# LETTER

# Increased soil emissions of potent greenhouse gases under increased atmospheric $CO_2$

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**Increasing concentrations of atmospheric carbon dioxide ($CO_2$) can affect biotic and abiotic conditions in soil, such as microbial activity and water content[1,2]. In turn, these changes might be expected to alter the production and consumption of the important greenhouse gases nitrous oxide ($N_2O$) and methane ($CH_4$) (refs 2, 3). However, studies on fluxes of $N_2O$ and $CH_4$ from soil under increased atmospheric $CO_2$ have not been quantitatively synthesized. Here we show, using meta-analysis, that increased $CO_2$ (ranging from 463 to 780 parts per million by volume) stimulates both $N_2O$ emissions from upland soils and $CH_4$ emissions from rice paddies and natural wetlands. Because enhanced greenhouse-gas emissions add to the radiative forcing of terrestrial ecosystems, these emissions are expected to negate at least 16.6 per cent of the climate change mitigation potential previously predicted from an increase in the terrestrial carbon sink under increased atmospheric $CO_2$ concentrations[4]. Our results therefore suggest that the capacity of land ecosystems to slow climate warming has been overestimated.**

By burning fossil fuels, cutting down forests and changing land use in other ways, humans are rapidly increasing the amount of $CO_2$ in the atmosphere and warming the planet[5]. Plant growth is known to increase after an abrupt surge in $CO_2$ levels[6]. Because stimulated assimilation of carbon by plants can increase soil carbon input and soil carbon storage, terrestrial ecosystems could help to reduce the increase in atmospheric $CO_2$ and thereby slow climate change[7]. However, the radiative forcing of land ecosystems is not determined by their uptake and release of $CO_2$ alone; increased $CO_2$ can also alter soil emissions of $N_2O$ and $CH_4$ (ref. 2). Although both of these gases occur in far lower atmospheric concentrations than does $CO_2$, their global warming potentials are much higher: 298 times higher for $N_2O$ and 25 times higher for $CH_4$ (ref. 5). Agricultural soils are the main source of human-induced $N_2O$ emissions[8]. Soils under natural vegetation produce roughly the same amount of $N_2O$ as all anthropogenic sources combined[8]. Wetlands, including rice paddies, contribute 32–53% to the global emissions of $CH_4$ (ref. 8). Upland soils, on the other hand, act as a sink for atmospheric $CH_4$ through oxidation by methanotrophic bacteria[9]. Thus, changes in $N_2O$ and $CH_4$ fluxes could greatly alter how terrestrial ecosystems influence climate[10].

Studies of greenhouse-gas (GHG) emissions span a variety of ecosystem types, and vary in experimental design and results, making it difficult to determine their global response to increased $CO_2$ from individual experiments. A quantitative synthesis of results across multiple studies can overcome this problem. Therefore, we used meta-analysis[11] to summarize the effect of atmospheric $CO_2$ enrichment on fluxes of $CH_4$ and $N_2O$ from soil, using 152 observations from 49 published studies (see Supplementary Table 1, Supplementary Data 1 and 2, Supplementary Notes 1). We also summarized the effect of increased $CO_2$ on possible drivers of altered $CH_4$ and $N_2O$ fluxes, using standing root biomass and soil water content from the studies in which the observations on $N_2O$ and $CH_4$ fluxes were collected (Supplementary Data 3 and 4). All observations were analysed using three different weighting functions (see Methods). As $CH_4$ and $N_2O$

emissions were not correlated with the concentration of $CO_2$ used for enrichment (Methods), we treat 'increased $CO_2$' as a category.

Overall, increased concentrations of atmospheric $CO_2$ stimulated emissions of $N_2O$ by 18.8% (Fig. 1a). This positive response was significant for studies receiving little or no fertilizer, for non-pot studies and for studies on natural vegetation—that is, studies that most closely resembled real-world conditions (Supplementary Table 2). Increased $CO_2$ stimulated $CH_4$ emissions in wetlands by 13.2% (Fig. 1a, Supplementary Table 3). In rice paddies, increased $CO_2$ stimulated $CH_4$ emissions by 43.4% (Fig. 1a, Supplementary Table 4). In upland systems, increased $CO_2$ caused on average a small and insignificant net uptake of $CH_4$ (Supplementary Table 5).

To compare the relative importance of changed GHG fluxes in uplands, wetlands and rice paddies, we expressed the absolute effect of increased $CO_2$ on $CH_4$ and $N_2O$ fluxes from these ecosystem types (Supplementary Tables 5–8) scaled by their respective total land area. For upland soils, we distinguished fertilized agricultural ecosystems and ecosystems receiving little or no fertilizer. Our estimates of total GHG fluxes under ambient (that is, present-day) $CO_2$ conditions correspond well to independent global syntheses of modern GHG fluxes (Supplementary Table 9), supporting our scaling approach.

The estimated stimulation by increased $CO_2$ of total soil $N_2O$ emissions corresponds to an additional source of 0.33 Pg $CO_2$ equivalents (equiv.) $yr^{-1}$ from agricultural ecosystems (1 Pg = $10^{15}$ g), and of 0.24 Pg $CO_2$ equiv. $yr^{-1}$ for all other upland ecosystems (Fig. 2). The $CO_2$-stimulation of $CH_4$ emissions corresponds to an additional source of 0.25 Pg $CO_2$ equiv. $yr^{-1}$ from rice paddies and of 0.31 Pg $CO_2$ equiv. $yr^{-1}$ from natural wetlands. Our data indicate a small and non-significant effect of $CO_2$ on global $CH_4$ fluxes from upland soils for
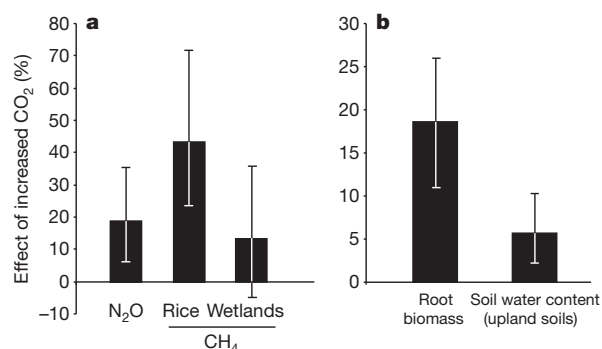


**Figure 1 | Results of a meta-analysis of the response of GHG emissions and their potential drivers to rising levels of atmospheric $CO_2$. a**, The effect of increased $CO_2$ on emissions of $N_2O$ from upland soil and $CH_4$ from rice paddies and wetlands. Results are based on 73, 21 and 24 observations, respectively. **b**, The effect of increased $CO_2$ on root biomass and soil water content. Results are based on 83 and 55 observations, respectively. Effect sizes in all meta-analyses were weighted by replication. Error bars, 95% confidence intervals.

