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Comparing the variations and influencing factors of CH_4 emissions from paddies and wetlands under CO_2 enrichment: A data synthesis in the last three decades

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A R T I C L E I N F O

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A B S T R A C T

Understanding and quantifying the impact of elevated tropospheric carbon dioxide concentration (e [CO_2]) on methane (CH_4) globally is important for effectively assessing and mitigating climate warming. Paddies and wetlands are the two important sources of CH_4 emissions. Yet, a quantitative synthetic investigation of the effects of e [CO_2] on CH_4 emissions from paddies and wetlands on a global scale has not been conducted. Here, we conducted a meta-analysis of 488 observation cases from 40 studies to assess the long-term effects of e [CO_2] (ambient [CO_2]+ 53–400 μmol mol^{-1}) on CH_4 emissions and to identify the relevant key drivers. On aggregate, e [CO_2] increased CH_4 emissions by 25.7% ($p < 0.05$) from paddies but did not affect CH_4 emissions from wetlands (−3.29%; $p > 0.05$). The e [CO_2] effects on paddy CH_4 emissions were positively related to that on belowground biomass and soil-dissolved CH_4 content. However, these factors under e [CO_2] resulted in no significant change in CH_4 emissions in wetlands. Particularly, the e [CO_2]-induced abundance of methanogens increased in paddies but decreased in wetlands. In addition, tillering number of rice and water table levels affected e [CO_2]-induced CH_4 emissions in paddies and wetlands, respectively. On a global scale, CH_4 emissions changed from an increase (+0.13 and + 0.86 Pg CO_2-eq yr^{-1}) under short-term e [CO_2] into a decrease and no changes (−0.22 and + 0.03 Pg CO_2-eq yr^{-1}) under long-term e [CO_2] in paddies and wetlands, respectively. This suggested that e [CO_2]-induced CH_4 emissions from paddies and wetlands changed over time. Our results not only shed light on the different stimulative responses of CH_4 emissions to e [CO_2] from paddy and wetland ecosystems but also suggest that estimates of e [CO_2]-induced CH_4 emissions from global paddies and wetlands need to account for long-term changes in various regions.

1. Introduction

Most likely due to extensive human activities, tropospheric carbon dioxide concentrations ([CO_2]) have risen from the pre-industrial level of 280 μmol mol^{-1} to the current level of 420 μmol mol^{-1} (NOAA, 2022). It's predicted that future CO_2 concentration would increase to between 600 μmol mol^{-1} (SSP2−4.5) and 1080 μmol mol^{-1} (SSP5−8.5) over the next century (IPCC). Such changes may lead to an increase in net primary productivity and also in decomposition rates of soil carbon in various ecosystems (forest, grassland, wetland, tundra, cropland,

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etc.), indirectly affecting greenhouse gases (GHGs, e.g., methane (CH_4) and nitrous oxide (N_2O)) emissions (Abbasi and Mueller, 2011; Bridgman et al., 2020; Oechel and Vourlitis, 1994; Phillips et al., 2001; Xia et al., 2020; Yun et al., 2012; Zhu et al., 2022). CH_4 is the second-most powerful GHGs after CO_2, contributing 18% to global warming (IPCC). Based on a top-down approach, it has been estimated that global CH_4 emissions in the last decade were about 572 Tg CH_4 yr^{-1}, of which 219 Tg CH_4 yr^{-1} (38%) and 215 Tg CH_4 yr^{-1} (38%) were attributed to agricultural sources and natural wetlands, respectively (Saunois et al., 2020). Paddies and wetlands are the largest agricultural and natural CH_4 sources, respectively, accounting for about 7–11% of total anthropogenic emissions and 21−74% of global natural emissions (Saunois et al., 2020). Therefore, the feedback of CH_4 emissions from paddies and wetlands to elevated CO_2 concentration (e [CO_2]) plays a critical role in future climate change.

CH_4 production from methanogens and CH_4 oxidation from methanotrophs decide CH_4 emissions from paddies and wetlands (Conrad, 2007; Lin et al., 2021). e [CO_2] generally stimulates paddy and wetland CH_4 emissions by the promotion of plant photosynthesis (Liu et al., 2018; Zheng et al., 2006), which can provide more methanogenic substrates and increase the abundance of methanogenic in soils (Dacey et al., 1994; Megonigal and Schlesinger, 1997; Qian et al., 2020). However, a few studies have shown that e [CO_2] could inhibit CH_4 emissions from paddies and wetlands due to the decrease in belowground biomass and dissolved CH_4 contents induced by e [CO_2] (Bridgman et al., 2020; Lin et al., 2021; Schrope et al., 1999; Yu et al., 2022c). For instance, recent studies showed that this inhibitory effect of e [CO_2] on CH_4 emissions was closely related to the improvement of plant root oxygen (O_2) secretion capacity and the increase of methanotrophs abundance under e [CO_2] (Yu et al., 2022b, 2022c). Furthermore, Yu et al. (2022c) also found that e [CO_2] did not necessarily enhance CH_4 emissions from paddies, and the effect of e [CO_2] on paddy CH_4 emissions might change over time. In their study, they used meta-analysis to show that the effects of long-term e [CO_2] on the abundance of methanogens and methanotrophs varied with time series, which was one of the important reasons for the differences in promoting and attenuating mechanisms between short- and long-term e [CO_2] on CH_4 emissions. However, the universality of this phenomenon has yet to be tested. Thus, accurate assessments of variations of CH_4 emissions from paddies and wetlands under long-term e [CO_2] are urgently required.

The vast majority of the world's rice is grown in flooded paddies (Bhattacharyya et al., 2017; Malyan et al., 2016), where the aerobic decomposition of organic matter such as rice root secretions and residual roots would gradually soil deplete most O_2, resulting in anoxic conditions and CH_4 production (Schrope et al., 1999; Yu et al., 2022b). Meanwhile, as productive man-made wetlands, paddies are greatly affected by human management practices, which would inevitably lead to differences in CH_4 emissions between them and natural wetlands (Qin et al., 2015; Xia et al., 2016). For instance, fertilization, straw incorporation, water regime and rice cultivar can affect the production, oxidation, and transport of CH_4 in paddies by mediating the abundance, structure, and activity of related microorganisms (Xia et al., 2014; Yu et al., 2022a). Recently, Yu et al. (2022c) found that the stimulatory effect of long-term e [CO_2] on CH_4 emissions from paddies was diminished because methanogenic substrates were less stimulated by long-term e [CO_2]. This indicates that the response of CH_4 emissions to long-term e [CO_2] in paddies is likely to have a large spatiotemporal variability. However, despite there having been many reports on e [CO_2]-induced CH_4 emissions in paddies and the influencing factors, a comprehensive understanding of their time scale responses is still lacking.

