Impacts of nitrogen deposition on soil methane uptake in global forests

Atmospheric Nitrogen Deposition to Global Forests

Xia, Nan; Du, Enzai; de Vries, Wim

https://doi.org/10.1016/B978-0-323-91140-5.00018-X

Chapter 9

Impacts of nitrogen deposition on soil methane uptake in global forests

Nan Xia[a,b], Enzai Du[a,b] and Wim de Vries[c,d]

[a]State Key Laboratory of Earth Surface Processes and Resource Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing, China; [b]School of Natural Resources, Faculty of Geographical Science, Beijing Normal University, Beijing, China; [c]Environmental Research, Wageningen University and Research, Wageningen, the Netherlands; [d]Environmental Systems Analysis Group, Wageningen University and Research, Wageningen, the Netherlands

1. Introduction

As a well-known greenhouse gas, atmosphere methane (CH_4) can absorb infrared radiation and has a global warming potential that is 29.8 times higher than CO_2 (Forster et al., 2021; Houghton et al., 2001; Rodhe, 1990). Atmospheric CH_4 concentrations have been increasing rapidly and causing a growing concern of its contribution to climate warming (Dlugokencky et al., 2011; Kirschke et al., 2013). Soil CH_4 can either be produced by methanogens (Le Mer and Roger, 2001; Thauer et al., 2008) or oxidized to CO_2 by methanotrophs (Bosse and Frenzel, 1997; Le Mer and Roger, 2001). Under aerobic conditions, the oxidization of CH_4 generally exceeds its production and thus results in a net soil CH_4 sink (Bodelier and Laanbroek, 2004). Covering nearly one third of the land surface area (Keenan et al., 2015), forest soils are an important sink of atmospheric CH_4 (Dutaur and Verchot, 2007; Le Mer and Roger, 2001). Anthropogenic nitrogen (N) emissions have increased N deposition to global forests (Lamarque et al., 2013; Schwede et al., 2018; Vet et al., 2014), resulting in various ecological consequences (Bobbink et al., 2010; Bowman et al., 2008; de Vries et al., 2011, 2017; Du et al., 2019, 2020a; Gilliam, 2006; Midolo et al., 2019). However, the response of soil CH_4 flux to N deposition is less quantified across global forest biomes in comparison with soil CO_2 fluxes (Bodelier and Steenbergh, 2014; de Vries et al., 2017).

Nitrogen deposition affects both the activities of methanogens and methanotrophs (Bodelier and Laanbroek, 2004; Schnell and King, 1994). In an N-deficient ecosystem, N inputs might release the N limitation of methanotrophic microorganisms and/or the biosynthesis of enzymes involved in methane oxidation and thus benefit soil CH_4 uptake (Bodelier et al., 2000; Bodelier and Laanbroek, 2004; Reay and Nedwell, 2004). In addition, external N inputs can stimulate tree growth (Du and de Vries, 2018; Schulte-Uebbing and de Vries, 2018; Sonnleitner et al., 2001) and increase evapotranspiration, indirectly favoring microbial CH_4 oxidation in soils. However, excess N inputs may decrease soil CH_4 uptake via a direct inhibition of CH_4 oxidation due to either osmotic stress caused by increased soil inorganic N concentrations or competitive inhibition of the enzyme methane mono-oxygenase by ammonia (Bodelier and Laanbroek, 2004; Schnell and King, 1994; Sitaula et al., 1995) and an indirect effect due to soil acidification and an imbalance of N and P (Veraart et al., 2015). Theoretically, external N additions likely exert nonlinear effects on soil CH_4 uptake in N-limited forests, including an initial stimulation of soil CH_4 uptake and then an inhibition when the N addition rate exceeds a certain threshold (see *red curve* in Fig. 9.1). In non N-limited forests, N additions generally decrease soil CH_4 uptake or increase soil CH_4 emissions (see blue line in Fig. 9.1).

Based on an earlier meta-analysis, Liu and Greaver (2009) demonstrated that forest soil CH_4 uptake was significantly reduced by N additions but the analysis was not conducted for each forest biome. In contrast, another meta-analysis indicated an overall neutral effect of N additions on forest soil CH_4 uptake (Aronson and Helliker, 2010). This inconsistency might be caused by mixing experimental results from all forest biomes and neglecting the nonlinear effects of N additions in the meta-analyses (Xia et al., 2020). Previous studies have indicated a poleward increase in N limitation from tropical forest to boreal forest (Du et al., 2020b; Elser et al., 2007), implying distinct responses of soil CH_4 flux to N addition across forest biomes. Therefore, the biome-specific effects of N deposition should be considered separately.

Atmospheric Nitrogen Deposition to Global Forests. https://doi.org/10.1016/B978-0-323-91140-5.00018-X

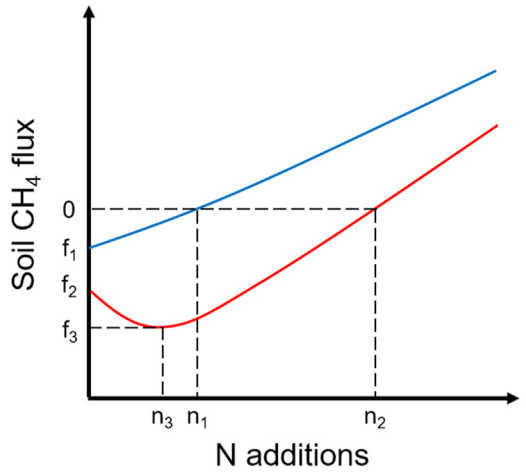

FIG. 9.1 Conceptual responses of soil CH_4 flux to N additions in N-limited (in red) and non N-limited forests (in blue). f_1 and f_2 indicate the soil CH_4 fluxes under ambient condition (N addition = 0) in non N-limited forests and N-limited forests, respectively. n_1 and n_2 indicate the thresholds of N addition that result in a shift from soil CH_4 sinks to soil CH_4 sources in non N-limited forests and N-limited forests, respectively. n_3 indicates the threshold of N addition that shift from positive to negative effects on soil CH_4 uptake in the N-limited forests.

According to an assessment conducted by the World Meteorological Organization (WMO) Global Atmosphere Watch program (GAW), ambient N deposition rarely exceeded 60 kg N ha^{-1} yr^{-1} across the globe (Vet et al., 2014). In view of an urban hotspot phenomenon, N deposition is even lower in the widespread natural forests in comparison with urban and rural forests (Du et al., 2022). Current understanding of the effects of N deposition on forest soil CH_4 uptake is mainly derived from manipulated N addition experiments. However, much higher N dosages (e.g., >100 kg N ha^{-1} yr^{-1}) have been frequently used in existing N addition experiments (Aronson and Helliker, 2010; Bodelier and Steenbergh, 2014; de Vries et al., 2017; Liu and Greaver, 2009; Xia et al., 2020). These experiments might lead to biases when evaluating the effects of actual N deposition on soil CH_4 uptake.

Forest soil CH_4 flux is regulated by several climate factors (Borken et al., 2006; Ni and Groffman, 2018) and soil properties (Benstead and King, 2001; Boeckx et al., 1997; Castro et al., 1995). Compared to methanogens, methanotrophs have a lower optimum temperature and are thus less sensitive to temperature (Borken et al., 2006; Dunfield et al., 1993). Under low temperature conditions (e.g., boreal forest), methanotrophs are likely more active than methanogens, resulting in lager soil CH_4 sinks. Precipitation has a strong control of soil moisture, which not only affects the activity of methanotrophs but also affects the diffusion rates of CH_4 and O_2 molecules (Smith et al., 2003). In soils with low moisture, CH_4 is more easily to diffuse into methanotrophs, which in turn promote a high oxidation rate. Soil pH affects the physiological functions of methanogens and methanotrophs directly (Benstead and King, 2001) and may interact with other factors (e.g., water stress, terpenes, and ammonium inputs) to limit methanotrophs activity (Amaral et al., 1998a; King, 1997). However, the reported effects of soil pH on soil CH_4 flux vary largely among sites and studies (Hütsch et al., 1994; Saari et al., 2004; Weslien et al., 2009).