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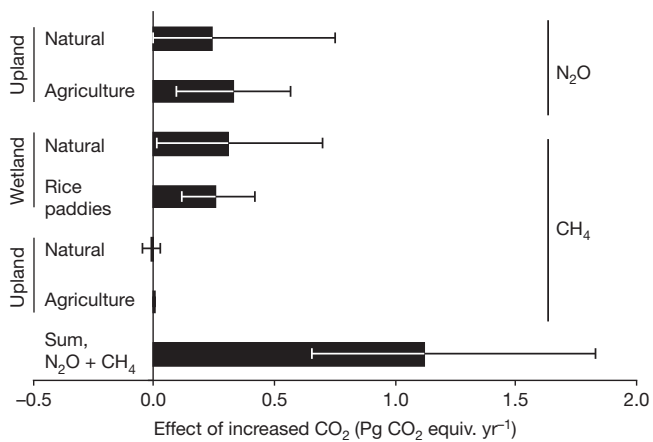
**Figure 2 | The effect of rising atmospheric $CO_2$ on GHG emissions, expressed on the global scale.** For $N_2O$ fluxes, the results for natural and agricultural soils were based on 35 and 19 observations, respectively. For $CH_4$ fluxes, the results for natural wetlands, rice paddies, natural upland soils and agricultural upland soils were based on 16, 21, 10 and 8 observations, respectively. Effect sizes in all meta-analyses were weighted by replication. Error bars, 95% confidence intervals.

agricultural ecosystems (0.003 Pg $CO_2$ equiv. yr$^{-1}$) and for all other upland ecosystems (−0.011 Pg $CO_2$ equiv. yr$^{-1}$). The combined effect of increased $CO_2$ on emissions of these GHGs is 1.12 Pg $CO_2$ equiv. yr$^{-1}$.

Rising atmospheric $CO_2$ is expected to increase soil C storage in terrestrial ecosystems, which may contribute to the current residual C sink on land[7]. Meta-analysis of $CO_2$ enrichment experiments indicates that the sink is larger for ecosystems receiving fertilizer[12]. Scaled up by the total area of agricultural and non-fertilized ecosystems, these meta-analyses suggest that increased atmospheric $CO_2$ levels may increase the soil C sink by as much as 4.0 Pg $CO_2$ yr$^{-1}$. Results presented here indicate that enhanced GHG emissions under increased $CO_2$ reduce the C mitigation effect of soil C storage by 28% (1.12 Pg/4.0 Pg). The magnitude and significance of this result is insensitive to the choice of the weighting function used in the meta-analysis (Supplementary Fig. 1, Supplementary Table 10).

Experiments included in our database increased atmospheric $CO_2$ concentration to 630 p.p.m.v. on average, a level expected for the second half of this century[13]. Biogeochemical models predict that at that time, the terrestrial C sink may be as much as 6.8 Pg $CO_2$ yr$^{-1}$ stronger than it is today[4] (when considering forcing by rising $CO_2$ alone). On the basis of our analysis, a $CO_2$-induced rise in GHG fluxes could negate 16.6% (1.12 Pg/6.8 Pg) of the expected increase of the entire terrestrial C sink (Supplementary Table 10).

This estimate (16.6%) is likely to be an underestimate for three reasons. First, most of the studies in our data set measured GHG fluxes during the growing season only, but we assumed these applied to the entire year. Winter emissions of $CH_4$ in wetlands and rice paddies are typically small[9]; however, winter emissions of $N_2O$ during freeze-thaw cycles can contribute substantially to annual $N_2O$ fluxes[14], and available data indicate that winter emissions of $N_2O$ are stimulated under increased $CO_2$ (ref. 15). A recently published data set[16] suggests that $N_2O$ emissions outside the growing season amount to 88% and 64% of the emissions during the growing season in agricultural systems and natural ecosystems, respectively (see Methods). Assuming that increased $CO_2$ affects $N_2O$ emissions proportionately throughout the year, its effect on $N_2O$ emissions outside the growing season would therefore amount to 0.29 Pg $CO_2$ equiv. yr$^{-1}$ from agricultural systems and 0.15 Pg $CO_2$ equiv. yr$^{-1}$ from natural ecosystems. Together, these fluxes negate an additional 7% of the expected increase of the terrestrial C sink.

Second, atmospheric N deposition is predicted to increase during this century[17]. Because average $CO_2$ responses of $N_2O$ emissions were higher in studies receiving additional N (Supplementary Tables 2 and 6), the positive effect of $CO_2$ on $N_2O$ emissions may strengthen as ecosystems become enriched in N.

Last, $CO_2$ effects on $N_2O$ emissions showed a weak but significant correlation with experiment duration (Supplementary Fig. 2), suggesting that $CO_2$ effects on $N_2O$ emissions may increase over time.

Why do GHG emissions respond positively to rising levels of atmospheric $CO_2$? Atmospheric $CO_2$ enrichment increased soil water contents for the studies contributing to our $N_2O$ database (Fig. 1b, Supplementary Table 11); this result is probably due to improved efficiency of water use by plants, which reduces soil water loss through transpiration[18]. Moreover, increased $CO_2$ has been shown to enhance soil biological activity across a broad range of ecosystems[1,2]. Both responses promote soil anoxia, and thus stimulate denitrification[19] (anaerobic microbial respiration of nitrate), one of the major sources of $N_2O$ from soils[3]. Increased $CO_2$ also enhanced root biomass in all three habitats (Fig. 1b, Supplementary Table 12). As denitrification is generally stimulated by high availability of labile C as a source of energy[20], and because new C enters mineral soil mainly through the root system, this increase in root biomass would stimulate denitrification rates—and $N_2O$ emissions—even further.