In wetland soils, persistent high water table levels limit O_2 availability, which creates a suitable redox condition for CH_4 production (Lin et al., 2021; Vann and Megonigal, 2003). However, CH_4 fluxes from wetlands are generally lower than that from paddies (Qin et al., 2015). Two mechanisms could explain the relatively low emissions from wetlands: (i) the produced CH_4 can be continuously oxidized in the process of transmission with higher water levels in most wetlands, except marsh wetlands (Qin et al., 2015; Saarnio et al., 2009); (ii) higher water table levels and fewer wetland plants weaken CH_4 transport capacity, leading to reduced CH_4 emissions (Mueller et al., 2020). For these reasons, hydrological characteristics, unlike paddies, are considered to be the key factors mediating plant community structure and carbon cycling in wetlands (Lin et al., 2021). Furthermore, previous studies reported that e [CO_2] had positive (Kao-Kniffin et al., 2011; Vann and Megonigal, 2003), negative (Bridgman et al., 2020; Lin et al., 2021), or even no effect (Silvola et al., 2003) on CH_4 emissions in wetlands, possibly because the key influencing factors were not consistent. For instance, plant parameters, wetland types, and water table levels could affect the response of e [CO_2] to CH_4 emissions (Bridgman et al., 2020; Lin et al., 2021). However, few studies have explored the specific key drivers. Therefore, it is necessary to systematically and comprehensively compare the responses of CH_4 emissions from paddies and wetlands and their influencing factors to e [CO_2], which is of great significance for proposing effective emission reduction measures to cope with severe global climate change.

Here, we synthesized the results of 40 studies (25 for paddies and 15 for wetlands; Table S1) in the last three decades. Three hypotheses were tested in this study: (i) on average, e [CO_2] (ambient [CO_2] (a [CO_2]) + 53–400 μmol mol^{-1}) increases CH_4 emissions from paddies and wetlands, which is associated with the increased substrates of CH_4 production in paddies and wetlands because of e [CO_2]; (ii) the main controlling factors of CH_4 emissions as affected by e [CO_2] probably are different between paddies and wetlands; and (iii) under long-term e [CO_2], the promoting effects of CH_4 emission in paddies and wetlands gradually are weakened. Therefore, this study will provide a scientific reference for the accurate assessment of the variations and influencing factors of CH_4 emissions from paddies and wetlands under long-term e [CO_2].

2. Materials and methods

2.1. Literature search and data collection

We used the Web of Science (http://apps.webofknowledge.com/) and China National Knowledge Infrastructure (CNKI) (http://www.cnki.net/) to search for peer-reviewed publications before June 30, 2022. The search terms "e [CO_2]" and "CH_4 emissions" and "paddies OR wetlands" were used for data collection. The following criteria were adopted to select appropriate articles: (i) observations of CH_4 emissions and the influence factors from paddies or wetlands under both a [CO_2] and e [CO_2] must be included; (ii) the accumulation of CH_4 emissions must be measured in paddies or wetlands, or total CH_4 emissions must be calculated by CH_4 fluxes during the growing season; (iii) field management measures in paddies (e.g. nitrogen (N) application rate, straw incorporation, water regime, and rice cultivar) and other influencing factors must be reported; (iv) information on the wetland subclasses, water table levels, and environmental factor in wetlands must be collected. It should be noted that the duration of e [CO_2] was also artificially divided, that was, if e [CO_2] durations were less than 5 yrs, they had short-term e [CO_2] effects, and if e [CO_2] durations were more than 10 yrs, they had long-term e [CO_2] effects. In addition, the influencing factors of e [CO_2]-induced CH_4 emissions in the literature selection criteria included plant parameters (aboveground biomass and belowground biomass), soil physicochemical properties (soil redox potential, dissolved organic carbon, mean annual temperature, etc.), and key functional microorganisms (methanogens and methanotrophs). Based on these criteria, 488 observations from 40 studies were included in our meta-analysis (Table S1). The global distribution of research sites involved in this study was shown in Fig. S1.

2.2. Meta-analysis

In this meta-analysis, we calculated the natural logarithm of the response ratio (ln$R$) to evaluate e [CO_2]-induced CH_4 emissions from paddies and wetlands in each paired experiment (Hedges et al., 1999):

$$\ln R = \ln(X_e / X_a) = \ln X_e - \ln X_a \tag{1}$$

where X_e and X_a represent CH_4 emissions under e [CO_2] and a [CO_2], respectively.

For some observations in the dataset provided herein, there are no standard deviation values in the compiled studies. Therefore, we adopted a function of the sample size to weigh effects sizes (Xia et al., 2017):

$$w = (N_e \times N_a) / (N_e + N_a) \tag{2}$$

where w represents the weight of each ln$R$ of observations, and N_e and N_a represent the number of replicates of CH_4 emissions from paddies or wetlands under e [CO_2] and a [CO_2], respectively.

The weighted mean effect size (ln$R$++) and 95% confidence intervals (95%*CIs*) were generated by a bootstrapping procedure with 4999 iterations, using MetaWin 2.0. Between-group heterogeneity tests (Q tests) were performed to determine the differential e [CO_2]-induced CH_4 emissions in the different groups (Tables S2 and S3). A significant p-value (<0.05) indicated that the responses differed among groups. A Gaussian distribution function was applied to feet the frequency of ln$R$s, and we found that the ln$R$s for the above variables were homogeneous (Fig. S2). If 95%*CIs* did not overlap with zero, the percentage changes (*PC*) in the variables under e [CO_2] were assumed to represent a significant increase (>zero) or decrease (<zero) compared with the residue removed ($p < 0.05$) (Xia et al., 2021):

$$PC = \left(e^{\ln R++} - 1\right) \times 100\% \tag{3}$$

Positive values denote an increase due to e [CO_2] whereas negative values indicate a decrease in the respective variables.

