > 1–3 t ha^{-1}, which has highly significant difference ($p < 0.001$) (Fig. 5b). The results from the fitted line regression also confirmed that soil N_2O emission is highly correlated with lime application rates ($R^2 = 0.38$, $p = 0.01$) (Fig. 4b). The highest reduction in soil N_2O emissions at the highest lime application rate could be attributed to the highest pH manipulation. In harmony with this statement, Oliver

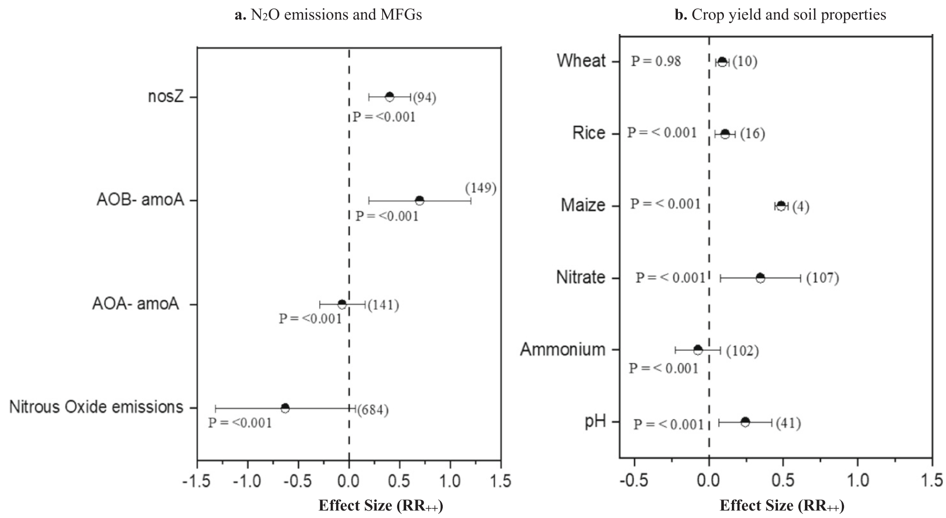

Fig. 3. Overall effect of lime application on (a) N_2O emissions and microbial functional genes and (b) crops yield and selected soil properties. Points represent the effect size (weighted response ratio). Error bars represent 95 % confidence intervals (CIs). Numbers in the brackets indicate number of paired observations. Abbreviation: AOA, ammonia oxidizing archaea; AOB, ammonia oxidizing bacteria.