Methane is produced only under anaerobic conditions, which are common in soils of rice paddies and natural wetlands but not uplands. Because methanogenic archaea rely on C assimilation by plants as their ultimate source of organic substrates[9], increased rates of soil C input with increased $CO_2$ can also stimulate $CH_4$ emissions. Indeed, the positive correlation between $CH_4$ emission rates and net ecosystem production in wetlands[21] suggests that plant productivity is a key process in the regulation of $CH_4$ emission from these ecosystems. The response to increased $CO_2$ of $CH_4$ emissions from rice paddies and wetlands showed significant correlation with the $CO_2$ response of root biomass ($r^2 = 0.17$, $P = 0.02$, Supplementary Fig. 6); this further suggests that increased $CO_2$ stimulates $CH_4$ production through its positive effect on plant growth and soil C input.

Global changes in climate and atmospheric composition have previously been suggested to affect GHG emissions from natural ecosystems. For instance, a global rise in temperature of 3.4 °C has been predicted to increase $CH_4$ emissions from wetlands by 78% (ref. 22). In addition to its direct effect on the global climate through radiative forcing, our results identify two indirect mechanisms through which rising atmospheric $CO_2$ amplifies climate change: by stimulating the release of $N_2O$ from terrestrial ecosystems, and by enhancing $CH_4$ release from wetlands and rice paddies. The meta-analytic approach used here, synthesizing results across 49 studies, shows that increased $N_2O$ and $CH_4$ emissions are both general and quantitatively important. Future assessments of terrestrial feedbacks to climate change should therefore consider these indirect effects of increased atmospheric $CO_2$ on the production by soil of trace gases like $N_2O$ and $CH_4$.

## METHODS SUMMARY

We extracted results for soil fluxes of $CH_4$ and $N_2O$, root biomass and soil water contents from $CO_2$ enrichment studies that were conducted in the field, in growth chambers or in glass houses. Soil fluxes of $CH_4$ from wetlands, rice paddies and upland soils were considered separately. We divided studies into two categories of N availability based on fertilization rates, that is, more or less than 30 kg N ha$^{-1}$ yr$^{-1}$. This cut-off point corresponds to maximum atmospheric N deposition in the United States and most of the European Union[23]. We also made a distinction between studies in pots and field studies, and between studies with planted or natural vegetation. Agricultural ecosystems were defined as cropland and managed grasslands receiving between 30 and 300 kg N ha$^{-1}$ yr$^{-1}$.

We quantified the effect of increased $CO_2$ on GHG fluxes by calculating the natural log of the response ratio ($R$), a metric commonly used in meta-analysis[24]:

$$\ln R = \ln(GHG_i/GHG_a)$$

where GHG is the flux of either $CH_4$ or $N_2O$ under increased (i) or ambient (a) conditions. We also used $\ln R$ to assess $CO_2$ responses of root biomass and soil water contents. We performed our analysis on effect sizes weighted by replication[25], on

unweighted effect sizes[12], and on effect sizes weighted by the inverse of the pooled variance[26].

Treatment effects were also expressed as the difference in annual GHG fluxes on an areal basis ($U$). This metric was essential for upland $CH_4$ flux, where values can be both positive and negative (making ln$R$ problematic).

We used METAWIN 2.1[27] to generate mean effect sizes and 95% bootstrapped confidence intervals (95% CI). Treatment effects were considered significant if the 95% CI did not overlap with 0. To scale up our results, we multiplied $U$ by the total vegetated land area covered by each category of experiment[28,29].

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## METHODS

**Data collection.** We extracted results for soil fluxes of $CH_4$ and $N_2O$, root biomass and soil water contents from atmospheric $CO_2$ enrichment studies, conducted in the field, in growth chambers or in glass houses. We used Google Scholar (Google Inc.) for an exhaustive search of journal articles published before January 2011, using as search terms either "elevated $CO_2$" or "$CO_2$ enrichment", and either "$N_2O$" and "soil", or "$CH_4$". Further papers were added from a comparable search using Web of Science. For a study to be included in our data set, the atmospheric $CO_2$ concentration for the ambient and elevated treatments had to be in the range 350–450 p.p.m.v. and 450–800 p.p.m.v., respectively. Means and sample sizes had to be reported for both ambient and elevated $CO_2$ treatments.

For each study, we noted experimental duration, plant species, N fertilization rates and the type of experimental facility. Estimates of standard deviation were tabulated when available, but were not required for inclusion in the analysis. We included studies involving experiments in pots (that is, any container with dimensions <1 m) or in the field, and studies on natural or planted vegetation. We only considered studies in which soil under both $CO_2$ treatments had the same treatment history. One study was discarded for this reason. Studies on soil water content and root biomass were only included if data on $N_2O$ or $CH_4$ fluxes were available from the same site. When root biomass and soil water content were reported for multiple soil depths, we calculated the overall treatment effects across the entire soil profile. We included separate observations of increased $CO_2$ effects from a single ecosystem under different experimental treatments (that is, in multi-factorial studies). Because wetlands are mostly anaerobic and therefore produce $CH_4$, whereas upland soils are mostly aerobic and oxidize $CH_4$, these two groups of ecosystems were considered in separate data sets. We also distinguished studies conducted in rice paddies, which like wetlands produce $CH_4$. Because the low number of studies on $N_2O$ fluxes from rice paddies (1) and wetlands (3) did not warrant the construction of separate data sets, these studies were not included in our analysis.

We divided the studies into two categories of N availability based on N fertilization rates, that is, more or less than $30 \, kg \, N \, ha^{-1} \, yr^{-1}$. This cut-off point was chosen because it is comparable to maximum atmospheric N depositions in the US and most of the EU[23]. We also distinguished between studies on natural or planted vegetation. Agricultural ecosystems were defined as grassland and cropland that received between 30 and $300 \, kg \, N \, ha^{-1} \, yr^{-1}$. The upper cut-off point was based on reported average fertilization rates for croplands in the world's most intensively fertilized region (that is, East Asia, at $150 \, kg \, N \, ha^{-1} \, yr^{-1}$)[16], and the assumption that average fertilizer N use per hectare will be twofold higher in 2050[30].