Based on a synthesis of experimental results in literature, we evaluated the impacts of N additions on soil CH_4 uptake in global forests. Specifically, the effects of low-level N addition (≤60 kg N ha^{-1} yr^{-1}) and high-level N addition (>60 kg N ha^{-1} yr^{-1}) on soil CH_4 flux were assessed separately. Moreover, we explored the key factors affecting the spatial variation in the responses of soil CH_4 flux to N additions, including experimental duration, N addition rate, N addition form, mean annual temperature (MAT), mean annual precipitation (MAP), ambient N deposition, soil pH and forest type. This chapter extends a previous meta-analysis by Xia et al. (2020) on the effects of low and high level N deposition on soil CH_4 uptake in forest biomes, by using an updated literature database and quantifying the response of soil CH_4 uptake per kg N addition for major forest biomes and the global-scale impact of N deposition on forest soil CH_4 uptake.

2. Materials and methods

2.1 Data set

By conducting a survey via the online library of ISI Web of Science (http://isiknowledge.com), Google Scholar (http://scholar.google.com) and China National Knowledge Infrastructure (http://www.cnki.net), we collected field experimental data on the effect of N addition on soil CH_4 flux in forest ecosystems across the globe. The key words "methane (or CH_4)", "nitrogen addition (or nitrogen deposition, nitrogen fertilization)" and "forest" were used. The database recorded the means and standard deviations of soil CH_4 fluxes in control plots and treatment plots, as well as information on site location (longitude and latitude), experimental treatments (the experimental duration, N addition rate, N addition form, i.e., NO_3^--N, NH_4^+-N, NH_4NO_3−N or urea), climate (mean annual temperature, MAT, and mean annual precipitation, MAP), ambient N deposition, soil pH and forest type (i.e., boreal, temperate, subtropical or tropical forests) (Table 9.1).

Experimental and climate data were either directly extracted from tables or digitized from figures by using a GetData Graph Digitizer (Version 2.18, http://www.getdata-graph-digitizer.com). Soil pH was retrieved from SoilGrids (http://soilgrids.org) and ambient N deposition was retrieved from a multiple-model estimate of N deposition (Tan et al., 2018) if it was not reported. In boreal and

TABLE 9.1 Information on location, climate, forest type, and design of the manipulated N addition experiments in forest ecosystems.

ID	Lon (°E)	Lat (°E)	MAT (°C)	MAP (mm)	Soil pH	N deposition (kg N ha^{-1} yr^{-1})	Forest type	N addition form	N addition rate (kg N ha^{-1} yr^{-1})	Experimental duration (yr)	References
1	−148.30	64.75	−2.8	284	5.80	0	BF	NH_4NO_3	0, 171	4	Gulledge and Schimel (2000)
2	−148.30	64.75	−2.8	284	5.80	0	BF	NH_4NO_3	0, 143	4	Gulledge and Schimel (2000)
3	29.37	61.85	3.8	582	4.07	4	BF	NH_4NO_3	0, 31	28	Saari et al. (2004)
4	25.62	61.32	3.3	680	3.60	5	BF	NH_4NO_3	0, 200	3	Maljanen et al. (2006)
5	125.48	51.37	−2.4	489	5.15	4	BF	NH_4NO_3	0, 25, 50, 75	3	Yan et al. (2016b)
6	121.51	50.83	−5.4	580	5.50	9	BF	NH_4NO_3	0, 10, 20, 40	0.5	Xu et al. (2014)
7	121.88	50.42	−5.4	500	5.50	10	BF	NH_4Cl/ KNO_3	0, 10, 40	1	Gao et al. (2013)
8	129.11	48.12	−0.5	718	5.50	9	TemF	NH_4NO_3	0, 50, 100, 150	1	Yan et al. (2016a)
9	128.89	47.18	−0.3	676	5.67	13	TemF	NH_4NO_3	0, 20, 40, 80	3	Song et al. (2017)
10	141.33	43.10	9.5	995	4.21	10	TemF	NH_4NO_3	0, 50	1	Kim et al. (2012)
11	128.10	42.40	4.1	855	5.90	23	TemF	NH_4Cl/ KNO_3	0, 45	0.25	Xu et al. (2011)
12	−85.40	42.40	9.7	890	5.47	6	TemF	NH_4NO_3	0, 10	2	Ambus and Robertson (2006)
13	−85.40	42.40	9.7	890	4.63	6	TemF	NH_4NO_3	0, 10	2	Ambus and Robertson (2006)
14	127.63	41.70	3.6	745	5.30	11	TemF	Urea	0, 10, 20, 40, 60, 80, 100, 120, 140	0.5	Geng et al. (2017)
15	−80.03	41.60	9.8	1125	4.00	15	TemF	NH_4NO_3	0, 100	1	Chan et al. (2005)
16	116.22	39.99	11.6	630	6.72	33	TemF	NH_4NO_3	0, 50, 100, 150	1	Wang (2012)
17	−74.58	39.92	12.3	1143	4.80	15	TemF	NH_4NO_3	0, 5, 67	0.33	Aronson et al. (2012)
18	112.15	36.69	8.6	662	7.08	31	TemF	NH_4NO_3	0, 50, 100, 200, 400	3.33	Yu et al. (2019)
19	118.70	32.18	15.5	1020	4.50	48	STF	NH_4NO_3	0, 50, 100, 150	1.5	Hu et al. (2011)
20	110.45	31.60	10.6	1650	5.70	27	STF	NH_4NO_3	0, 50	0.42	Pan (2013)
21	119.70	30.23	15.9	1450	6.50	40	STF	NH_4NO_3	0, 40, 120	2	He (2019)

Continued

TABLE 9.1 Information on location, climate, forest type, and design of the manipulated N addition experiments in forest ecosystems.—cont'd

ID	Lon (°E)	Lat (°E)	MAT (°C)	MAP (mm)	Soil pH	N deposition (kg N ha^{-1} yr^{-1})	Forest type	N addition form	N addition rate (kg N ha^{-1} yr^{-1})	Experimental duration (yr)	References
22	115.06	26.74	17.9	1505	4.26	33	STF	NH_4Cl/ $NaNO_3$	0, 40, 120	1	Li et al. (2015)
23	115.07	26.75	18.0	1489	5.50	23	STF	NH_4NO_3	0, 50, 100	0.75	Zhang (2013)
24	117.47	26.18	19.4	1700	5.40	36	STF	NH_4NO_3	0, 40, 80	6	Wu (2018)
25	112.54	23.18	21.0	1927	4.07	44	STF	NH_4NO_3	0, 100	1.5	Gao et al. (2017)
26	112.17	23.17	21.0	1927	3.80	33	STF	NH_4NO_3	0, 50, 100, 150	1	Zhang et al. (2008)
27	112.17	23.17	21.0	1927	3.90	33	STF	NH_4NO_3	0, 50, 100	1	Zhang et al. (2008)
28	112.17	23.17	21.0	1927	4.00	33	STF	NH_4NO_3	0, 50, 100	1	Zhang et al. (2008)
29	112.17	23.17	21.0	1927	5.50	40	STF	NH_4NO_3	0, 150	2.66	Zheng et al. (2016)
30	112.17	23.17	21.0	1927	5.50	40	STF	NH_4NO_3	0, 150	2.66	Zheng et al. (2016)
31	112.17	23.17	21.0	1927	5.50	40	STF	NH_4NO_3	0, 150	2.66	Zhang et al. (2011)
32	112.83	22.57	22.5	1534	3.87	43	STF	NH_4NO_3	0, 50, 100	1	Zhang et al. (2012)
33	107.60	22.38	21.8	1200	3.95	22	STF	Urea	0, 48, 167, 334	2	Zhang et al. (2017)
34	−79.83	9.10	27.2	2715	5.10	9	TroF	Urea	0, 125	12	Veldkamp et al. (2013)
35	−82.25	8.75	20.3	5461	4.70	5	TroF	Urea	0, 125	4	Veldkamp et al. (2013)
36	117.39	5.37	25.2	3098	4.70	3	TroF	Urea	0, 100	4	Mori et al. (2017)
37	−79.20	−4.08	19.4	2230	4.20	5	TroF	Urea	0, 50	4.67	Martinson et al. (2020)
38	−79.20	−4.08	15.7	1950	3.70	5	TroF	Urea	0, 50	4.67	Martinson et al. (2020)
39	−79.20	−4.08	9.4	4500	3.80	5	TroF	Urea	0, 50	4.67	Martinson et al. (2020)

Abbreviations: *BF*, boreal forest; *STF*, subtropical forest; *Tem*, Temperate forest; *TroF*, tropical forest.

temperate forests, soil CH_4 fluxes were generally measured during the growing season, while in subtropical and tropical forests, the measurements were conducted the whole year round. During the nongrowing season, temperature of boreal and temperate forests is relatively low and measurements of soil CH_4 fluxes are lacking. Therefore, our analysis ignored the part of soil CH_4 flux in boreal and temperate forests during the nongrowing season.