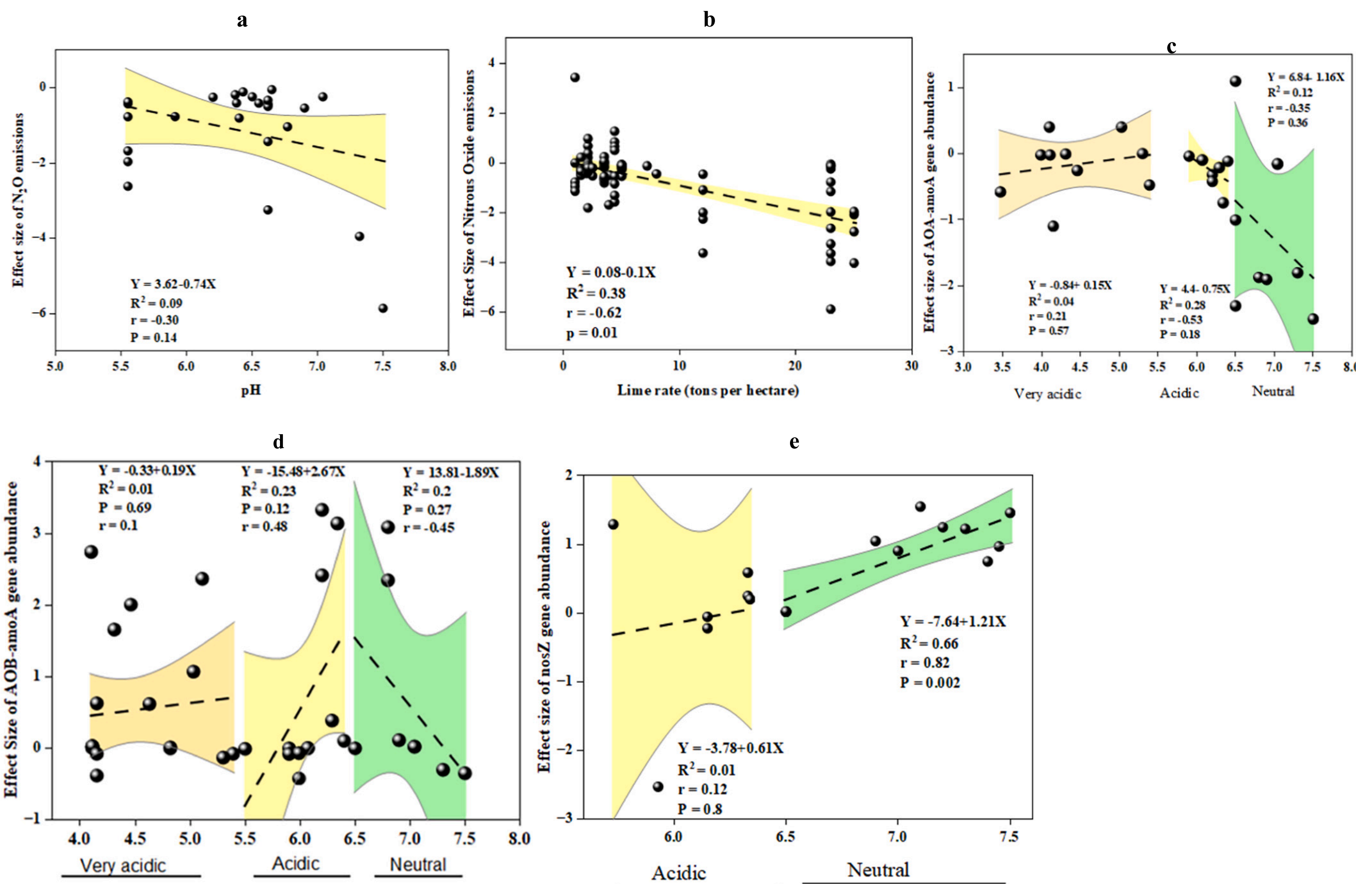

Fig. 4. Relationship between pH and N_2O emissions (a) lime application rates and RR of N_2O emissions (b) soil acidification and RR of AOA-amoA gene abundance (c) soil acidification and RR of AOB-amoA gene abundance (d) and soil acidification and RR of nosZ gene abundance.

et al. (2021) reported that liming rate is the most important factor influencing pH changes in acidic soil conditions, and a higher liming rate will solve subsoil acidity issues. Similarly, the highest reduction in soil N_2O emissions at a higher lime rate could be attributed to acidic soils' high buffering capacity, which requires a higher lime rate to neutralize acidity, as indicated by (Bravo Tutivén et al., 2022). Therefore, lime applications are considered a way to mitigate soil N_2O emissions, with the highest application rates being the most effective.

Liming alleviates soil acidity, which markedly affects the microbial activity responsible for nitrification and denitrification pathways, thus influencing soil N_2O emissions. Interestingly, the higher reduction in N_2O emissions following lime application was observed under neutral