**Response metrics.** We evaluated our data sets by using meta-analysis. As a metric for the response of GHG emissions to increased $CO_2$, we used the natural log of the response ratio[24]. This metric starts with an estimate of the relative change in GHG emissions between ambient and increased $CO_2$ treatments, and log-transforms it to improve its statistical behaviour.

$$\ln R = \ln(GHG_i/GHG_a)$$

where GHG is the flux of either $CH_4$ or $N_2O$ under increased (i) or ambient (a) conditions. We also used $\ln R$ as a metric for $CO_2$ responses of root biomass and soil water contents. Fluxes of $CH_4$ from upland soils could not be analysed using this metric, because our data set included both sites with negative (that is, $CH_4$ uptake) and positive ($CH_4$ emissions) fluxes. For this reason, we also used the difference in annual emissions, expressed on an areal basis ($U$) as a metric:

$$U = (GHG_i - GHG_a)$$

with $GHG_i$ and $GHG_a$ as before. All but one study on wetland soils found net $CH_4$ emissions under both ambient and increased $CO_2$ conditions (Supplementary Data 2). This one study, which reported that increased $CO_2$ turned wetland soils from a net sink of $CH_4$ into a net source, was therefore excluded when calculating $\ln R$, but included when calculating $U$.

Several studies only measured $N_2O$ and $CH_4$ fluxes during the growing season. In these cases, we assumed that the effect of increased $CO_2$ on annual fluxes occurred entirely during this period. When the length of the growing season was not explicitly indicated, we assumed a growing season of 150 days. When studies measured gas fluxes for multiple years, fluxes were averaged over time.

**Weighting functions.** We performed analyses using non-parametric weighting functions and generated confidence intervals (CIs) on weighted effects sizes using bootstrapping. Because effect size estimates and subsequent inferences in meta-analysis may depend on how individual studies are weighted[12], we used three different weighting functions. First, weighted by replication: $W_R = (n_a \times n_i)/(n_a + n_i)$, where $n_a$ and $n_i$ are the number of replicates under ambient and increased $CO_2$, respectively[25]. For pot studies, $n$ equalled the number of replicate experimental

facilities (that is, growth chambers, glass houses, and so on), rather than the number of pots per $CO_2$ treatment. Second, unweighted. Each observation was assigned an equal weight: $W_U = 1$. Third, weighted by the inverse of the pooled variance, the weighting function conventionally used in meta-analyses[26]: $W_V = 1/(var_a/GHG_a^2 + var_i/GHG_i^2)$, with $GHG_a$ and $GHG_i$ as before, and $var_a$ and $var_i$ as their respective variance.

When variance estimates were missing for a study, we calculated the average coefficient of variation (CV) within each data set, and then approximated the missing variance by multiplying the reported mean by the average CV and squaring the result.

When multiple effects were extracted from the same experimental site, we adjusted the weights defined above by the total number of observations from that site. This approach ensured that all experimental comparisons in multifactor studies could be included in the data set without dominating the overall effect size. For three experimental sites, multiple studies were done on the same GHG fluxes at different points in time. We adjusted the weights of observations from these studies by the total number of observations per site. Thus, the final weights used in the analyses were $w_{f,i} = W_{f,i}/n_c$, where $n_c$ was the number of observations from the same site as the $i$th observation, and $f$ was the index that referred to one of the three weighting functions defined above.

Mean effects sizes ($\overline{\ln R}$, $\overline{U}$) for different categories of studies were estimated as:

$$\overline{\ln R} = \sum_i \left( \ln R_i \times w_{f,i} \right) \Big/ \sum_i w_{f,i}$$

$$\overline{U} = \sum_i \left( U_i \times w_{f,i} \right) \Big/ \sum_i w_{f,i}$$

We used METAWIN 2.1[27] to generate these mean effect sizes and 95% bootstrapped CIs (4,999 iterations). Treatment effects were considered significant if the 95% CI did not overlap with 0. The results for the analyses on $\ln R$ were back-transformed and reported as percentage change under increased $CO_2$ (that is, $100 \times (R - 1)$) to ease interpretation.

We tested whether $\ln R$ for GHG emissions was correlated with $\ln R$ for root biomass using the statistical package SPSS 19. Similarly, we tested whether $\ln R$ for GHG emissions was correlated with experiment duration or the level of $CO_2$ enrichment. The effect of increased $CO_2$ on soil emissions of $N_2O$, but not $CH_4$, showed a weak positive correlation with experiment duration (Supplementary Figs 2 and 3). $\ln R$ was not significantly correlated with the degree of $CO_2$ enrichment for either $N_2O$ or $CH_4$ emissions (Supplementary Figs 4 and 5). This result is probably due to the large variation in treatment effects between studies, masking effects of the degree in $CO_2$ enrichment. Alternatively, the results may reflect that plant growth is a saturating function of $CO_2$ concentrations. Since experiments increased atmospheric $CO_2$ to a similar extent for all data sets (Supplementary Table 13), we did not normalize effect sizes for the level of $CO_2$ enrichment.

Results using the different weighting functions were qualitatively similar. However, the variance-based weighting function, $W_v$, yielded weights that varied over 1,000 times in magnitude (Supplementary Data 1 and 2). By assigning extreme importance to individual observations, average effect sizes were largely determined by a small number of studies. Because variance estimates are notoriously unreliable (especially given the small samples common in many of these studies), we favoured the use of the alternative weighting functions (which assigned less extreme weights). In this Letter, we provide results of the analyses on effect sizes that were weighted by replication; results for all weighting functions can be found in Supplementary Tables 2–8, 11 and 12.