2.3. Upscaling estimation

We calculated changes in CH_4 emissions from global paddies and wetlands under short- and long-term e [CO_2] using the following equation (van Groenigen et al., 2011; Xia et al., 2021):

$$E = A \times H \tag{4}$$

while E represents the change (net increase or decrease) in CH_4 emissions as affected by e [CO_2] (Pg CO_2-eq yr^{-1}), A represents the replicate-weighted mean positive or negative changes in CH_4 emissions between e [CO_2] and a [CO_2] treatments, and H represents the habitat area of global paddies or wetlands (1.67×10^8 ha for paddies and 1.21×10^9 ha for wetlands) (Davidson et al., 2018; FAO).

3. Results

3.1. e [CO_2]-induced CH_4 emissions from paddies and wetlands

Globally, mean CH_4 emissions were 185 and 246 kg CH_4 ha^{-1} yr^{-1} from paddies and wetlands under a [CO_2], respectively, but they increased to 218 and 296 kg CH_4 ha^{-1} yr^{-1} under e [CO_2], respectively (Fig. 1a). However, when weighted the effect sizes, e [CO_2] increased overall CH_4 emissions by 25.7% (95%*CIs*: 18.2%–33.4%; $p < 0.05$) from paddies, while it decreased CH_4 emissions by 3.29% (95%*CIs*: −21.0%–15.0%; $p > 0.05$) from wetlands (Fig. 1b). So, there were significant differences in the *PC* of e [CO_2]-induced CH_4 emissions from paddies and wetlands ($p < 0.05$, Fig. 1b).

There was no difference in the effects of different experimental facilities, e [CO_2] levels, N fertilization rates, and water regimes on e [CO_2]-induced CH_4 emissions in paddies ($p > 0.05$; Fig. 2a and S3). However, e [CO_2] increased CH_4 emissions by 29.9% (95%*CIs*: 21.3%–39.0%; $p < 0.05$) and 49.0% (95%*CIs*: 21.8%–85.9%; $p < 0.05$) under zero and half of straw incorporations conditions, respectively, but decreased CH_4 emissions by 4.19% (95%*CIs*: −9.37%–2.57%; $p > 0.05$) under all straw incorporations condition in paddies (Fig. 2a). CH_4 emissions generally increased by 34.7% (95%*CIs*: 26.6%–43.2%; $p < 0.05$) and 27.3% (95%*CIs*: 20.9%–34.6%; $p < 0.05$), when the duration of e [CO_2] was smaller than 5 yrs and 5–10 yrs (Fig. 2a), respectively. Interestingly, long-term e [CO_2] (more than 10 yrs) decreased CH_4 emissions from paddies by 26.5% (95%*CIs*: −38.4% to −12.7%; $p < 0.05$) (Fig. 3a). For wetlands, the related management practices did not affect CH_4 emissions under e [CO_2] ($p > 0.05$, Fig. 2b).

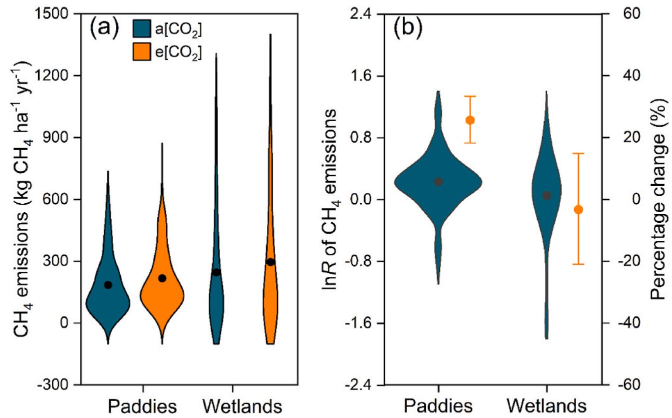

Fig. 1. Violin plots of (a) global CH_4 emissions under a [CO_2] and e [CO_2] and (b) the response ratio (ln$R$) of CH_4 emissions to e [CO_2] from paddies ($n = 124$) and wetlands ($n = 41$). a [CO_2], ambient CO_2 concentration; e [CO_2], elevated CO_2 concentration. Black dots represent mean values. Orange dots indicate the percentage changes, and error bars of the dots represent 95% confidence intervals (95%*CIs*). Error bars that do not overlap with zero indicate statistically significant differences ($p < 0.05$).

3.2. Relationships between effect sizes of e [CO_2] on CH_4 emissions and influencing factors

With respect to plant parameters, aboveground and belowground biomass were increased under e [CO_2] by 22.8% and 30.5% (95%*CIs*: 18.7%–26.6% and 20.7%–38.8%; $p < 0.05$), respectively (Fig. 3). However, there were no significant changes in aboveground/belowground biomass in the overall dataset under e [CO_2] because the 95%*CIs* of percentage change of aboveground/belowground biomass overlapped zero. In contrast, e [CO_2] significantly decreased aboveground/belowground biomass by 9.63% in paddies (95%*CIs*: −19.6%% to −0.09%; $p < 0.05$) (Fig. 3). The linear regression analysis suggested that the response ratio of CH_4 emissions from paddies and wetlands under e [CO_2] was positively correlated with the response ratio of belowground biomass, and negatively correlated with the response ratio of aboveground/belowground biomass ($p < 0.05$; Fig. 4b and c).