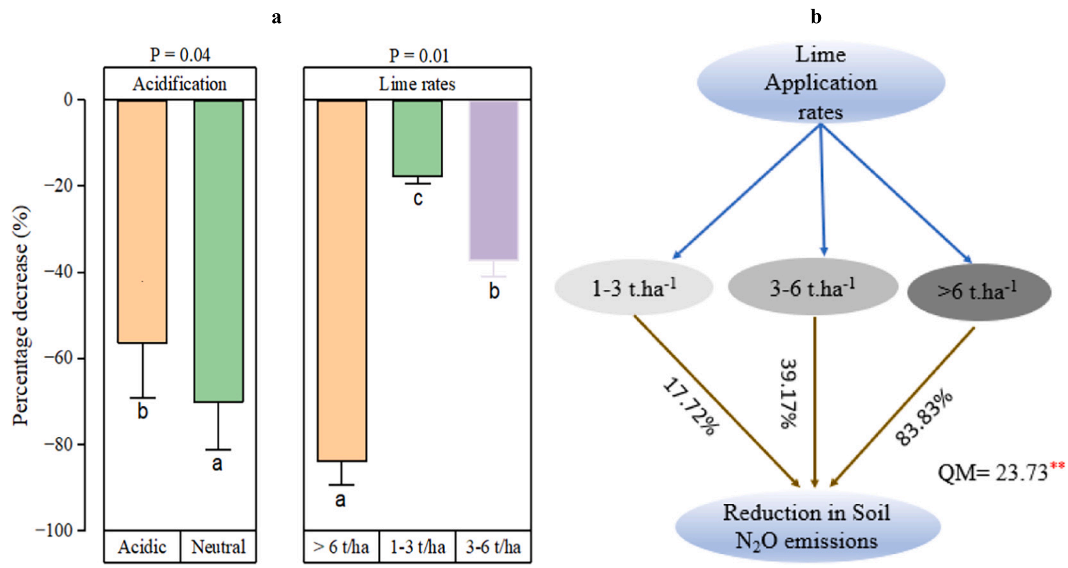

Fig. 5. Percentage decrease in N_2O emissions under different soil acidification and lime application rates (a) Percentage decrease in N_2O emissions with significance value indicating between group heterogeneity (QM) under subgroup of lime application rates (b).

soil conditions (70.00 %) compared to the acidic soil conditions (56.26 %) (Fig. 5a). These findings could be explained by the fact that there is a better improvement in the activities of N_2O emissions-related microbial communities at neutral soil acidity conditions. Similar to our work, the findings of Qu et al. (2014) reported that the higher values of N_2O emissions from acidic soils, while neutral soil pH produced less N_2O emissions. Furthermore, Wang et al. (2018) considered lime application to acidic soil as a potential tool for the mitigation of N_2O emissions since acidic or low-pH soil has enhanced N_2O emissions. Therefore, soil N_2O emissions were reduced following lime application, with the neutral soil pH condition having more pronounced effects.

The higher reduction in N_2O emission in response to lime application at the neutral soil acidity condition may also have resulted from the increase in denitrifying activity at a given soil acidity condition, which was supported by a study of Simek and Cooper (2002), which stated that denitrification rates are highest at the near-neutral pH. Similarly, Liu et al. (2014) also concluded that the enzyme nitrous oxide reductase (N_2O-R) encoded by the *nosZ* gene is the sole and main enzyme in the denitrification process; this enzyme reduces N_2O and converts it to N_2 gas at neutral, near neutral, or above pH 7. Philippot et al. (2009) stated that denitrifying enzymes, especially N_2O reductases and their encoding genes, which are responsible for the reduction of N_2O and the N_2O to N_2 ratio, are less active and susceptible at a low soil pH and produce more N_2O as an intermediate product. Therefore, the degree to which soil N_2O emissions decreased with lime application depends on microbial activities at a particular level of soil acidification caused by different lime application rates.

Similarly, we noticed that the response of N_2O emissions to lime application was affected by a coexistence of other external and internal factors. There are factors that could further synergistically promote the reduction of N_2O emissions in response to lime application. For instance, the highest synergistic promotion in the reduction of N_2O emissions was observed under temperate climatic conditions with fine-textured soil, soil WFPS of 60–90 %, and soils that had not received straw additions. Numerous previous meta-analyses and research reports have substantiated our findings.

Previous research has shown that soils in temperate regions have lower N_2O emissions due to their low acidification or higher pH. Heavy rainfall is a characteristic of tropical regions, and this may result in considerable NO_3^- leaching (Liu et al., 2019) and soil acidification. These authors stated that tropical soils are often more acidic than soils in other climatic conditions as a result of significant rainfall, which is the possible cause for the lowest reduction in soil N_2O emissions. The average soil pH of temperate regions was higher than that of tropical climate zones, which is favorable for better development and activity of nitrifiers. This could account for the biggest drop in soil N_2O emissions in response to lime applications in temperate climate conditions (Barnard et al., 2005). Our results were also consistent with those of Nugroho et al. (2007), who stated that in temperate regions, soils with slightly higher pH levels result in lower N_2O emissions. Similarly, previous research has shown that soil N_2O emissions were enhanced at 60 % WFPS compared to the other soil moisture regimes by promoting the microbial activities responsible for N_2O emissions due to the concurrent occurrence of nitrification and denitrification at this specific soil moisture regime. In line with the above statements, we have found less stimulation of a reduction in N_2O emission at WFPS of 60 % in response to lime application. Our findings are strongly supported by the findings of (Butterly et al., 2009; Vilain et al., 2010; Yang et al., 2016).