**Scaling of results.** We scaled up the results from the experiments by multiplying them by the total land area covered by the particular type of habitat that was being summarized. In other words, we took the mean effects and confidence intervals for $U$ calculated above and scaled them:

$$F = \overline{U} \times H$$

where $F$ is expressed in Pg $CO_2$ equiv. $yr^{-1}$, and $H$ is the amount of habitat in uplands, wetlands, or rice paddies (103.1, 5.7, and 1.3 million $km^2$, respectively[28,29]). Because N fertilization increases $N_2O$ emissions[16,17] and enhances plant growth, we distinguished between upland agricultural ecosystems (that is, 19.0 million $km^2$ of fertilized grasslands and croplands[16], minus 1.3 million $km^2$ of rice paddies[28]) and ecosystems receiving little or no fertilizer (103.1 – 19.0 + 1.3 = 85.4 million $km^2$).

We estimated the contribution of winter $N_2O$ emissions to total $N_2O$ emissions from a recently published data set[16]. For agricultural soils and soils under natural vegetation, studies conducted over the growing season and lasting 100–200 days were compared to studies conducted over the entire year (that is, lasting >300 days). Because tropical and subtropical systems do not experience marked

growing seasons, we excluded studies from those regions. For agricultural soils, we only considered studies on grassland and cropland receiving 30–300 kg N ha$^{-1}$ yr$^{-1}$ (that is, the same restrictions that applied to our data sets 1 and 2 for the global extrapolation shown in Fig. 2). The difference in mean $N_2O$ emissions between the two categories of study duration was assumed to be representative of $N_2O$ emissions outside the growing season.

To estimate the CI for the combined effect of increased $CO_2$ on all six GHG fluxes shown in Fig. 2, we calculated the square root of the sum of the squared CIs. Because the original CIs were asymmetric, we did this separately for the upper and lower CIs. All studies on rice paddies were conducted on planted vegetation, experimental conditions resembling real-world conditions. When we combined our extrapolated data to calculate the overall $CO_2$ effect on $CH_4$ emissions, we therefore included all available data from rice paddies (Fig. 2, Supplementary Fig. 1). To compare the emissions of GHG with soil C sequestration under increased $CO_2$, we used results from the analyses weighted by replication and from unweighted analyses as reported in ref. 12, applying the same study selection criteria as for studies in our current data set. These results were expressed as a function of total land area, using the same approach that was used to scale up our results on GHG fluxes.

30. Tilman, D. *et al.* Forecasting agriculturally driven global environmental change. *Science* **292,** 281–284 (2001).