On average, e [CO_2] did not affect redox potential in both paddies and wetlands (95*CIs*: −9.34%–12.3%; $p > 0.05$) (Fig. 3). e [CO_2] increased dissolved organic carbon by 17.3% (95%*CIs*: 11.8%–22.9%; $p < 0.05$), with an increased rate of 18.8% (95%*CIs*: 14.3%–23.3%; $p < 0.05$) in paddies and 14.1% (95%*CIs*: 2.16%–29.5%; $p < 0.05$) in wetlands. In addition, overall dissolved CH_4 significantly increased by 32.7% (95%*CIs*: 3.98%–85.8%; $p < 0.05$) in paddies and wetlands under e [CO_2] (Fig. 3). Yet, dissolved CH_4 was significantly increased in paddies by 43.7% (95%*CIs*: 8.02%–113%; $p < 0.05$) under e [CO_2] (Fig. 3), while it did not change in wetlands. The linear regression equation showed that e [CO_2]-induced CH_4 emissions were positively correlated with the response ratio of dissolved CH_4, but not with the response ratio

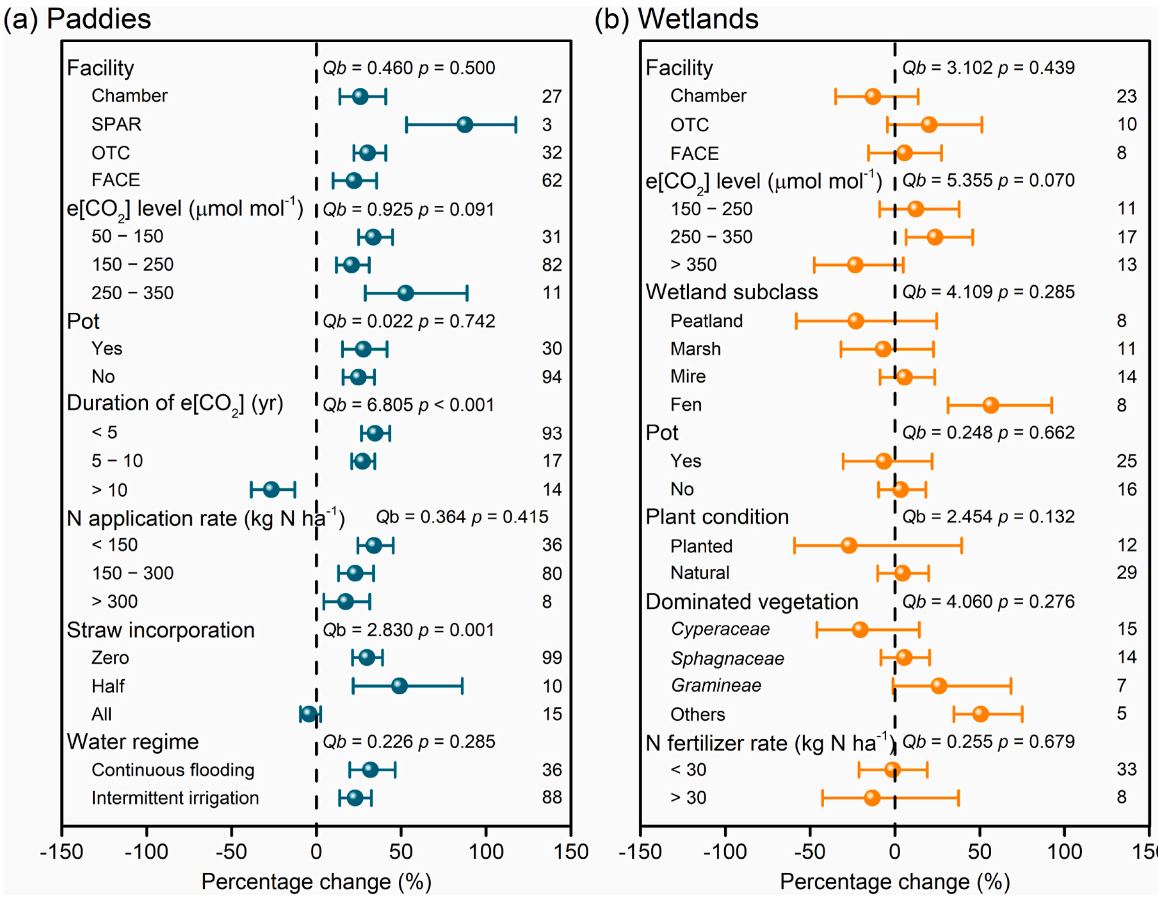

Fig. 2. Effects of e $[CO_2]$ on CH_4 emissions from (a) paddies and (b) wetlands with different managemental conditions. Values are means ± 95% confidence intervals (95%*CIs*) of the percentage changes. The number of paired observations is shown beside each condition. Between-group heterogeneity (*Qb*) represents the effects of categorical variables. Significant *Qb* values ($p < 0.05$) indicate that the effects of categorical variables were significant.

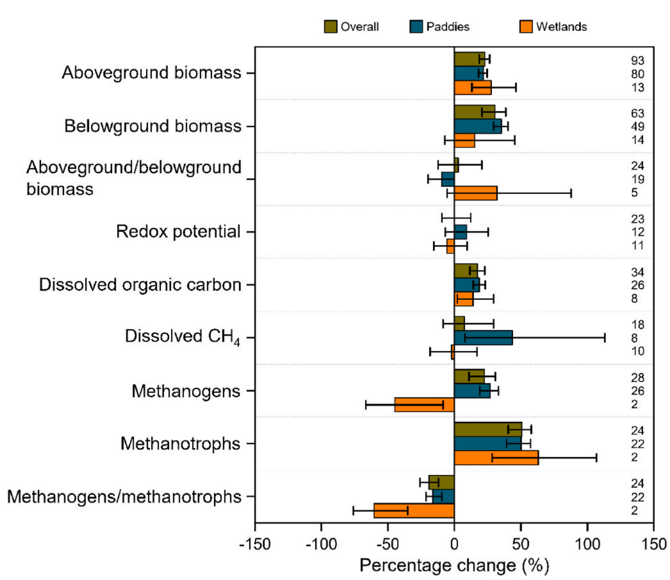

Fig. 3. Effects of e $[CO_2]$ on plant parameters, soil properties, and microorganisms in paddies and wetlands. Error bars represent 95% confidence intervals (95%*CIs*). 95%*CIs* that do not overlap with zero indicate statistically significant differences ($p < 0.05$). The number of paired observations is shown beside each condition.

of redox potential and dissolved organic carbon ($p < 0.05$; Fig. 4d–f).