Overall, our database included experimental results of 74-N addition trials across 39 forests from 30 sites (Fig. 9.2). Specifically, 52 trials were conducted by using NH_4NO_3 in 28 forests, 17 trials by using urea in eight forests, and five paired trials by using both nitrate (KNO_3 or $NaNO_3$) and ammonium (NH_4Cl) based N forms in three forests (Table 9.1). For the paired trials, the rates of soil CH_4 flux were averaged for each N dosage and used as one treatment for further analysis. Finally, there were 12, 28, 28 and six fertilization trials from seven boreal forests, 11 temperate forests, 15 subtropical forests and six tropical forests, respectively (Table 9.1). However, the tropical forest studied by Martinson et al. (2020) was a mountain rain forest with low soil mineral N availability and a closed soil N cycle, which was different from most tropical forests. Therefore, we considered this study as a special case and excluded the 3 N addition trials. Afterward, data of tropical forests were combined with those of subtropical forests for further analysis since there were too few trials in tropical forests for a robust statistical analysis (n = 4).

2.2 Statistical analysis

To qualify the effect of N additions on soil CH_4 flux, we defined a response ratio (*RR*, g CH_4 kg^{-1} N) as given in Eq. (9.1),

$$RR = \frac{(Flux_t - Flux_c)}{N_{add}} \times c \tag{9.1}$$

where $Flux_t$ and $Flux_c$ indicate the mean soil CH_4 fluxes in the treatment plots and control plots (mg CH_4 m^{-2} h^{-1}), N_{add} indicates the N addition for each treatment (kg N ha^{-1} yr^{-1}), and the constant c is a unit correction factor from mg CH_4 m^{-2} h^{-1} to g CH_4 ha^{-1} yr^{-1}. In subtropical and tropical forests, the unit correction factor ($c = 87{,}600$) was calculated based on the duration of a whole year. The unit correction factors ($c = 29{,}200$ for boreal forest and 51,100 for temperate forest) were estimated using durations of 4 months (mid-May to mid-September) for boreal forest and 7 months (April to October) for temperate forest (Piao et al., 2007) while neglecting the remaining time of the year. A positive value of the response ratio indicates a reduction in soil CH_4 uptake or an increase in soil CH_4 emission due to N addition, while a negative value indicates an opposite effect.

The variance (v_i) of the response ratio is estimated according to Eq. (9.2) as given below (Schulte-Uebbing and de Vries, 2018),

$$v_i = \left[\frac{n_t + n_c}{n_t \times n_c} + \frac{(n_t - 1) \times sd_t^2 + (n_c - 1) \times sd_c^2}{n_t + n_c - 2}\right] \times \left(\frac{c}{N_{add}}\right) \tag{9.2}$$

where sd_t, sd_c, n_t, n_c indicate the standard deviation and number of replicates for the treatment plots and control plots, respectively. Using a random effect model (Borenstein et al., 2009), we estimated the mean response ratios and corresponding standard errors for the forest biomes with weight (w_i) equal to the inverse of the sum of the within-study variance (v_i, due to sampling error) and between-study variance (τ^2, due to variations in experimental conditions) according to Eq. (9.3),

$$w_i = \frac{1}{v_i + \tau^2} \tag{9.3}$$

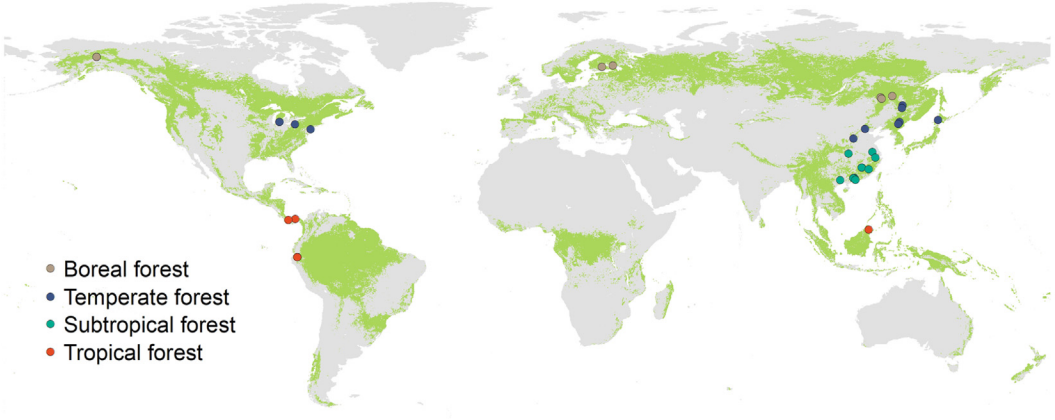

FIG. 9.2 Geographical distribution of nitrogen addition experiments from 39 forests across 30 sites. *Green shadows* indicate the distribution of global forest.

We conducted one-way ANOVA analysis and a post-hoc test to compare the response ratio of soil CH_4 flux to N addition among boreal, temperate, as well as subtropical and tropical forests. In addition, we used the Student's t test to compare the response ratio between low-level N addition ($\leq$60 kg N ha^{-1} yr^{-1}) and high-level N addition (>60 kg N ha^{-1} yr^{-1}) in different forest biomes respectively. The low-level N addition is in the range of N deposition over the world (Vet et al., 2014). Moreover, biome-scale effects of N deposition on soil CH_4 sink were estimated based on the response ratio of soil CH_4 flux to low-level N addition, mean forest-specific total N deposition (base year 2010) (Schwede et al., 2018) and the area of each forest biomes (base year 2010) (Keenan et al., 2015).

Then we used the "*glmulti*" package to conduct a model selection analysis for the potential driving factors affecting the variation of response ratios of soil CH_4 flux to low-level N addition ($\leq$60 kg N ha^{-1} yr^{-1}) based on the corrected Akaike information criterion (Calcagno and de Mazancourt, 2010). The relative importance value of each driving factor was estimated as the sum of the Akaike weights for the models in which the variable appeared. A cut-off relative importance value of 0.8 was used to differentiate between the important and unimportant variables (Calcagno and de Mazancourt, 2010). Conditional regression analysis (Breheny and Burchett, 2013) was conducted to visualize the role of each driving factor on response ratio while holding all the other important variables constant (by default the median for numeric variables). The variance inflation factor (VIF <3 indicates weak collinearity) was computed to diagnose the multicollinearity of the driving factors for the final model (Zuur et al., 2010). The variance explained by each driving factor was estimated by averaging sequential sums of squares over all orderings of regressors using the "*relaimpo*" package (Groemping, 2006). All analyses were conducted by R software (version 4.0.0, R Development Core Team, http://www.r-project.org/) using a significance level of $P = .05$. Values were mean ± standard error, if not specially noted.

3. Results and discussion

3.1 Variation in ambient soil methane uptake across forest biomes

Forest soils in control plots were significant CH_4 sinks, on average taking up 0.07 ± 0.02, 0.04 ± 0.01 and 0.02 ± 0.00 mg CH_4 m^{-2} h^{-1} in boreal (n = 7), temperate (n = 11) as well as subtropical and tropical (n = 18) forests, respectively. The rate of soil CH_4 uptake in boreal forest was higher than those in temperate ($P = .08$) and subtropical and tropical forests ($P = .003$). The rate of soil CH_4 uptake in temperate forest showed no significant differences from subtropical and tropical forests ($P = .15$). Compared with boreal forest, the lower rates of soil CH_4 uptake in other forest biomes might be attributed to a suppression of CH_4 oxidation by higher temperature (Dutaur and Verchot, 2007), more precipitation (Le Mer and Roger, 2001), higher background N availability (Vet et al., 2014; Schwede et al., 2018; Du and de Vries, 2018), and/or a stronger phosphorus limitation to methanotrophic microorganisms (Veraart et al., 2015).