## Supplementary Tables

**Supplementary Table 1.** Overview of $CO_2$ enrichment studies included in our meta-analyses.

| Citation | Ecosystem | Facility | Location | Coordinates | Site name | Increased [$CO_2$] (p.p.m.v.) | GHG | Additional citations root biomass | soil water content |
|---|---|---|---|---|---|---|---|---|---|
| **Upland** | | | | | | | | | |
| Ambus and Robertson 1999[1] | Trembling aspen | OTC[2] | Pellston, MI, USA | 45°34'-N, 84°40'-W | UMBS-OTC | 700 | $N_2O + CH_4$ | - | 33[1] |
| Arnone III and Bohlen 1998 | Grassland | GH | Basel, CH | 47°34'-N, 7°35'-E | Dept. of Integrative Biology | 570 | $N_2O$ | 87 | 34 |
| Baggs et al. 2003; Baggs and Blum 2004; Ineson et al. 1998 | Grassland | FACE | Eschikon, CH | 47°27'-N, 8°41'-E | Swiss FACE | 600 | $N_2O + CH_4$ | 53 | 35,36 |
| Billings et al. 2002 | Desert ecosystem | FACE | Mercury, NV, USA | 36°49'-N, 115°55'-W | NDFF | 550 | $N_2O$ | 77 | 74 |
| Blankinship et al. 2010; Niboyet et al. 2011 | Grassland | FACE | Stanford, CA, USA | 37°24'-N, 122°14'-W | JRGCE | 680 | $N_2O + CH_4$ | 39,75 | 75 |
| Cantarel et al. 2011 | Grassland | FACE | Theix, FR | 45°47'-N, 03°05'-E | CCCE | 600 | $N_2O$ | - | 40 |
| Dijkstra et al. 2010b | Grassland | GC | Fort Collins, CO, USA | 40°34'-N, 105°47'-E | USDA-ARS | 780 | $N_2O + CH_4$ | 46 | 46 |
| Dubbs and Whalen 2010; Phillips et al. 2001a,b | Loblolly pine forest | FACE | Duke Forest, NC, USA | 35°58'-N, 78°56'-W | FACTS-I | ambient + 200 | $N_2O + CH_4$ | 52 | 48 |
| Hagedorn et al. 2000 | Beech / Spruce forest | OTC | Birmensdorf, CH | 47°21'-N, 8°26'-E | WSL | ambient + 200 | $N_2O$ | 49 | 51 |
| Hungate et al. 1997 | Grassland | OTC | Stanford, CA, USA | 37°24'-N, 122°13'-W | MECCA | ambient + 360 | $N_2O$ | 54 | - |
| Kammann et al. 2008 | Grassland | FACE | Giessen, DE | 50°32'-N, 8°41'-E | Giessen FACE | ambient + 20% | $N_2O$ | - | 58 |
| Kanerva et al. 2007 | Grassland | OTC | Rehtijärvi, FI | 60°40'-N, 23°28'-E | Rehtijärvi | 530 | $N_2O + CH_4$ | - | - |
| Kettunen et al. 2005, 2006, 2007a,b | Grassland | GC | University of Joensuu, FI | 62°35'-N, 29°46'-E | Dept. of Biology | 720 | $N_2O + CH_4$ | 61,62,64 | 61-64 |
| Lam et al. 2011 | Winter wheat | FACE | Changping, CN | 40°10'-N, 116°14'-E | FACE | 565 | $N_2O + CH_4$ | - | - |
| Larsen et al. 2011 | Heathland | FACE | Copenhagen, DK | 55°53'-N, 11°58'-E | CLIMAITE | 510 | $N_2O$ | - | - |
| Martín-Olmedo et al. 2002 | Spring barley | GC | Edinburgh, UK | 55°55'-N, 3°11'-W | University of Edinburgh | 716 | $N_2O$ | 70 | 70 |
| Mosier et al. 2002 | Shortgrass steppe | OTC | Nunn, CO, USA | 40°50'-N,104°42'-W | LTER | 720 | $N_2O + CH_4$ | 76 | 73 |
| Pleijel et al. 1998 | Winter wheat | OTC | Östad säteri, SE | 57°54'-N, 12°24'-E | Östad säteri | 700 | $N_2O$ | - | - |
| Rütting et al. 2010 | Grassland | FACE | Bulls, NZ | 40°14'-S, 175°16'-E | NZ-FACE | 475 | $N_2O$ | 31 | 31 |
| Smith et al. 2010 | Sorghum / Soybean rotation | OTC | Auburn, AL, USA | 32°36'-N, 85°30'-W | USDA-ARS | 683 | $N_2O + CH_4$ | 81 | 86 |
| Welzmiller et al. 2008 | Sorghum | FACE | Maricopa, AZ, USA | 33°4'-N, 111°59'-W | Maricopa-FACE | 550 | $N_2O$ | - | 44 |
| **Wetland** | | | | | | | | | |
| Dacey et al. 1994; Marsh et al. 2005 | Marsh | OTC | Chesapeake Bay, FL, USA | 38°51'-N, 76°32'-W | Chesapeake Bay | ambient + 340 | $CH_4$ | 45,69 | - |
| Ellis et al. 2009 | Peatland (transplanted) | FACE | Abergwyngregyn, UK | 53°14'-N, 4°01'-E | Bangor-FACE | 558 | $CH_4$ | - | - |
| Hutchin et al. 1995 | Marsh | OTC | Bangor, UK | 53°-N, 4°-E | ITE-Bangor | 550 | $CH_4$ | - | - |
| Kang et al. 2001 | Peatland | GH | Bangor, UK | 53°-N, 4°-E | Solardomes | 700 | $N_2O + CH_4$ | 60 | - |
| Liikanen et al. 2003 | Eulittoral zone of lake | GH | University of Joensuu, FI | 62°35'-N, 29°46'-E | Dept. of Biology | 720 | $N_2O + CH_4$ | - | - |
| Megonigal and Schlesinger 1997 | Golden club | GC | Durham, NC, USA | 36°0'-N, 78°56'-W | Duke University | 720 | $CH_4$ | 71 | - |
| Saarnio et al. 1998; Saarnio and Silvola 1999 | Peatland | GH | University of Joensuu, FI | 62°35'-N, 29°46'-E | Dept. of Biology | 720 | $CH_4$ | - | - |
| Silvola et al. 2003 | Peatland | FACE | Kopparas mire, SE | 57°08'-N, 14°30'-E | BERI-SE | 560 | $CH_4$ | 37 | - |
| Silvola et al. 2003 | Peatland | FACE | La Chaux-des-Breuleux, CH | 47°13'-N, 07°03'-E | BERI-CH | 560 | $CH_4$ | 37 | - |
| Silvola et al. 2003 | Peatland | FACE | Roudsea Wood, UK | 54°14'-N, 03°01'-W | BERI-UK | 560 | $CH_4$ | - | - |
| Silvola et al. 2003 | Peatland | FACE | Salmisuo mire, FI | 62°47'-N, 30°56'-E | BERI-FI | 560 | $CH_4$ | 37 | - |
| Silvola et al. 2003 | Peatland | FACE | Wageningen, NL | 52°49'-N, 06°26'-E | BERI-NL | 560 | $CH_4$ | 37 | - |
| Vann and Megonigal 2003 | Golden club / Swamp cypress | GH | Durham, NC, USA | 36°0'-N, 78°56'-W | Duke University Phytotron | 700 | $CH_4$ | 72 | - |
| Wolf et al. 2007 | Three-square | GH | Edgewater, MD, USA | 38°53'-N, 76°33'-W | SERC | 735 | $CH_4$ | 91 | - |
| **Rice paddies** | | | | | | | | | |
| Allen et al. 2003 | Rice paddy | GC | Gainesville, FL, USA | 29°48'-N, 82°25'-E | SPAR chambers | 660 | $CH_4$ | 32 | - |
| Inubushi et al. 2003; Zheng et al. 2006 | Rice paddy | FACE | Shizukuishi, JP | 39°38'-N, 140°57'-E | Rice FACE 1a | 550 | $CH_4$ | 57,92 | - |
| Cheng et al. 2006, 2008; Lou et al. 2008 | Rice paddy | GC | Tsukuba, JP | 36°01'-N, 140°07'-E | Climatron facility | 570/680/743 | $N_2O + CH_4$ | 41,43,68 | - |
| Tokida et al. 2010 | Rice paddy | FACE | Shizukuishi, JP | 39°38'-N, 140°57'-E | Rice FACE 1b | 570 | $CH_4$ | 88 | - |
| Zheng et al. 2006 | Rice paddy | FACE | Wuxi city, CN | 31°37'-N, 120°28'-E | Rice FACE 2 | 550 | $CH_4$ | 92 | - |
| Ziska et al. 1998 | Rice paddy | OTC | Los Banos, PH | 14°13'-N, 121°15'-E | IRRI-OTC | 660 | $CH_4$ | 94 | - |

[1]Complete references can be found in the Supplementary notes.

[2]Abbreviations: OTC = Open Top Chamber, FACE = Free Air Carbon dioxide Enrichment, GH = Greenhouse, GC = Growth chamber

**Supplementary Table 2.** Summary of the results of the meta-analysis on the response of soil $N_2O$ emissions to atmospheric $CO_2$ enrichment, using the response metric $lnR$ (see Methods). Results are shown for the entire data set and for 7 different categories of studies. The meta-analysis was performed on studies weighted by replication, on unweighted studies, and on studies weighted by the inverse of the pooled variance.