e $[CO_2]$ significantly increased overall methanogens by 22.5% (95% *CIs*: 11.05–30.8%; $p < 0.05$) (Fig. 3). Specifically, e $[CO_2]$ increased the abundance in paddies by 26.9% (95%*CIs*: 19.1%–33.3%; $p < 0.05$), while it decreased the abundance by 44.9% in wetlands (95%*CIs*: −66.8% to −8.66%; $p < 0.05$). For methanotrophs, e $[CO_2]$ increased the overall abundance by 50.7% (95%*CIs*: 40.6%–57.9%; $p < 0.05$); it significantly increased the abundance by 50.1% (95%*CIs*: 39.2%–57.3%; $p < 0.05$) in paddies and by 63.1% (95%*CIs*: 28.5%–107%; $p < 0.05$) in wetlands (Fig. 3). Conversely, e $[CO_2]$ decreased methanogens/methanotrophs by 19.1% (95%*CIs*: −26.1% to −12.0%; $p < 0.05$), and such changes were more pronounced in wetlands than in paddies ($p < 0.05$). Regression analysis showed that the response ratio of e $[CO_2]$-induced CH_4 emissions positively correlated with methanogens and methanogens/methanotrophs ($p < 0.05$), but did not correlate with methanotrophs (Fig. 4h and i).

The response ratio of e $[CO_2]$-induced CH_4 emissions was positively correlated with mean annual temperature (MAT) in paddies and wetlands ($p < 0.05$; Fig. 4j). Similarly, in paddies, the response ratios of e $[CO_2]$-induced CH_4 emissions were related with changes of rice tiller numbers in a linear relationship ($p < 0.05$; Fig. 4k). The response ratios of e $[CO_2]$-induced CH_4 emissions from wetlands showed a downward parabolic relationship with water table levels (Fig. 4l). When the depth of the wetland water table levels was about 1–2 cm, response ratios of e $[CO_2]$-induced CH_4 emissions reached the maximum value. In contrast, the negative effect of e $[CO_2]$-induced CH_4 emissions occurred when water table levels were below −9 cm or above 12 cm.

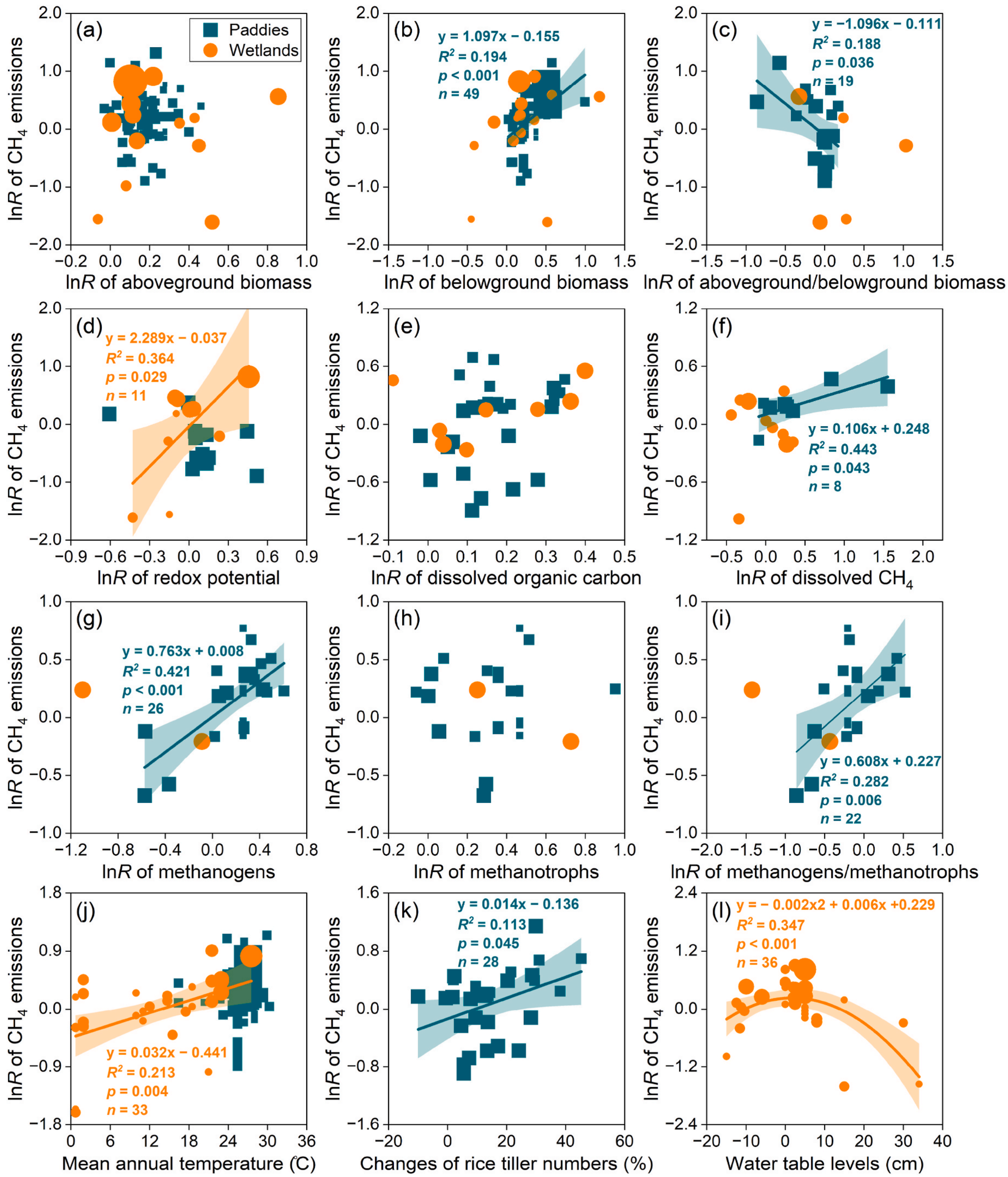

Fig. 4. Relationships between the response ratios of CH_4 emissions and (a) aboveground biomass, (b) belowground biomass, (c) aboveground/belowground biomass, (d) redox potential, (e) dissolved organic carbon, (f) dissolved CH_4, (g) methanogens, (h) methanotrophs, (i) methanogens/methanotrophs, (j) mean annual temperature, (k) changes of rice tiller numbers, and (l) water table levels after paddies (dark cyan squares) or wetlands (orange circles) were affected by e [CO_2]. Shaded sections represent the 95% confidence intervals (95%*CIs*) of the regression line. The square and circle sizes indicate the relative weights based on linear regression analysis (the larger the shape, the greater the weight).