In addition, the highest stimulation of soil N_2O emissions reduction in response to lime application under the fine-textured soil is attributed to its low gas diffusivity, which enabled it to take longer for N_2O gas to be converted to N_2 gas. This claim was amply confirmed by the findings of Weitz et al. (2001), who identified a decrease in N_2O emission from fine-textured soils and suggested that a low gas diffusivity may have given more time for a more thorough conversion of N_2O to N_2. Similarly, Groffman and Tiedje (1991) found that fine-textured soils have lower denitrification rates and N_2O emissions than coarse-textured soils. Moreover, soil that had not received straw additions highly stimulated the decrease in soil N_2O emissions in response to lime application. In a similar vein, the results report by Köster et al. (2011) stated that straw is generally shown to increase the production of N_2O by providing readily available C as an energy source for denitrification, readily available N released during the decomposition of straw for nitrifiers and denitrifiers (Hu et al., 2013; Li et al., 2016), and by creating anaerobic microsites for denitrification (Chen et al., 2013). Similar findings were also reported by Baggs et al. (2000) and Huang et al. (2004) about how crop residue increased N_2O emissions. Therefore, a reduction in soil N_2O emissions as a result of lime application is highly context-dependent, depending on the aforementioned external and internal factors.

4.2. Variation in soil MFGS abundance in response to lime application under different conditions and soil acidification

The variable responses in archaeal and bacterial gene abundance to different soil acidifications are also strongly supported by our findings (Fig. 4c and d). Our current findings are supported by the previous study, which stated that the abundance of the archaeal *amoA* gene decreased with increased soil pH, while that of the bacterial *amoA* gene increased with increased soil pH (Nicol et al., 2008). We also indicated that soil pH is negatively and positively correlated with archaeal and bacterial *amoA* genes abundance, respectively (Table S3). Leininger et al. (2006) also reported the higher abundance of the AOA *amoA* gene over the AOB *amoA* gene in acidic soils since AOA has a stronger and special ability to tolerate low soil pH conditions. Study by Hu et al. (2013) also confirmed that the relative abundance of the ammonia oxidizers, AOA and AOB, was driven by factors like soil pH, and there was a decrease in the AOA/AOB ratio with an increase in soil pH. Another interesting result from the present study is the highest positive responses of AOB *amoA* to lime application observed at acidic soil pH conditions (5.5–6.5), indicating less tolerance of this microbial group to soil acidification, as indicated in Leininger et al. (2006) and Nicol et al. (2008).

Contrary to the acidic soil pH condition, at the neutral soil pH condition, both archaeal *amoA* gene abundance and bacterial *amoA* gene abundance showed similar decreasing trends (Fig. 4c and d). The earlier reports from different meta-analyses also reported that the abundance of both bacteria and archaeal *amoA* genes showed an almost similar trend at neutral soil acidity conditions, which was in harmony with our findings. The observed reduction in *amoA* of AOB at neutral soil pH condition could be due to its lower affinity for NH_4^+, which decreased with lime application. Similarly, previous studies found that AOA *amoA* has a higher affinity for low NH_4^+ than AOB (Martens-Habbena et al., 2009; Martens-Habbena and Stahl, 2011). The lower affinity of AOB over AOA for low NH_4^+ is also reported by Prosser and Nicol (2012). The variable responses of bacterial *amoA* gene abundance to lime application were also observed at different lime application rates. The highest enhancement of AOB *amoA* gene abundance in response to lime application was observed at lower lime application rates, which could be attributed to the lower tolerance of this bacteria to soil acidification since there is less pH manipulation at lower lime application rates. Studies by Simek et al. (2002); Nicol et al., 2008) strongly support the above claims.

Soil acidification has a general effect on denitrification and its product ratio of N_2O:N_2. The denitrifying gene, *nosZ*, is an important gene involved in the reduction of NO_2 and is the main target gene to quantify soil denitrification, as described by (Braker et al., 2000; Kuypers et al., 2018). From our study, we found that lime application resulted in a significant increase in the abundance of the *nosZ* gene, with the neutral soil pH condition showing a higher response compared to acidic soil pH condition (Fig. 4e). The possible explanation for the difference in the *nosZ* gene abundance under acidic and neutral soil pH conditions could be due to the difference in the activity of nitrous oxide reductase. Consistent with the current findings, Pauleta et al. (2013); Bakken and Frostegård, 2020) have also stated that under acidic soil conditions, the expression of the *nosZ* gene is substantially decreased. Moreover, a conceptual diagram illustrates the difference in N_2O reductase activity in the denitrification pathways under different soil acidifications, resulting in a difference in N_2O emissions (Fig. 6).