| | | Weighted by replication | | | Unweighted | | | Weighted by (1 / var) | | |
| | | | 95% CI | | | 95% CI | | | 95% CI | |
| | n= | average | bootstrapping | | average | bootstrapping | | average | bootstrapping | |
| $lnR$ (%) | | | min. | max. | | min. | max. | | min. | max. |
|---|---|---|---|---|---|---|---|---|---|---|
| overall | 73 | 18.8 | 6.3 | 35.4 | 18.4 | 5.4 | 36.8 | 13.1 | 4.9 | 28.7 |
| *N fertilization (kg ha$^{-1}$ yr$^{-1}$)* | | | | | | | | | | |
| <30 | 35 | 9.7 | 0.4 | 26.9 | 10.3 | 3.4 | 42.3 | 12.2 | 1.5 | 35.4 |
| >30 | 38 | 30.2 | 4.5 | 61.0 | 28.1 | 4.4 | 63.0 | 14.9 | 2.4 | 36.3 |
| *Pot study* | | | | | | | | | | |
| no | 40 | 28.8 | 10.0 | 55.0 | 28.4 | 9.2 | 60.5 | 12.5 | 6.8 | 25.9 |
| yes | 33 | 2.9 | -6.7 | 18.6 | 5.4 | -6.7 | 24.3 | 14.7 | -8.5 | 50.0 |
| *Plant community* | | | | | | | | | | |
| natural | 22 | 24.5 | 5.2 | 57.4 | 29.7 | 5.8 | 65.0 | 21.5 | 5.8 | 79.7 |
| planted | 51 | 15.2 | 0.1 | 38.3 | 12.4 | -0.7 | 37.3 | 7.1 | -0.5 | 14.4 |
| | | | | | | | | | | |
| *Agricultural ecosystems* | 19 | 37.9 | 7.2 | 83.1 | 40.2 | 7.1 | 101.0 | 32.0 | 2.8 | 69.4 |

**Supplementary Table 3.** Summary of the results of the meta-analysis on the response of $CH_4$ emissions from wetlands to atmospheric $CO_2$ enrichment, using the response metric $lnR$ (see Methods). Results are shown for the entire data set and for 6 different categories of studies. The meta-analysis was performed on studies weighted by replication, on unweighted studies, and on studies weighted by the inverse of the pooled variance.

| | | Weighted by replication | | | Unweighted analysis | | | Weighted by (1 / var) | | |
| | | | 95% CI | | | 95% CI | | | 95% CI | |
| | n= | average | bootstrapping | | average | bootstrapping | | average | bootstrapping | |
| $lnR$ (%) | | | min. | max. | | min. | max. | | min. | max. |
|---|---|---|---|---|---|---|---|---|---|---|
| overall | 24 | 13.2 | -4.8 | 35.7 | 23.8 | 1.2 | 51.8 | 20.5 | 7.1 | 33.8 |
| *N fertilization (kg ha$^{-1}$ yr$^{-1}$)* | | | | | | | | | | |
| <30 | 16 | 13.2 | -6.6 | 37.5 | 23.0 | 0.4 | 52.4 | 16.9 | 2.9 | 35.5 |
| >30 | 8 | 12.8 | -36.6 | 69.9 | 26.3 | -32.2 | 89.5 | 26.4 | -7.8 | 46.1 |
| *Pot study* | | | | | | | | | | |
| no | 7 | 3.0 | -18.0 | 22.9 | 3.0 | -18.3 | 23.2 | 11.3 | -13.6 | 25.2 |
| yes | 17 | 28.6 | -3.1 | 66.8 | 38.9 | 1.3 | 74.9 | 28.1 | 7.6 | 47.0 |
| *Plant community* | | | | | | | | | | |
| natural | 19 | 9.9 | -9.2 | 31.8 | 15.4 | -8.7 | 41.2 | 11.9 | -6.4 | 27.2 |
| planted | 5 | 68.4 | 35.9 | 110.4 | 82.3 | 35.9 | 119.1 | 40.5 | 32.0 | 72.1 |

**Supplementary Table 4.** Summary of the results of the meta-analysis on the response of $CH_4$ emissions from rice paddies to atmospheric $CO_2$ enrichment, using the response metric ln$R$ (see Methods). Results are shown for the entire data set and for 2 different categories of studies. The meta-analysis was performed on studies weighted by replication, on unweighted studies, and on studies weighted by the inverse of the pooled variance.

| | | *Weighted by replication* | | | *Unweighted* | | | *Weighted by (1 / var)* | | |
| | n= | average | 95% CI | | average | 95% CI | | average | 95% CI | |
| | | | bootstrapping | | | bootstrapping | | | bootstrapping | |
| ln$R$ | | | min. | max. | | min. | max. | | min. | max. |
| (%) | | | | | | | | | | |
| overall | 21 | 43.4 | 23.5 | 71.6 | 42.3 | 25.0 | 66.3 | 32.4 | 22.0 | 51.4 |
| *Pot study* | | | | | | | | | | |
| no | 11 | 40.7 | 16.2 | 84.8 | 42.1 | 16.9 | 91.6 | 52.5 | 23.4 | 127.5 |
| yes | 10 | 49.5 | 25.5 | 65.1 | 42.4 | 23.5 | 62.7 | 25.0 | 18.7 | 40.3 |

**Supplementary Table 5.** Summary of the results of the meta-analysis on the response of $CH_4$ fluxes in upland soils to atmospheric $CO_2$ enrichment, using the response metric $U$ (see Methods). Results are shown for the entire data set and for 7 different categories of studies. The meta-analysis was performed on studies weighted by replication and on unweighted studies.

| | | *Weighted by replication* | | | *Unweighted* | | |
| | n= | average | 95% CI | | average | 95% CI | |
| $U$ | | | bootstrapping | | | bootstrapping | |
| (kg $CH_4$-C ha$^{-1}$yr$^{-1}$) | | | min. | max. | | min. | max. |
| overall | 33 | 0.00 | -0.09 | 0.07 | -0.02 | -0.12 | 0.07 |
| *N fertilization (kg ha$^{-1}$ yr$^{-1}$)* | | | | | | | |
| <30 | 23 | -0.04 | -0.17 | 0.09 | -0.08 | -0.21 | 0.04 |
| >30 | 10 | 0.05 | -0.04 | 0.15 | 0.07 | -0.04 | 0.20 |
| *Pot study* | | | | | | | |
| no | 19 | 0.01 | -0.10 | 0.10 | 0.02 | -0.09 | 0.13 |
| yes | 14 | -0.03 | -0.38 | 0.05 | -0.16 | -0.40 | -0.04 |
| *Plant community* | | | | | | | |
| natural | 10 | -0.05 | -0.23 | 0.18 | -0.06 | -0.24 | 0.21 |
| planted | 23 | 0.02 | -0.04 | 0.07 | -0.01 | -0.09 | 0.07 |
| *Agricultural ecosystems* | 8 | 0.05 | -0.06 | 0.15 | 0.04 | -0.08 | 0.13 |