3.3. *Global upscaling estimate of long-term e [CO_2]-induced CH_4 emissions from paddies and wetlands*

Upscaling our results, e [CO_2] increased overall CH_4 emissions from global paddies and wetlands by 0.14 Pg CO_2-eq yr^{-1} (95%*CIs*: 0.09 to 0.18 Pg CO_2-eq yr^{-1}; $p < 0.05$) and 0.73 Pg CO_2-eq yr^{-1} (95%*CIs*: −0.01 to 1.55 Pg CO_2-eq yr^{-1}; $p > 0.05$), respectively (Table 1). Specifically, under short-term e [CO_2] (smaller than 5 yrs), global CH_4 emissions increased by 0.18 Pg CO_2-eq yr^{-1} (95%*CIs*: 0.13 to 0.23 Pg CO_2-eq yr^{-1}; $p < 0.05$) and 0.80 Pg CO_2-eq yr^{-1} (95%*CIs*: 0.01 to 1.69 Pg CO_2-eq yr^{-1}; $p < 0.05$) from paddies and wetland, respectively (Table 1). However, long-term e [CO_2] (more than 10 yrs) decreased CH_4 emissions by 0.23 Pg CO_2-eq yr^{-1} (95%*CIs*: −0.37 to −0.09 Pg CO_2-eq yr^{-1}; $p < 0.05$) from paddies, while it did not affect global CH_4 emissions from wetlands (Table 1).

Table 1
Estimates of effects of the duration of e $[CO_2]$ on CH_4 emissions from paddies and wetlands on a global scale.

Ecosystems	Duration of e $[CO_2]$	No. of observations	Area (ha)	CO_2-eq changes (Pg)	95%*CIs*	
					Min.	Max.
Paddies	Overall	124	1.67×10^8 [a]	0.14	0.09	0.18
	<5 yrs	93		0.18	0.13	0.23
	5–10 yrs	17		0.16	0.12	0.21
	>10 yrs	14		−0.22	−0.37	−0.09
Wetlands	Overall	41	1.21×10^9 [b]	0.73	−0.01	1.55
	<5 yrs	37		0.80	0.01	1.69
	5–10 yrs	0		N.D. [c]	N.D.	N.D.
	>10 yrs	4		0.03	−0.25	0.26

e$[CO_2]$, elevated CO_2 concentration. 95%*CIs* that do not overlap with zero indicate statistically significant differences ($p < 0.05$). [a] Source from FAO. (2020). [b] Source from Davidson et al. (2018). [c] N.D. represents no data.

4. Discussion

4.1. Comparison of e $[CO_2]$-induced CH_4 emissions from paddies and wetlands

In line with our hypothesis (i), e $[CO_2]$ stimulated global CH_4 emissions from paddies ($p < 0.05$; Fig. 1b). Indeed, e $[CO_2]$ typically increased rice plant photosynthesis (Malyan et al., 2016) and thus spurred paddy soil carbon input. This was supported by higher belowground biomass and dissolved organic carbon concentrations (Fig. 3), which provided more substrates for methanogens (Qian et al., 2022a), and therefore stimulated CH_4 production in paddies. This was also confirmed by the positive effect of e $[CO_2]$ on methanogens in paddies (Figs. 3 and 4). Soil biogeochemical processes are jointly regulated by hydrological and vegetal regimes (Mueller et al., 2020). e $[CO_2]$ increased belowground biomass through the photosynthesis of aboveground plants (Fig. S4), and then indirectly led to the increase in CH_4 emissions by providing more substrates for methanogens (Lin et al., 2021; van Groenigen et al., 2011). In general, N application rates can further promote plant growth and rhizodeposit mineralization under e $[CO_2]$ (Li et al., 2022; Xie et al., 2012), and may indirectly affect the response of CH_4 emissions in paddies and wetlands to e $[CO_2]$. However, in our study, there was no significant change in the response of CH_4 emissions to e $[CO_2]$ under different N application rates in paddies and wetlands (Fig. 2 and S3). This suggests that the mechanism of carbon-N coupling under e $[CO_2]$ needs to be further explored.

Unlike CH_4 emissions from paddies, however, e $[CO_2]$ did not affect overall CH_4 emissions from wetlands (Fig. 1b). This was presumably because root exudation rates did not increase significantly due to no priming effects of belowground biomass in wetlands as affected by e $[CO_2]$ (Bridgman et al., 2020), resulting in no change of methanogens (Fig. 3). The response of e $[CO_2]$ on wetland underground biomass was positively correlated with MAT (Fig. S4). In our data set, e $[CO_2]$ experiments were mostly carried out in wetlands with low MAT (Fig. S1), indicating that the effects of MAT on wetland underground biomass may mask that of e $[CO_2]$. In addition, this was further supported by the unaffected dissolved CH_4 content under e $[CO_2]$ (Fig. 3), suggesting that wetland CH_4 emissions had little response to the indirect effects of e $[CO_2]$. Accordingly, the response of wetland CH_4 emissions to e $[CO_2]$ was different from paddies, which was not consistent with our hypothesis (i).

It was reported that e $[CO_2]$ increased CH_4 fluxes from paddy and wetland by 0.30 Pg CO_2-eq yr^{-1} and 1.90 Pg CO_2-eq yr^{-1}, respectively (Liu et al., 2018). However, we only found a little increase (+0.13 and + 0.73 Pg CO_2-eq yr^{-1} from paddies and wetlands, respectively) in e $[CO_2]$-induced CH_4 emissions on a global scale (Table 1). This was because our meta-analysis included a larger dataset that minimized the uncertainty in estimates. Consistent with our hypothesis (iii), the effects of long- and short-term e $[CO_2]$ on CH_4 emissions in global paddies and wetlands were different, namely, short-term e $[CO_2]$ increased CH_4 emissions (+0.30 and + 0.80 Pg CO_2-eq yr^{-1}) from paddies and wetlands, while showing a decrease or no change (−0.22 or +0.03 Pg CO_2-eq yr^{-1}) under long-term e $[CO_2]$ (Table 1). This may be another reason why our estimates of CH_4 emissions as affected by e $[CO_2]$ were lower than those of previous studies (Yu et al., 2022c).