By multiplying the average rate of soil CH_4 uptake in control plots with the area of each forest biome (Keenan et al., 2015), annual soil CH_4 fluxes were estimated to be -2.49 ± 0.68, -1.38 ± 0.45 and -3.71 ± 0.56 Tg CH_4 yr^{-1} in global boreal, temperate as well as subtropical and tropical forest biomes, respectively (Table 9.2). Overall, our results showed that global forest soils contributed to a CH_4 sink of 7.55 ± 1.68 Tg CH_4 yr^{-1}, accounting for only a half of the estimated annual forest soil CH_4 sink (13.9 Tg CH_4 yr^{-1}) in a model-based study by Murguia-Flores et al. (2018).

TABLE 9.2 Biome-scale estimates of soil CH_4 fluxes and the effects of nitrogen deposition in global forest biomes.

Forest biome	Area (million ha)	Soil CH_4 flux rate (mg CH_4 m^{-2} h^{-1})	Biome CH_4 flux (Tg CH_4 yr^{-1})	Mean N deposition (kg N ha^{-1} yr^{-1})	Response ratio (g CH_4 kg^{-1} N)	Biome effect (Tg CH_4 yr^{-1})
Boreal	1225	-0.07 ± 0.02^{b}	-2.47 ± 0.68	1.2	-11.49 ± 7.94^{b}	-0.02 ± 0.01
Temperate	673	-0.04 ± 0.01^{ab}	-1.38 ± 0.45	7.3	4.89 ± 7.57^{ab}	0.02 ± 0.04
Subtropical and tropical	2118	-0.02 ± 0.00^{a}	-3.71 ± 0.56	8.3	10.39 ± 6.57^{a}	0.18 ± 0.12
Total	4016		-7.55 ± 1.68			0.18 ± 0.17

Note: The area of each biome (base year 2010) was derived from FAO Global Forest Resources Assessment (Keenan et al., 2015). Mean N deposition (base year 2010) of each forest biome was derived from Schwede et al. (2018). Different lowercase letters (e.g., a, b) mean significant difference of mean soil CH_4 flux between forest biomes ($P < .05$), and same letters mean no significant difference. The average response ratio of soil CH_4 flux to low-level N addition ($\leq$60 kg N ha^{-1} yr^{-1}, reasonably indicative to the effects of N deposition) were used to indicate the effect of N deposition.

3.2 Biome-specific effects of nitrogen additions on soil methane flux

Our results showed that the response of soil CH_4 flux to N addition varied across forest biomes, and the effect of low-level N addition ($\leq$60 kg N ha^{-1} yr^{-1}) on soil CH_4 flux was different from that of high-level N addition (>60 kg N ha^{-1} yr^{-1}) (Fig. 9.3). When both low and high-level were combined, N addition increased soil CH_4 uptake in boreal forest (-6.12 ± 5.99 g CH_4 kg^{-1} N), while it decreased soil CH_4 uptake in temperate forest (6.79 ± 5.31 g CH_4 kg^{-1} N) as well as subtropical and tropical (8.55 ± 3.27 g CH_4 kg^{-1} N) forests (Fig. 9.3a). The response of soil CH_4 flux to low-level N addition, being in the range of atmospheric N deposition, however, was -11.49 ± 7.94 g CH_4 kg^{-1} N in boreal forest, 4.89 ± 7.57 g CH_4 kg^{-1} N in temperate forest and 10.39 ± 6.57 g CH_4 kg^{-1} N in subtropical and tropical forests, respectively. The difference in response to low-level and high-level N additions was significant in boreal forest ($P = .04$), but insignificant in temperate ($P = .26$) as well as subtropical and tropical ($P = .31$) forests (Fig. 9.3b). Overall, these results indicate a necessity to distinguish among forest biomes and separately assess the effect of low-level N addition from that of high-level N addition in boreal forest. However, many previous meta-analyses did not differentiate the effect of low-level N deposition from that of high-level N addition (Liu and Greaver, 2009; Aronson and Helliker, 2010), which might have overestimated the negative effect of the natural N deposition on forest soil CH_4 sink.

Based on the average response ratio of soil CH_4 flux to low-level N addition ($\leq$60 kg N ha^{-1} yr^{-1}), the average N deposition (Schwede et al., 2018) and the area of each forest biome (Keenan et al., 2015), we roughly estimated the biome-scale effects of N deposition on soil CH_4 sink in global forests. Specifically, N deposition increased CH_4 uptake by 0.02 ± 0.01 Tg CH_4 yr^{-1} in boreal forest, while it decreased soil CH_4 uptake by 0.02 ± 0.04 and 0.18 ± 0.12 Tg CH_4 yr^{-1} in temperate as well as subtropical and tropical forests, respectively (Table 9.2). Since there is no significant difference of the response ratio between low and high-level N deposition for temperate forest and subtropical/tropical forests, we also estimated the biome-scale effects using mean response ratios for all N addition experiments, being 6.79 and 8.55 g CH_4 kg^{-1} N for temperate forest and subtropical/tropical forests, respectively.

Overall, N deposition was estimated to decrease soil CH_4 sink by 0.18 ± 0.17 Tg CH_4 yr^{-1} in global forests using the low N deposition responses (Table 9.2). The results showed that when the response ratios to low and high-level N additions were combined in the analysis, CH_4 uptake decreased by 0.03 ± 0.03 Tg CH_4 yr^{-1} in temperate forest and 0.15 ± 0.06 Tg CH_4 yr^{-1} in subtropical and tropical forests. The overall estimates of biome-scale effects, using the mean response ratios to all N additions, were thus slightly lower than those based on the response ratios to low-level N additions in global temperate, subtropical and tropical forests (0.18 ± 0.09 and 0.20 ± 0.16 Tg CH_4 yr^{-1}, respectively).

Comparison of the mean N deposition induced decrease in soil CH_4 sink of 0.18 Tg CH_4 yr^{-1} with the total soil CH_4 sink of 7.55 Tg CH_4 yr^{-1} in global forest (see Table 9.2) implies that this reduction is nearly negligible (2%). Considering that CH_4 is 29.8 times more effective, on a per-unit-mass basis, than CO_2 in absorbing long-wave radiation on a 100-year time horizon (Forster et al., 2021), the warming effect of N deposition induced reduction of soil CH_4 sink in global forest is equivalent to an emission of 4.68 Tg CO_2 yr^{-1}. This effect on climate warming is negligible in view of the large carbon sink (2.4 Pg C yr^{-1}) in global established forest (Pan et al., 2011).

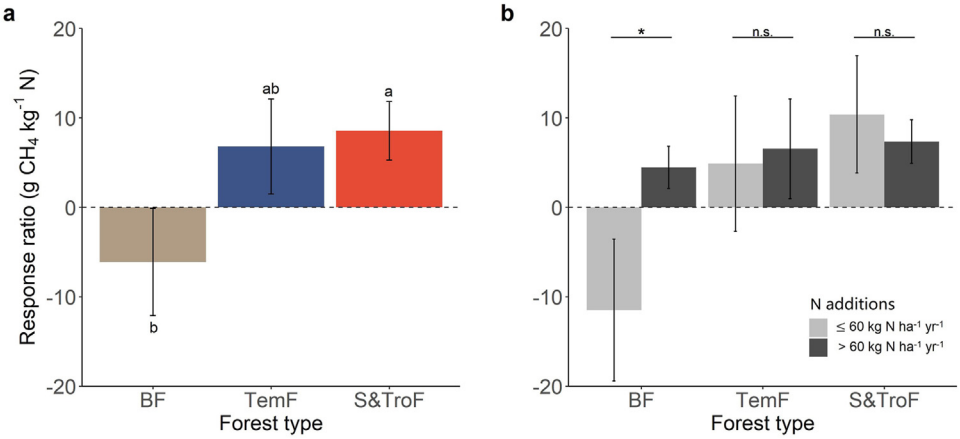

FIG. 9.3 Response ratios of soil CH_4 flux to all N additions (a), low-level ($\leq$60 kg N ha^{-1} yr^{-1}) and high-level N additions (>60 kg N ha^{-1} yr^{-1}) (b) in boreal (BF), temperate (TemF), and subtropical and tropical forests (S&TroF). Error bars are standard errors. Same lowercase letters mean no significant difference and different letters mean significant difference between forest biomes ($P < .05$). The asterisk (*) indicates a significant difference between low-level and high-level N additions ($P < .05$).