4.3. Effects of lime applications on selected soil properties and crop yield

The availability of all essential nutrients exists between the pH ranges of 6.0 and 7.0 and is considered optimal for many crops (Rosen and Bierman, 2005). Liming has a direct impact on different soil properties, which increases the availability and mobility of most essential plant nutrients (Bolan et al., 2003; Jaskulska et al., 2014). This is predominantly how lime application increases crop yield in acidic soil. The results of our current study revealed that liming increased the yields of all the crops, and the improved grain yield caused by lime application greatly depends on crop species (Fig. 3b). In line with our study, Holland et al. (2018) reported that crop species vary greatly in terms of their potential to tolerate and sensitivity to acidic soil. Moreover, a study by Fageria and Nascente (2014) reported that various species require variable amounts of lime.

NH_4^+ is used as the substrate for nitrification, and the end product of nitrification, NO_3^-, is used as the substrate for denitrification (Prosser, 2011). The concentration of these forms of nitrogen directly affects the microbial nitrification and denitrification processes. In the present study, the concentration of NH_4^+-N decreased and resulted in increased NO_3^--N, with the lime application indicating nitrification, which can play a vital role in N_2O emissions (Fig. 3b). Generally, the liming of

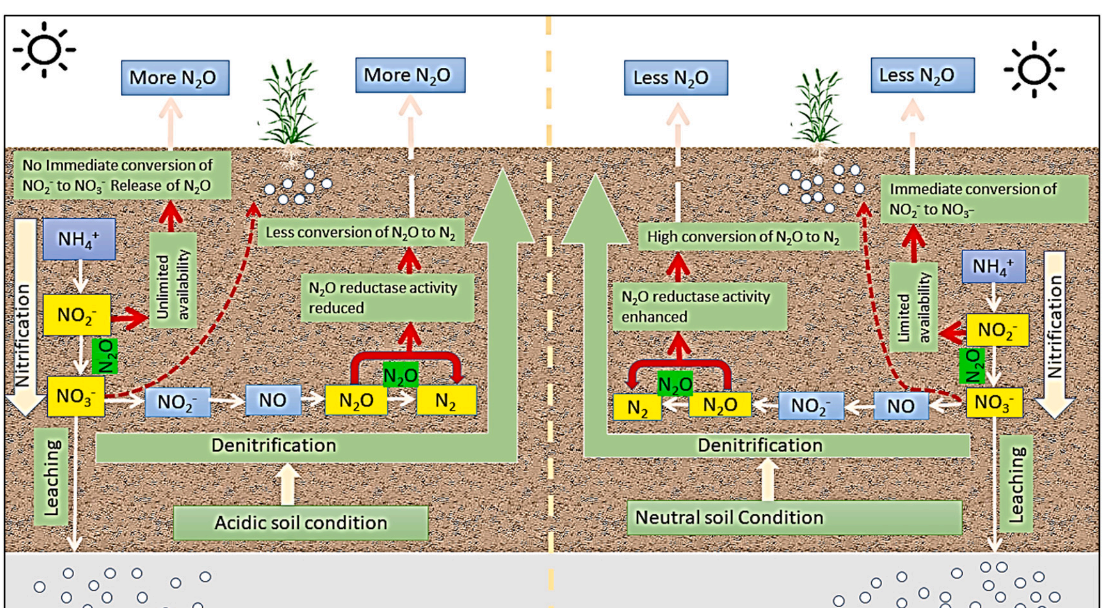

Fig. 6. Conceptual diagram showing N_2O emission from nitrification and denitrification pathways under different soil acidification.

acidic soils stimulates soil nitrification activity. The increased concentration of NO_3^-- N with lime application from our work is supported by Barton et al. (2013); Vázquez et al. (2020) which stated that an increase in soil pH facilitated the conversion of NO_2^- to NO_3^-. Similarly, soil pH and NH_4^+ supply are thought to be important factors influencing nitrification (Homyak et al., 2014; Hanan et al., 2016) and they can interact to magnify their effect on nitrification. Further-more, studies by Nugroho et al. (2007), Ulyett et al. (2014), and Che et al. (2015), reported that lime application increased soil nitrification.