Why did paddy and wetland CH_4 emissions respond differently to short-term and long-term e $[CO_2]$? Regarding paddies, compared to short-term e $[CO_2]$, long-term e $[CO_2]$ practices declined the stimulation of belowground biomass induced by e $[CO_2]$ (Fig. S5). This resulted in a decrease in the increment of methanogenic substrates and thus inhibited CH_4 production in paddies (Yu et al., 2022c). In terms of wetlands, the stimulation of CH_4 emissions by long-term e $[CO_2]$ may be sporadic due to temporal variations in the reduction of discharge pathways as water table levels change (Lin et al., 2021) or the increasing competition from other microorganisms for methanogenic substrates (Marsh et al., 2005). On the other hand, the decreased stimulation effect of long-term e $[CO_2]$ on CH_4 emissions from paddies or wetlands may be due to the adaptation of methanogens and methanotrophs to environmental changes. That is, if the duration of e $[CO_2]$ is taken into account, the intensity of e $[CO_2]$-induced CH_4 emissions in paddies and wetlands would be weakened due to reverse changes in the functions of the above key microorganisms (Yu et al., 2022c). Therefore, our results suggested that previous studies may have overestimated e $[CO_2]$-induced CH_4 emissions from global paddies and wetlands (Qian et al., 2022a; Shen et al., 2023; Wang et al., 2022; Zhu et al., 2022).

4.2. Different influencing factors of e $[CO_2]$-induced CH_4 emissions from paddies and wetlands

The significant variation in the percentage changes of e $[CO_2]$-induced CH_4 emissions from paddies and wetlands (Fig. 1) suggested that there were differences in possible influencing factors between paddies and wetlands (Fig. 5). Why did the similar anaerobic environment of paddies and wetlands lead to different influencing factors?

e $[CO_2]$ increased CH_4 emissions from paddies accompanied by a decrease in methanogens/methanotrophs, indicating that CH_4 transport capacities were probably enhanced as affected by e $[CO_2]$ (Figs. 3 and 4k). This was reflected by the increase in rice tiller numbers (Fig. 4k). Allen et al. (2003) reported that, in paddies, e $[CO_2]$ increased rice tiller numbers, which could explain why the increased aerenchyma numbers led to more CH_4 transport to the atmosphere. However, more aerenchyma tissues as affected by e $[CO_2]$ were likely to lead to more O_2 diffusion into the soil and facilitate CH_4 oxidation (Schrope et al., 1999; Yu et al., 2022c). Thus, under e $[CO_2]$ in the future, it is necessary to select high-yield rice varieties with lower tiller numbers to cope with more CH_4 emissions from paddies (Jiang et al., 2017; Yu et al., 2022b). These interpretations could contribute to the reduction of CH_4 from paddies under long-term e $[CO_2]$.

In wetlands, it was clear that water table levels directly influenced CH_4 emission responses under e $[CO_2]$, which essentially differed from the flood-water environment in paddies (Boardman et al., 2011; Lin et al., 2021). This was because e $[CO_2]$ stimulation of plant production

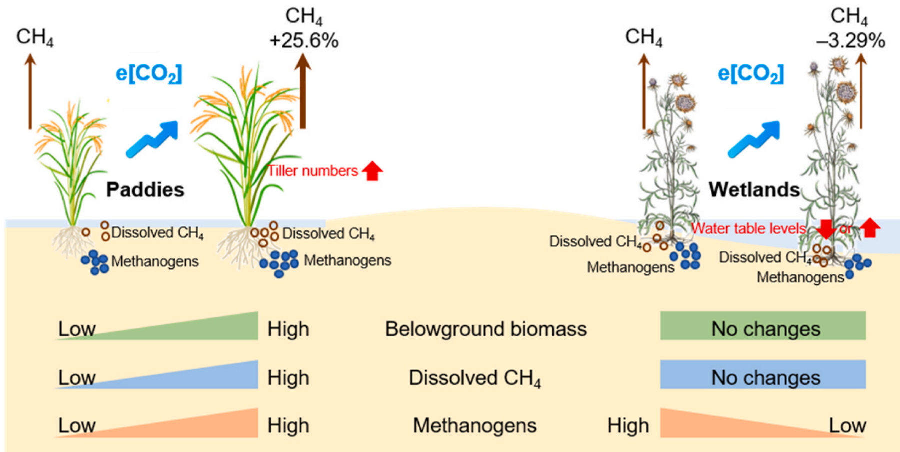

Fig. 5. A schematic diagram illustrating the effects of e [CO_2] on CH_4 emissions from paddies and wetlands. e [CO_2], elevated CO_2 concentration. "+" and "−" represent increase and decrease in CH_4 emissions from paddies and wetlands in response to e [CO_2], respectively. The widths of the brown arrows denote the magnitude of CH_4 emissions influenced by e [CO_2].

was diminished by the increase in water table levels above (Zhu et al. (2022). In the present study, the response of wetland CH_4 emissions to e [CO_2] might be weakened regardless of the decrease or increase of water table levels (Fig. 4l), indicating that CH_4 emissions under e [CO_2] can be reduced by regulating wetland water levels. Under future climate conditions, environmental factors such as uneven rainfall, rising sea levels, or drought might change water table levels in wetlands, which would indirectly affect the response of CH_4 emissions in wetlands to e [CO_2]. But as a result, no matter whether the water table levels of coastal wetlands rise due to the increase in relative sea levels or that of inland freshwater wetlands fall due to uneven rainfall or drought, they will lead to the reduction of e [CO_2]-induced CH_4 emissions, which may have a certain positive effect on the mitigation of climate warming (Bridgman et al., 2020; Silvola et al., 2003). As for the mechanism, on the one hand, the decrease in water table levels might lead to the change of anaerobic conditions of wetland soils and the increase of soil redox potential, thus inhibiting the production of CH_4. On the other hand, the rise of water table levels might inhibit CH_4 transport, thus reducing CH_4 emissions in wetlands (Lin et al., 2021; Mueller et al., 2020; Vann and Megonigal, 2003; Zhao et al., 2023). However, the current statistical data is relatively small, and the relevant mechanism needs to be further studied. Furthermore, based on the limited data in our study, the response of CH_4 emissions to e [CO_2] may also be diverse under different wetland types and vegetation cover conditions (Fig. 2). Therefore, consistent with our hypothesis (ii), the different responses of CH_4 emissions from paddies and wetlands to e [CO_2] might be related to various influencing factors (Fig. 5).