3.3 Main drivers of response ratio of soil methane flux to low-level nitrogen addition

The spatial variation in the response ratio of soil CH_4 flux to low-level N additions ($\leq$60 kg N ha^{-1} yr^{-1}), reasonably indicative to the effects of actual N deposition, was mainly explained by soil pH and N addition rate (Fig. 9.4a). Conditional regression analysis indicates that the response ratio increased with both higher soil pH (variance explained 17.3%, $P = .02$) (Fig. 9.4b) and N addition rate (variance explained 18.7%, $P = .01$) (Fig. 9.4c). Other factors, including experimental duration, N addition form, MAT, MAP, N deposition and forest type had an unimportant role in shaping the variation of the response ratio of soil CH_4 flux to N addition.

Soil pH plays an important role in the dynamics of soil CH_4 uptake because soil acidity directly affects the physiological functions of organisms, and determines the form and concentration of toxic elements and nutrients (Benstead and King, 2001). Aerobic CH_4 oxidation is mainly driven by methanotrophs in the topsoil (Le Mer and Roger, 2001), which are most active under low soil pH (Amaral et al., 1998b; Saari et al., 2004). Therefore, as soil pH increases, the activity of methanotrophs decreases, thereby inhibiting the absorption/oxidation of soil CH_4, and changing the response ratio from a negative to a positive value. In addition, soil pH can interact with ammonium inputs to affect the growth and activity of methanotrophs (Amaral et al., 1998a; King, 1997). Nitrification increases with an increase in soil pH, implying a decrease in NH_4 concentration (Dancer et al., 1973; Katyal et al., 1988). However, experimental studies indicate that the ammonium toxicity to soil CH_4 consumption does not vary substantially with pH in moderately acidic soils (pH < 5), but the ammonium toxicity increases with soil pH when pH > 5 (Benstead and King, 2001). This interaction may also account in part for the shift from positive to negative effects on soil CH_4 uptake with changes in soil pH (Fig. 9.4b).

Nitrogen addition rate also affected the spatial variation in the response ratio of soil CH_4 flux to N additions. Soil CH_4 uptake decreased with increasing N addition rate, resulting in response ratio shift from negative value to positive value, i.e., a nonlinear effect on soil CH_4 uptake (Fig. 9.4c). Low-level dosages of N addition may release the N limitation of methanotrophic microorganisms and thus increase soil CH_4 uptake in N-deficient conditions (Bodelier et al., 2000; Bodelier and Laanbroek, 2004; Reay and Nedwell, 2004). In contrast, excess N inputs may decrease soil CH_4 uptake via a direct inhibition of CH_4 oxidation due to increased soil inorganic N concentrations (Bodelier and Laanbroek, 2004; Schnell and King, 1994; Sitaula et al., 1995) and an indirect effect due to soil acidification and an imbalance of N and P (Veraart et al., 2015).

4. Uncertainties and implications

Uncertainties remain in our analysis of the effects of N deposition on soil CH_4 sink across global forest biomes. First, there were limited numbers of manipulated N addition experiments by using low-level dosage of inorganic N addition, especially in tropical forests. Our search of the literature only gave experimental results for six tropical forests at four sites. Moreover, the three low-level N addition trials that we excluded from our database were all carried out in an atypical tropical forest site (Martinson et al., 2020). Therefore, further efforts are needed to evaluate the effect of N deposition on soil CH_4 flux in tropical forests by conducting N addition experiments with low-level addition of inorganic N. The advantage of the N addition trials in tropical forests is, however, that they were carried out during a whole year. In contrast, the estimates of soil CH_4 uptake and its response to N addition ignored nongrowing season soil CH_4 flux in boreal and temperate

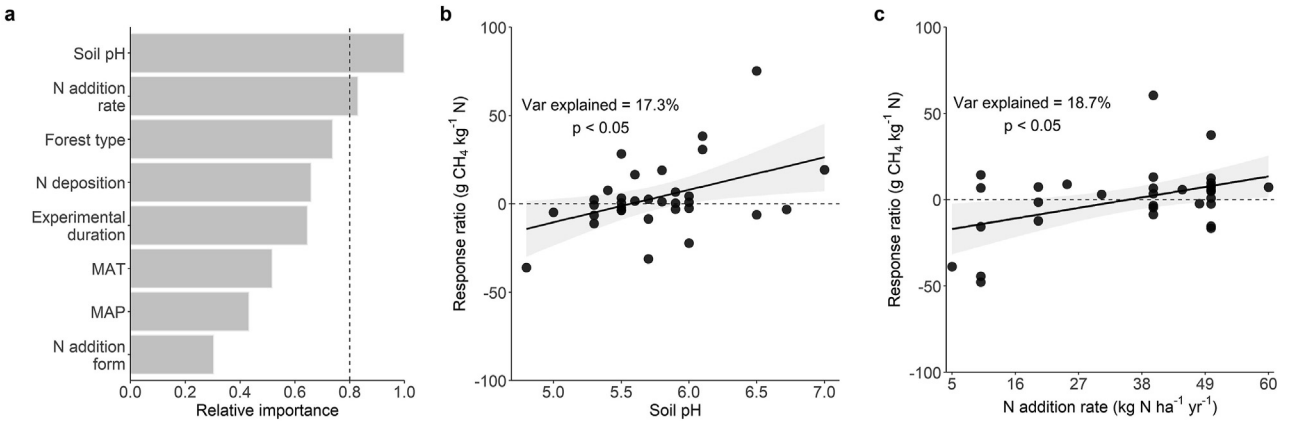

FIG. 9.4 The relative importance of potential drivers of the spatial variation in the response ratio of soil CH_4 flux to low-level N additions ($\leq$60 kg N ha^{-1} yr^{-1}) (a) and the conditional regression plots for soil pH (b) and N addition rate (c). The gray shadows represent 95% confidence intervals for the fitted curves.

forests. This likely underestimated the annual soil CH_4 flux in boreal and temperate forests. If the amount of soil CH_4 sink in nongrowing season is accounted, forest soils may contribute a higher proportion of global soil CH_4 sink, but it will not affect the estimated nearly negligible (2%) N induced impact on this sink.

A recent literature review indicates that the forest soil CH_4 sink in the northern hemisphere has significantly declined during the past three decades and this trend has been attributed to an increase of precipitation (Ni and Groffman, 2018). Our analysis implies that increasing N deposition in developing countries (e.g., China and India) (Abrol et al., 2017; Liu et al., 2013) may partially contribute to the reduction of the soil CH_4 sink. However, N deposition in Europe and the United States has shifted from an increase to a decrease since early or middle 1990s (Du, 2016; Waldner et al., 2014), implying a possible decrease in the effect on soil CH_4 sink since then.

The findings also have implications for improving the performance of process-based models to simulate and quantify the effect of global N deposition on soil CH_4 sinks. So far, the existing models simply account for a negative effect of N inputs on soil CH_4 uptake by involving an inhibition factor (Curry, 2007; Murguia-Flores et al., 2018; Ridgwell et al., 1999). However, our analysis indicates that N addition below a certain threshold level can exert a positive effect on soil CH_4 uptake in boreal forest, implying that existing models most likely overestimate the negative effect of N deposition on forest soil CH_4 sinks, especially in boreal regions. This indicates a necessity of models to separately consider the effect of low-level N addition from that of high-level N addition and distinguish the effects across forest biomes.

5. Conclusions and outlook

Our synthesis of experimental results indicates that soil CH_4 flux was significantly affected by N additions in global forest biomes. On a global scale, N deposition was estimated to induce a significant reduction of forest soil CH_4 sink, although it is negligible (2%) compared with the total soil CH_4 sink in global forest. In boreal forest, we found a shift from a positive to a negative effect on soil CH_4 uptake with increasing N addition, while N addition consistently decreased soil CH_4 uptake in temperate as well as subtropical and tropical forests.