4.4. Mechanisms of how lime application reduce N_2O emissions

Lime-induced changes in pH directly affect soil microbial processes (Bakken and Frostegård, 2020), and changes in soil microbial parameters and substrate availability will also affect the production and consumption of N_2O emissions (Clough et al., 2004; Paradelo et al., 2015; Shaaban et al., 2016; Khaliq et al., 2019; Royer-Tardif et al., 2019). Previous study reported the reduction in N_2O emissions following lime application. However, the mechanisms of reduction of N_2O under different soil acidifications were not clear and required detailed study. It was notable from our study that the difference in the reduction of N_2O emissions following lime application is explained by differences in the microbial activity and substrate availability (NO_3^--N and NH_4^+-N) under different soil acidification. It was reported from our SEM that the differences in the reduction of N_2O emission magnitudes under different lime rates are due to differences in the degree of soil pH manipulation (Fig. 7a and b) (Shaaban et al., 2020). Moreover, the results of relative influence indicated lime application rates as the highest determinant factor affecting the response of soil N_2O emissions to lime, followed by soil pH (Fig. 7c).

Variables in the activities of N_2O-associated microbial activities under different soil acidifications are main factor responsible for the difference in the N_2O reduction following lime application. Overall, N_2O emissions decreased by 56.26 % and 70.00 % under acidic and neutral