4.3. Future work

This meta-analysis focused on the effects of e [CO_2] alone on CH_4 emissions from paddies and wetlands. The results showed that the factors contributing to the e [CO_2]-induced stimulation effects were different in paddies and wetlands and the effects may vary over time scales. However, some uncertainties remain: (i), future climate change is a cross-cutting change involving multiple factors such as temperature, ozone, drought, radiation, and N deposition. Their comprehensive impacts are poorly considered. (ii), due to the high operating costs of e [CO_2] platforms, global *in-situ* experimental data on long-term e [CO_2] effects in paddy and wetland ecosystems are limited. The present studies cover only the short ranges of e [CO_2] duration and lack comparisons of short- and long-term e [CO_2] effects on CH_4 emissions in paddies and wetlands (Marsh et al., 2005; Yu et al., 2022c). (iii), e [CO_2] is a gradual rather than an abrupt increase, whereby the study of the response of CH_4 emissions to gradual e [CO_2] limits our ability to infer long-term effects on the time scale (Shen et al., 2023; Wang et al., 2022). Nevertheless, it could be inferred that the stimulation effects of e [CO_2] on CH_4 emissions from paddies and wetlands might be weakened and even inhibited as the duration of e [CO_2] increases over time (Fig. 2). Therefore, we suggest that more combined laboratory and field experiments under long-term e [CO_2] are needed to verify the relevant mechanisms, to better elucidate the effects of e [CO_2] on carbon cycling in paddies and wetlands.

We preliminarily clarified the main controlling factors of CH_4 emissions from paddies and wetlands to e [CO_2] (Fig. 4). This is meaningful for how to reduce the emissions and reveal their underline mechanism. However, a more rigorous ecological simulation environment of future climate needs to be developed to further validate the response of carbon cycling to climate change by integrating more biogeochemical factors. In recent years, it has been widely accepted that microorganisms play important roles in global carbon biogeochemical cycles. However, current biogeochemical models predicting the feedback of terrestrial ecosystems to climate change generally do not include microorganisms (Liu et al., 2018). Therefore, it is necessary to further in-depth study the microbial mechanisms of CH_4 emissions in response to climate change. Furthermore, in addition to e [CO_2], related microorganisms also have sensitive responses to other climate factors, such as temperature, ozone, drought, radiation, and N deposition. Thus, while studying the response of carbon cycling to climate change, it is necessary to pay close attention to the response of related microbial ecology to the interactions of climate factors (Niu et al., 2020; Wang et al., 2018).

More importantly, current studies on e [CO_2]-induced CH_4 emissions from paddies and wetlands are mainly concentrated in some countries in the Northern hemisphere, whereas studies on the effects of e [CO_2] on CH_4 emissions from paddies in some Southeast Asian and South African countries, and wetlands in Congo Basin in Africa and Amazon Plain in South America are seriously lacking (Fig. S1). Although the estimated area of paddies is becoming more accurate, the diversification of field management measures will inevitably affect the response of paddy CH_4 emissions to e [CO_2] (Qian et al., 2022b; Yu et al., 2022c; Yun et al., 2012). Thus, according to the response of e [CO_2]-induced CH_4 emissions to field management measures in different regions, the optimal solution of economic and environmental benefits of paddies under future climate conditions could be obtained. For wetlands, CH_4 emissions are calculated as the products of flux density and CH_4-producing area or surface area (Yuan et al., 2021; Zhang et al., 2021). However, there are still uncertainties in the estimation of their area, which might also have a certain impact on the estimation of e [CO_2]-induced CH_4

emissions from wetlands. On the other hand, wetland reclamation is intensifying in recent years, which will inevitably lead to the continuous reduction of wetland areas (Ma et al., 2019). At the same time, the conversion of natural wetlands into farmland or aquaculture ponds could exacerbate the carbon and N cycles, which in turn increases greenhouse gas emissions (Davidson et al., 2021; Li et al., 2021; Yang et al., 2022). Therefore, under future climate conditions, the studies of exploring the response of wetland CH_4 emissions to e [CO_2] require comprehensive exploration of more accurate area estimation and *in-situ* observation tests in various wetland types to reduce the uncertainty of assessment.

5. Conclusion

e [CO_2] stimulated overall CH_4 emissions from global paddies by increasing belowground biomass, methanogens, and methanogens/methanotrophs. However, in our study, the current statistical data showed that e [CO_2] might not affect CH_4 emissions from global wetlands. Particularly, rice tiller number mediated the response of CH_4 emissions to e [CO_2] in paddies, and water table levels modulated e [CO_2]-induced CH_4 emissions in wetlands. Our scaling-up estimate found that global CH_4 emissions were increased under short-term e [CO_2] while were decreased (no change) under long-term e [CO_2] in paddies (wetlands). Although the results need to be confirmed in long-term field experiments, our findings suggest that e [CO_2]-induced CH_4 emissions from paddies and wetlands may be smaller than previously thought.

Credit author statement

Haiyang Yu: Data curation, Investigation, Writing–original draft. **Xuechen Zhang:** Conceptualization, Writing–review & editing. **Xiangtian Meng:** Data curation. **Dan Luo:** Investigation. **Zhengfu Yue:** Supervision. **Yaying Li:** Writing–review & editing. **Yongxiang Yu:** Writing–review & editing. **Huaiying Yao:** Conceptualization, Writing–review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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