Compared with previous assessments based on a meta-analysis approach (Liu and Greaver, 2009; Aronson and Helliker, 2010), our work improves current understanding of actual N deposition effect on soil CH_4 sinks in global forests. It shows that the response of soil CH_4 flux at low-level N additions increases with soil pH and N addition rate, confirming current insights that higher pH values and N availability may reduce soil CH_4 uptake by inhibiting the activity of methanotrophs and possibly increasing the toxicity of ammonium. Furthermore, the observed biome-specific effects of N deposition on soil CH_4 sinks confirms that the poleward increase in N limitation from tropical forest to boreal forest affects CH_4 oxidation.

Across all forest biomes, the effect of N deposition on soil CH_4 flux is poorly understood in tropical forest due to a lack of experimental studies. This leads to a major uncertainty in the overall effect of N deposition on soil CH_4 sink in global forest. To better understand future trend of soil CH_4 sink in global forest, more experimental and modeling efforts are needed to incorporate the effects of N deposition and other global changing factors.

Acknowledgments

This work was supported by the Fundamental Research Funds for the Central Universities, the National Natural Science Foundation of China (41877328) and State Key Laboratory of Earth Surface Processes and Resource Ecology (2021-TS-02).

References

Abrol, Y.P., Adhya, T.K., Aneja Raghuram, V.P.N., Pathak, H., Kulshrestha, U., Sharma, C., Singh, B. (Eds.), 2017. The Indian Nitrogen Assessment: Sources of Reactive Nitrogen, Environmental and Climate Effects, Management Options, and Policies. Elsevier B.V., Amsterdam, the Netherlands.

Amaral, J.A., Ekins, A., Richards, S.R., Knowles, R., 1998a. Effect of selected monoterpenes on methane oxidation, denitrification, and aerobic metabolism by bacteria in pure culture. Appl. Environ. Microbiol. 64 (2), 520–525.

Amaral, J.A., Ren, T., Knowles, R., 1998b. Atmospheric methane consumption by forest soils and extracted bacteria at different pH values. Appl. Environ. Microbiol. 64 (7), 2397–2402.

Ambus, P., Robertson, G.P., 2006. The effect of increased N deposition on nitrous oxide, methane and carbon dioxide fluxes from unmanaged forest and grassland communities in Michigan. Biogeochemistry 79 (3), 315–337.

Aronson, E., Helliker, B., 2010. Methane flux in non-wetland soils in response to nitrogen addition: a meta-analysis. Ecology 91 (11), 3242–3251.

Aronson, E.L., Vann, D.R., Helliker, B.R., 2012. Methane flux response to nitrogen amendment in an upland pine forest soil and riparian zone. J. Geophys. Res-Biogeo. 117, G03012.

Benstead, J., King, G.M., 2001. The effect of soil acidification on atmospheric methane uptake by a Maine forest soil. FEMS Microbiol. Ecol. 34 (3), 207–212.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. 20, 30–59.

Bodelier, P.L., Roslev, P., Henckel, T., Frenzel, P., 2000. Stimulation by ammoniumbased fertilizers of methane oxidation in soil around rice roots. Nature 403 (6768), 421–424.

Bodelier, P.L., Laanbroek, H.J., 2004. Nitrogen as a regulatory factor of methane oxidation in soils and sediments. FEMS Microbiol. Ecol. 47 (3), 265–277.

Bodelier, P.L., Steenbergh, A.K., 2014. Interactions between methane and the nitrogen cycle in light of climate change. Curr. Opin. Environ. Sustain. 9, 26–36.

Boeckx, P., Van Cleemput, O., Villaralvo, I., 1997. Methane oxidation in soils with different textures and land use. Nutrient Cycl. Agroecosyst. 49 (1), 91–95.

Bowman, W.D., Cleveland, C.C., Halada, Ľ., Hreško, J., Baron, J.S., 2008. Negative impact of nitrogen deposition on soil buffering capacity. Nat. Geosci. 1 (11), 767–770.

Borenstein, M., Hedges, L.V., Higgins, J.P., Rothstein, H.R., 2009. Introduction to Meta-Analysis. John Wiley and Sons, West Sussex, UK.

Borken, W., Davidson, E.A., Savage, K., Sundquist, E.T., Steudler, P., 2006. Effect of summer throughfall exclusion, summer drought, and winter snow cover on methane fluxes in a temperate forest soil. Soil Biol. Biochem. 38 (6), 1388–1395.

Bosse, U., Frenzel, P., 1997. Activity and distribution of methane-oxidizing bacteria in flooded rice soil microcosms and in rice plants (*Oryza sativa*). Appl. Environ. Microbiol. 63 (4), 1199–1207.

Breheny, P., Burchett, W., 2013. Visualization of regression models using *visreg*. R J 9, 56–71.

Calcagno, V., de Mazancourt, C., 2010. *glmulti*: an R package for easy automated model selection with (generalized) linear models. J. Stat. Softw. 34 (12), 1–29.

Castro, M.S., Steudler, P.A., Melillo, J.M., Aber, J.D., Bowden, R.D., 1995. Factors controlling atmospheric methane consumption by temperate forest soils. Global Biogeochem. Cy. 9 (1), 1–10.

Chan, A.S., Steudler, P.A., Bowden, R.D., Gulledge, J., Cavanaugh, C.M., 2005. Consequences of nitrogen fertilization on soil methane consumption in a productive temperate deciduous forest. Biol. Fert. Soils 41 (3), 182–189.

Curry, C.L., 2007. Modeling the soil consumption of atmospheric methane at the global scale. Global Biogeochem. Cy. 21, GB4012.

Dancer, W.S., Peterson, L.A., Chesters, G., 1973. Ammonification and nitrification of N as influenced by soil pH and previous N treatments. Soil Sci. Soc. Am. Proc. 37 (1), 67–69.

de Vries, W., Kros, J., Reinds, G.J., Butterbach-Bahl, K., 2011. Quantifying impacts of nitrogen use in European agriculture on global warming potential. Curr. Opin. Environ. Sustain. 3 (5), 291–302.

de Vries, W., Du, E., Butterbach Bahl, K., Schulte-Uebbing, L., Dentener, F., 2017. Global-scale impact of human nitrogen fixation on greenhouse gas emissions. In: Oxford Research Encyclopedia of Environmental Science. Oxford University Press, USA.

Dlugokencky, E.J., Nisbet, E.G., Fisher, R., Lowry, D., 2011. Global atmospheric methane: budget, changes and dangers. Philos. T. R. Soc. A. 369 (1943), 2058–2072.

Du, E., 2016. Rise and fall of nitrogen deposition in the United States. P Natl. Acad. Sci. U. S. A. 113 (26), E3594–E3595.

Du, E., de Vries, W., 2018. Nitrogen-induced new net primary production and carbon sequestration in global forests. Environ. Pollut. 242 (PT.B), 1476–1487.

Du, E., Fenn, M.E., de Vries, W., Ok, Y.S., 2019. Atmospheric nitrogen deposition to global forests: status, impacts and management options. Environ. Pollut. 250, 1044–1048.

Du, E., Lu, X., Tian, D., Mao, Q., Jing, X., Wang, C., Xia, N., 2020a. Impacts of nitrogen deposition on forest ecosystems in China. In: Atmospheric Reactive Nitrogen in China. Springer, Singapore, pp. 185–213.

Du, E., Terrer, C., Pellegrini, A.F., Ahlström, A., van Lissa, C.J., Zhao, X., Xia, N., Wu, X.H., Jackson, R.B., 2020b. Global patterns of terrestrial nitrogen and phosphorus limitation. Nat. Geosci. 13 (3), 221–226.

Du, E., Xia, N., Guo, Y., Tian, Y., Li, B., Liu, X., de Vries, W., 2022. Ecological effects of nitrogen deposition on urban forests: An overview. Front. Agric. Sci. Eng. 9 (3), 445–456.

Dunfield, P., Dumont, R., Moore, T.R., 1993. Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biol. Biochem. 25 (3), 321–326.

Dutaur, L., Verchot, L.V., 2007. A global inventory of the soil CH_4 sink. Global Biogeochem. Cy. 21 (4), GB4013.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10 (12), 1135–1142.

Forster, P., Storelvmo, T., Armour, K., Collins, W., Dufresne, J.-L., Frame, D., Lunt, D.J., Mauritsen, T., Palmer, M.D., Watanabe, M., Wild, M., Zhang, H., 2021. The earth's energy budget, climate feedbacks, and climate sensitivity. In: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Gao, W., Cheng, S., Fang, H., Chen, Y., Wang, Y., Zhang, P., Xu, M., 2013. Early responses of soil CH_4 uptake to increased atmospheric nitrogen deposition in a cold-temperate coniferous forest. Acta Ecol. Sin. 33 (23), 7505–7515.