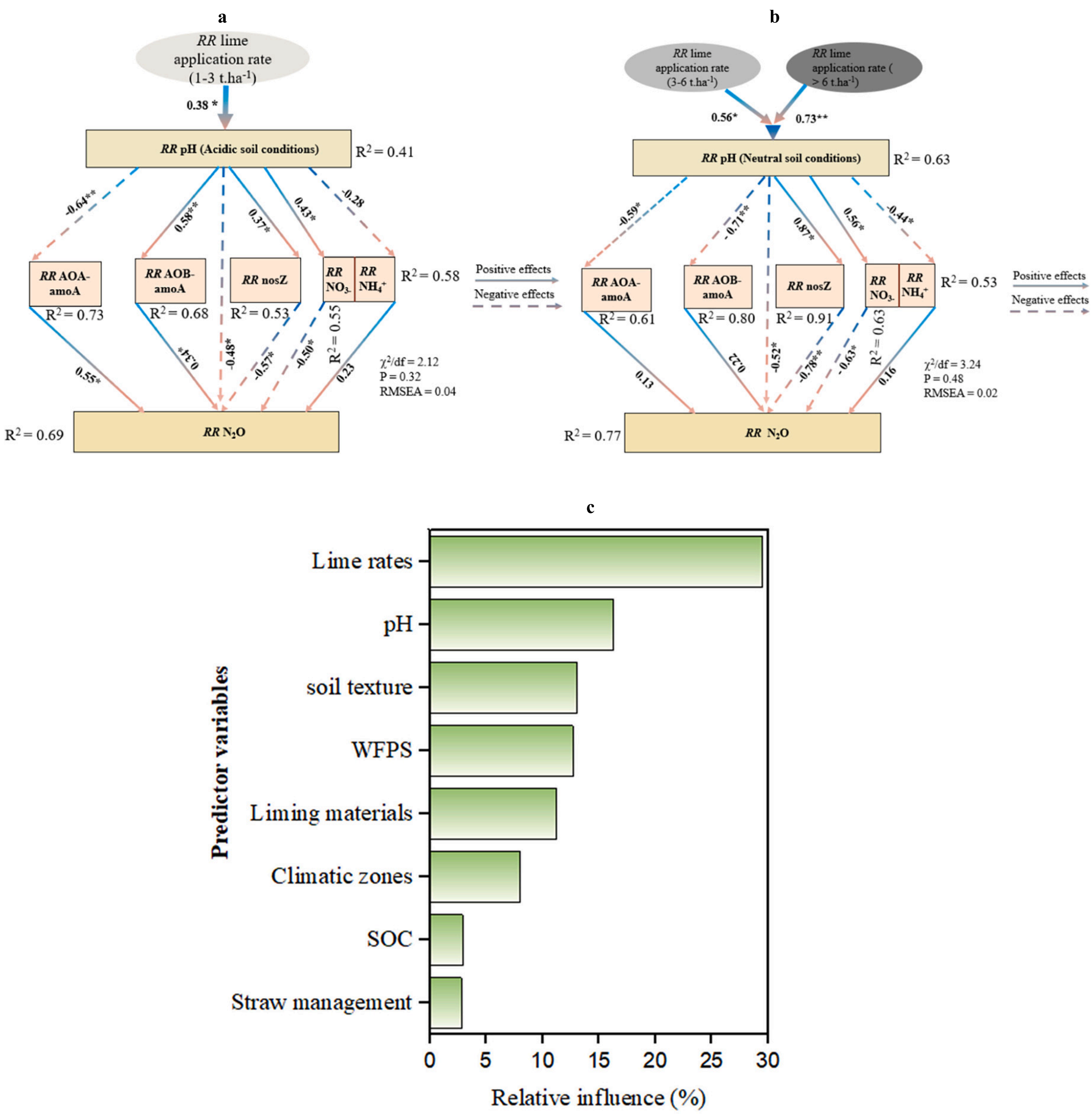

Fig. 7. Structural equation modeling showing how lime reduce N_2O emissions under different soil acidification. (a): acidic soil conditions (b) neutral soil conditions, (c) the relative influence (%) of predictor variables for the boosted regression tree model of N_2O emissions. Number near the arrow are path coefficients. * indicate that the significance level at $p < 0.05$ and ** indicate that the significance level at $p < 0.01$, respectively. The R^2 value represents the explained variance. RR represents response ratio.

soil conditions, respectively. Under acidic soil conditions, even though there is a sharp increase in the abundance of AOB *amoA* genes following lime application, the reduced soil N_2O emissions attributed to the conducive conditions for *nosZ* gene abundance (Fig. 7a and b), which modify the product ratio of $N_2O:N_2$. Higher reduction in N_2O emissions under neutral compared to acidic soil conditions is associated with the more conducive conditions for denitrification (Simek and Cooper, 2002). Similarly, reduced AOB activity under neutral soil conditions also contributed to N_2O emission reduction due to N_2O yield from AOB activity being double that of AOA (Nicol et al., 2008; Hink et al., 2018).

In the current study, lime applications greatly affect the substrate availability. Overall, a decrease in NH_4^+ and an increase in NO_3^- were observed from our current meta-analysis. SEM results from our current study indicated that NH_4^+ and NO_3^- affect N_2O emissions positively and negatively, respectively (Fig. 7a and b). The higher decrease in NH_4^+ under neutral soil conditions contributed to N_2O emissions due to decreased AOB activity having less affinity for NH_4^+ (Martens-Habbena et al., 2009; Martens-Habbena and Stahl, 2011). Lime also decreases N_2O emissions mainly through increased NO_3^-, where N_2O acts as an electron acceptor instead of NO_3^- (Shaaban et al., 2020).

5. Conclusion

Previous studies reported a reduction in N_2O emissions following lime application. However, the mechanisms of reduction of N_2O under different soil acidifications are not clear and require detailed study. As a result, it is imperative to gain insights into how lime application affects N_2O emissions and associated microbial activities under varying soil acidification and other factors in agricultural ecosystems. Our structural equation modeling (SEM) suggested that the differences in the reduction of N_2O emission magnitudes under different lime rates are due to differences in the degree of soil pH manipulation. Lime application rates and pH were the highest determinant factors affecting the response of soil N_2O emissions to liming. Our results from SEM indicated that the main drivers of the variable responses in soil N_2O emissions to lime application under different soil acidifications are the variable responses of N_2O-associated microbial activities and substrate availability. Overall, N_2O emissions decreased by 56.26 % and 70.00 % under acidic and neutral soil conditions, respectively. SEM from the current study illustrated that a higher reduction in N_2O emissions under neutral compared to acidic soil conditions is associated with more conducive conditions for *nosZ* gene abundance, reduced AOB *amoA* gene abundance due to reduced NH_4^+, and increased NO_3^-. Therefore, soil N_2O emissions were reduced following lime application, with the neutral soil pH condition having more pronounced effects. Based on our findings, we concluded that applying lime to acidic soils is a suitable option for reducing soil N_2O emissions by affecting the activity of associated MFGs and substrate availability in agricultural ecosystems.

CRediT authorship contribution statement

Kiya Adare Tadesse: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Conceptualization. **Tianfu Han:** Writing – review & editing, Software, Methodology, Data curation. **Zhe Shen:** Writing – review & editing, Software, Conceptualization. **Nano Alemu Daba:** Writing – review & editing, Software, Formal analysis, Conceptualization. **Jiwen Li:** Writing – review & editing, Visualization, Software. **Muhammad Numan Khan:** Writing – review & editing, Software. **Asad Shah:** Writing – review & editing, Visualization. **Huimin Zhang:** Validation, Supervision, Resources, Project administration, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106175.

Data availability

Data will be made available on request.

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