Gao, W., Yang, H., Li, S., Kou, L., 2017. Responses of soil CO_2, CH_4 and N_2O fluxes to N, P, and acid additions in mixed forest in subtropical China. J. Res. Ecol. 8 (2), 154–164.

Geng, J., Cheng, S., Fang, H., Yu, G., Li, X., Si, G., He, S., Yu, G., 2017. Soil nitrate accumulation explains the nonlinear responses of soil CO_2 and CH_4 fluxes to nitrogen addition in a temperate needle-broadleaved mixed forest. Ecol. Indicat. 79, 28–36.

Gilliam, F.S., 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. J. Ecol. 94 (6), 1176–1191.

Groemping, U., 2006. Relative importance for linear regression in R: the package *relaimpo*. J. Stat. Softw. 17 (1), 925–933.

Gulledge, J., Schimel, J.P., 2000. Controls on soil carbon dioxide and methane fluxes in a variety of taiga forest stands in interior Alaska. Ecosystems 3 (3), 269–282.

He, S., 2019. Effect of Nitrogen Input on Soil Methane Uptake in Moso Bamboo (Phyllostachys Edulis) Forest. Master's thesis. Zhejiang Agriculture and Forestry University, China.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A., 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.

Hu, Z., Zhang, H., Chen, S., Li, Q., Li, H., Shen, S., 2011. Effects of simulated nitrogen deposition on N_2O and CH_4 fluxes of soil in forest belt. China Environ. Sci. 31 (6), 892–897.

Hütsch, B.W., Webster, C.P., Powlson, D.S., 1994. Methane oxidation in soil as affected by land use, soil pH and N fertilization. Soil Biol. Biochem. 26 (12), 1613–1622.

Katyal, J.C., Carter, M.F., Vlek, P., 1988. Nitrification activity in submerged soils and its relation to denitrification loss. Biol. Fertil. Soil. 7 (1), 16–22.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: results from the FAO global forest Resources assessment 2015. For. Ecol. Manag. 352, 9–20.

Kim, Y.S., Imori, M., Watanabe, M., Hatano, R., Yi, M.J., Koike, T., 2012. Simulated nitrogen inputs influence methane and nitrous oxide fluxes from a young larch plantation in northern Japan. Atmos. Environ. 46, 36–44.

King, G., 1997. Responses of atmospheric methane consumption by soils to global climate change. Global Change Biol. 3 (4), 351–362.

Kirschke, S., Bousquet, P., Ciais, P., Saunois, M., Canadell, J.G., Dlugokencky, E.J., Bergamaschi, P., Bergmann, D., Blake, D.R., Bruhwiler, L., Cameron-Smith, P., Castaldi, S., Chevallier, F., Feng, L., Fraser, A., Heimann, M., Hodson, E.L., Houweling, S., Josse, B., Fraser, P.J., Krummel, P.B., Lamarque, J.-F., Langenfelds, R.L., Quéré, C.L., Naik, V., O'Doherty, S., Palmer, P.L., Pison, I., Plummer, D., Poulter, B., Prinn, R.G., Rigby, M., Ringeval, B., Santini, M., Schmidt, M., Shindell, D.T., Simpson, I.J., Spahni, R., Steele, L.P., Strode, S.A., Sudo, K., Szopa, S., van der Werf, G.R., Voulgarakis, A., van Weele, M., Weiss, R.F., Williams, J.E., Zeng, G., 2013. Three decades of global methane sources and sinks. Nat. Geosci. 6, 813–823.

Lamarque, J.F., Dentener, F., McConnell, J., Ro, C.-U., Shaw, M., Vet, R., Bergmann, D., Cameron-Smith, P., Dalsoren, S., Doherty, R., Faluvegi, G., Ghan, S.J., Josse, B., Lee, Y.H., MacKenzie, I.A., Plummer, D., Shindell, D.T., Skeie, R.B., Stevenson, D.S., Strode, S., Zeng, G., Curran, M., Dahl-Jensen, D., Das, S., Fritzsche, D., Nolan, M., 2013. Multi-model mean nitrogen and sulfur deposition from the AtmosphericChemistry and Climate Model Intercomparison Project (ACCMIP): evaluation ofhistorical and projected future changes. Atmos. Chem. Phys. 13 (16), 7997–8018.

Le Mer, J., Roger, P., 2001. Production, oxidation, emission and consumption of methane by soils: a review. Eur. J. Soil Biol. 37 (1), 25–50.

Li, X., Cheng, S., Fang, H., Yu, G., Dang, X., Xu, M., Wang, L., Si, G., Geng, J., He, S., 2015. The contrasting effects of deposited NH_4^+ and NO_3^- on soil CO_2, CH_4 and N_2O fluxes in a subtropical plantation, southern China. Ecol. Eng. 85, 317–327.

Liu, L.L., Greaver, T.L., 2009. A review of nitrogen enrichment effects on three biogenic GHGs: the CO_2 sink may be largely offset by stimulated N_2O and CH_4 emission. Ecol. Lett. 12 (10), 1103–1117.

Liu, X., Zhang, Y., Han, W., Tang, A., Shen, J., Cui, Z., Vitousek, P., Erisman, J., Goulding, K., Christie, P., Fangmeier, A., Zhang, F., 2013. Enhanced nitrogen deposition over China. Nature 494 (7438), 459–462.

Maljanen, M., Jokinen, H., Saari, A., Strömmer, R., Martikainen, P.J., 2006. Methane and nitrous oxide fluxes, and carbon dioxide production in boreal forest soil fertilized with wood ash and nitrogen. Soil Use Manag. 22 (2), 151–157.

Martinson, G.O., Müller, A.K., Matson, A.L., Corre, M.D., Veldkamp, E., 2020. Nitrogen and phosphorus control soil methane uptake in tropical montane forests. J. Geophys. Res-Biogeo. 126 (8), G005970.

Midolo, G., Alkemade, R., Schipper, A.M., Benítez-López, A., Perring, M.P., de Vries, W., 2019. Impacts of nitrogen addition on plant species richness and abundance: a global meta-analysis. Global Ecol. Biogeogr. 28 (3), 398–413.

Mori, T., Imai, N., Yokoyama, D., Mukai, M., Kitayama, K., 2017. Effects of selective logging and application of phosphorus and nitrogen on fluxes of CO_2, CH_4 and N_2O in lowland tropical rainforests of Borneo. J. Trop. For. Sci. 29 (2), 248–256.

Murguia-Flores, F., Arndt, S., Ganesan, A.L., Murray-Tortarolo, G., Hornibrook, E.R., 2018. Soil Methanotrophy Model (MeMo v1. 0): a process-based model to quantify global uptake of atmospheric methane by soil. Geosci. Model Dev. (GMD) 11 (6), 2009–2032.

Ni, X., Groffman, P.M., 2018. Declines in methane uptake in forest soils. P. Natl. Acad. Sci. U. S. A. 115 (34), 8587–8590.

Pan, D.R., 2013. Study on Greenhouse Gas Emission for Grassland Soil below Different Forest Soils under Precipitation Reduction and Nitrogen Deposition in Shennongjia Mountain. Master's thesis. Gansu Agricultural University, China.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Lewis, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333 (6045), 988–993.

Piao, S., Friedlingstein, P., Ciais, P., Viovy, N., Demarty, J., 2007. Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. Global Biogeochem. Cy. 21 (3), GB3018.

Reay, D.S., Nedwell, D.B., 2004. Methane oxidation in temperate soils: effects of inorganic N. Soil Biol. Biochem. 36 (12), 2059–2065.

Ridgwell, A.J., Marshall, S.J., Gregson, K., 1999. Consumption of atmospheric methane by soils: a process-based model. Global Biogeochem. Cy. 13 (1), 59–70.

Rodhe, H., 1990. A comparison of the contribution of various gases to the greenhouse effect. Science 248 (4960), 1217–1219.

Saari, A., Rinnan, R., Martikainen, P.J., 2004. Methane oxidation in boreal forest soils: kinetics and sensitivity to pH and ammonium. Soil Biol. Biochem. 36 (7), 1037–1046.

Schnell, S., King, G.M., 1994. Mechanistic analysis of ammonium inhibition of atmospheric methane consumption in forest soils. Appl. Environ. Microbiol. 60 (10), 3514–3521.

Schulte-Uebbing, L., de Vries, W., 2018. Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate, and boreal forests: a meta-analysis. Global Change Biol. 24 (2), 416–431.

Schwede, D.B., Simpson, D., Tan, J., Fu, J.S., Dentener, F., Du, E., deVries, W., 2018. Spatial variation of modelled total, dry and wet nitrogen deposition to forests at global scale. Environ. Pollut. 243 (PT.B), 1287–1301.

Sitaula, B.K., Bakken, L.R., Abrahamsen, G., 1995. CH_4 uptake by temperate forest soil: effect of N input and soil acidification. Soil Biol. Biochem. 27 (7), 871–880.

Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J., Rey, A., 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. Eur. J. Soil Sci. 54 (4), 779–791.

Song, L., Tian, P., Zhang, J., Jin, G., 2017. Effects of three years of simulated nitrogen deposition on soil nitrogen dynamics and greenhouse gas emissions in a Korean pine plantation of northeast China. Sci. Total Environ. 609, 1303–1311.

Sonnleitner, M.A., Günthardt-Goerg, M.S., Bucher-Wallin, I.K., Attinger, W., Reis, S., Schulin, R., 2001. Influence of soil type on the effects of elevated atmospheric CO_2 and N deposition on the water balance and growth of a young spruce and beech forest. Water Air Soil Pollut. 126 (3), 271−290.

Tan, J., Fu, J.S., Dentener, F., Sun, J., Emmons, L., Tilmes, S., Sudo, K., Flemming, J., Eiof, J.J., Gravel, S., Bian, H., Davila, Y., Henze, D.K., Lund, M.T., Kucsera, T., Takemura, T., Keating, T., 2018. Multi-model study of HTAP II on sulfur and nitrogen deposition. Atmos. Chem. Phys. 18, 6847−6866.

Thauer, R.K., Kaster, A.K., Seedorf, H., Buckel, W., Hedderich, R., 2008. Methanogenic archaea: ecologically relevant differences in energy conservation. Nat. Rev. Microbiol. 6 (8), 579−591.

Veraart, A.J., Steenbergh, A.K., Ho, A., Kim, S.Y., Bodelier, P.L.E., 2015. Beyond nitrogen: the importance of phosphorus for CH_4 oxidation in soils and sediments. Geoderma 259, 337−346.

Veldkamp, E., Koehler, B., Corre, M.D., 2013. Indications of nitrogen-limited methane uptake in tropical forest soils. Biogeosciences 10 (8), 5367−5379.

Vet, R., Artz, R.S., Carou, S., Shaw, M., Ro, C.U., Aas, W., Baker, A., Bowersox, V.C., Dentener, F., Galy-Lacaux, C., Hou, A., Pienaar, J.J., Gillett, R., Forti, M.C., Gromov, S., Hara, H., Khodzher, T., Mahowald, N.M., Nickovic, S., Rao, P.S.P., Reid, N.W., 2014. A global assessment of precipitation chemistry and deposition of sulfur, nitrogen, sea salt, base cations, organic acids, acidity and pH, and phosphorus. Atmos. Environ. 93, 3−100.

Waldner, P., Marchetto, A., Thimonier, A., Schmitt, M., Rogora, M., Granke, O., Mues, V., Hansen, K., Karlsson, G.P., Zlindra, D., Clarke, N., Verstraeten, A., Lazdins, A., Schimming, C., Iacoban, C., Lindroos, A.J., Vanguelova, E., Benham, S., Meesenburg, H., Nicolas, M., Kowalska, A., Apuhtin, V., Napa, U., Lachmanova, J., Kristoefel, F., Bleeker, A., Ingerslev, M., Vesterdal, L., Molina, J., Fischer, U., Seidling, W., Jonard, M., O'Dea, P., Johnson, J., Fischer, R., Lorenz, M., 2014. Detection of temporal trends in atmospheric deposition of inorganic nitrogen and sulphate to forests in Europe. Atmos. Environ. 95, 363−374.

Wang, R., 2012. Effects of Simulated Atmospheric Nitrogen Deposition on the Exchange Fluxes of Greenhouse Gases in the Temperate Forest Soil. Master's thesis. Beijing Forestry University, China.

Weslien, P., Kasimir Klemedtsson, Å., Börjesson, G., Klemedtsson, L., 2009. Strong pH influence on N_2O and CH_4 fluxes from forested organic soils. Eur. J. Soil Sci. 60 (3), 311−320.

Wu, D., 2018. Effects of N Deposition on Soil Microbial Community Structure and Greenhouse Gas Fluxes in a Natural *Castanopsis carlesii* Forest. Master's thesis, Fujian Normal University, China.

Xia, N., Du, E., Wu, X., Tang, Y., Wang, Y., de Vries, W., 2020. Effects of nitrogen addition on soil methane uptake in global forest biomes. Environ. Pollut. 264, 114751.

Xu, M., Cheng, S., Fang, H., Yu, G., Gao, W., Wang, Y., Dang, X., Li, L., 2014. Low-level nitrogen addition promotes net methane uptake in a boreal forest across the Great Xing'an Mountain Region, China. For. Sci. 60 (5), 973−981.

Xu, X., Han, L., Luo, X., Han, S., 2011. Synergistic effects of nitrogen amendments and ethylene on atmospheric methane uptake under a temperate old-growth forest. Adv. Atmos. Sci. 28 (4), 843−854.

Yan, G., Xing, Y., Wang, M., Wang, J., Han, S., Wang, Q., 2016a. Effects of nitrogen deposition on CH_4 uptake and CO_2 emission from temperate forests in Northeastern China. In: International Conference on Sustainable Energy and Environmental Engineering. Atlantis Press, Paris, pp. 323−335.

Yan, G., Xing, Y., Wang, M., Wang, J., Han, S., Wang, Q., 2016b. Response of CH_4 and CO_2 fluxes to simulated nitrogen deposition in a boreal forest in the Northeastern China. In: International Conference on Civil, Structure and Environmental Engineering. Atlantis Press, Paris, pp. 127−137.

Yu, H., Chen, Y., Zhang, H., Zhou, Z., 2019. The effect of inorganic nitrogen addition on soil nitrogen and greenhouse gas flux for the *Pinus tabulaeformis* forest in Taiyue Mountain, Shanxi Province. J. Nanjing For. Univ. (Nat. Sci. Ed.) 43 (3), 85−91.

Zhang, K., Zheng, H., Chen, F., Li, R., Yang, M., Ouyang, Z., Lan, L., Xiang, X., 2017. Impact of nitrogen fertilization on soil-atmosphere greenhouse gas exchanges in eucalypt plantations with different soil characteristics in southern China. PLoS One 12 (2), e0172142.

Zhang, L., 2013. Response of Greenhouse Gas Fluxes to the Addition of Nitrogen and Phosphorous in Subtropical Fir Forest. Master's thesis. Southwest University, China.

Zhang, W., Mo, J., Zhou, G., Gundersen, P., Fang, Y., Lu, X., Zhang, T., Dong, S., 2008. Methane uptake responses to nitrogen deposition in three tropical forests in southern China. J. Geophys. Res. Atmos. 113, D11116.

Zhang, W., Zhu, X., Liu, L., Fu, S., Chen, H., Huang, J., Lu, X., Liu, Z., Mo, J., 2012. Large difference of inhibitive effect of nitrogen deposition on soil methane oxidation between plantations with N-fixing tree species and non-N-fixing tree species. J. Geophys. Res-Biogeo. 117, G00N16.

Zhang, T., Zhu, W., Mo, J., Liu, L., Dong, S., 2011. Increased phosphorus availability mitigates the inhibition of nitrogen deposition on CH_4 uptake in an old-growth tropical forest, southern China. Biogeosciences 8 (9), 2805−2813.

Zheng, M., Zhang, T., Liu, L., Zhang, W., Lu, X., Mo, J., 2016. Effects of nitrogen and phosphorus additions on soil methane uptake in disturbed forests. J. Geophys. Res-Biogeo 121 (12), 3089−3100.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Method. Ecol. Evol. 1 (1), 3−14.