**Supplementary Table 6.** Summary of the results of the meta-analysis on the response of $N_2O$ fluxes to atmospheric $CO_2$ enrichment, using the response metric $U$ (see Methods). Results are shown for the entire data set and for 7 different categories of studies. The meta-analysis was performed on studies weighted by replication and on unweighted studies.

| | | | *Weighted by replication* | | | *Unweighted* | |
| | | | 95% CI | | | 95% CI | |
| $U$ | n= | average | bootstrapping | | average | bootstrapping | |
| ($kg\,N_2O$-N $ha^{-1}yr^{-1}$) | | | min. | max. | | min. | max. |
|---|---|---|---|---|---|---|---|
| overall | 73 | 0.56 | 0.10 | 1.66 | 0.62 | 0.06 | 1.90 |
| *N fertilization (kg ha$^{-1}$ yr$^{-1}$)* | | | | | | | |
| <30 | 35 | 0.06 | 0.00 | 0.19 | 0.09 | 0.00 | 0.27 |
| >30 | 38 | 1.13 | 0.18 | 3.86 | 1.21 | 0.00 | 4.01 |
| *Pot study* | | | | | | | |
| no | 40 | 0.86 | 0.17 | 2.66 | 1.05 | 0.20 | 3.25 |
| yes | 33 | 0.03 | -0.27 | 0.28 | 0.00 | -0.63 | 0.45 |
| *Plant community* | | | | | | | |
| natural | 22 | 0.21 | 0.03 | 0.49 | 0.29 | 0.03 | 0.60 |
| planted | 51 | 0.79 | 0.05 | 2.71 | 0.82 | -0.08 | 2.86 |
| | | | | | | | |
| *Agricultural ecosystems* | 19 | 0.40 | 0.12 | 0.68 | 0.42 | 0.11 | 0.76 |

**Supplementary Table 7.** Summary of the results of the meta-analysis on the response of $CH_4$ fluxes from wetlands to atmospheric $CO_2$ enrichment, using the response metric $U$ (see Methods). Results are shown for the entire data set and for 6 different categories of studies. The meta-analysis was performed on studies weighted by replication and on unweighted studies.

| | | | *Weighted by replication* | | | *Unweighted analysis* | |
| | | | 95% CI | | | 95% CI | |
| $U$ | n= | average | bootstrapping | | average | bootstrapping | |
| ($kg\,CH_4$-C $ha^{-1}yr^{-1}$) | | | min. | max. | | min. | max. |
|---|---|---|---|---|---|---|---|
| overall | 25 | 28.2 | 11.0 | 54.7 | 46.2 | 18.5 | 83.4 |
| *N fertilization (kg ha$^{-1}$ yr$^{-1}$)* | | | | | | | |
| <30 | 16 | 16.4 | 0.6 | 37.0 | 23.1 | 4.5 | 50.9 |
| >30 | 9 | 89.7 | 22.6 | 192.6 | 100.7 | 26.0 | 189.9 |
| *Pot study* | | | | | | | |
| no | 7 | 9.7 | -3.7 | 23.1 | 9.7 | -3.5 | 23.4 |
| yes | 18 | 51.1 | 14.8 | 107.0 | 66.4 | 24.5 | 116.6 |
| *Plant community* | | | | | | | |
| natural | 19 | 15.0 | 0.1 | 35.5 | 19.9 | 2.3 | 46.1 |
| planted | 6 | 134.7 | 45.5 | 261.6 | 142.5 | 48.4 | 250.5 |

**Supplementary Table 8.** Summary of the results of the meta-analysis on the response of $CH_4$ fluxes from rice paddies to atmospheric $CO_2$ enrichment, using the response metric $U$ (see Methods). Results are shown for the entire data set and for 2 different categories of studies. The meta-analysis was performed on studies weighted by replication and on unweighted studies.

| $U$<br>$(kg\,CH_4\text{-}C\,ha^{-1}yr^{-1})$ | n= | Weighted by replication | | | Unweighted | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | average | 95% CI bootstrapping | | average | 95% CI bootstrapping | |
| | | | min. | max. | | min. | max. |
| overall | 21 | 58.7 | 26.2 | 96.4 | 57.7 | 31.4 | 88.1 |
| *Pot study* | | | | | | | |
| no | 11 | 47.6 | 13.2 | 96.6 | 51.3 | 13.9 | 104.9 |
| yes | 10 | 82.6 | 33.7 | 112.8 | 64.0 | 33.1 | 97.7 |

**Supplementary Table 9.** Comparison between spatially extrapolated $N_2O$ and $CH_4$ fluxes from ambient $CO_2$ treatments within our data set, based on studies weighted by replication and unweighted studies, and estimates reported in IPCC-AR4.

| | land area (M $km^2$) | Estimated global flux | | | |
| --- | --- | --- | --- | --- | --- |
| | | *Weighted by replication* | *Unweighted* | IPCC-AR4* | Unit |
| **$N_2O$** | | | | | |
| upland soils (natural) | 85.4 | 3.6 | 3.7 | 3.3 - 9.0 | $Tg\,N_2O\text{-}N\,yr^{-1}$ |
| upland soils (agriculture) | 17.7 | 2.3 | 2.5 | 1.7 - 4.8 | $Tg\,N_2O\text{-}N\,yr^{-1}$ |
| **$CH_4$** | | | | | |
| natural wetlands | 5.7 | 82.5 | 77.3 | 100 - 231 | $Tg\,CH_4\,yr^{-1}$ |
| rice paddies | 1.3 | 26.9 | 30.1 | 31 - 112 | $Tg\,CH_4\,yr^{-1}$ |
| upland soils (natural) | 85.4 | -10.8 | -13.7 | | $Tg\,CH_4\,yr^{-1}$ |
| upland soils (agriculture) | 17.7 | -0.3 | -0.1 | | $Tg\,CH_4\,yr^{-1}$ |
| upland soils (combined) | 103.1 | -11.0 | -13.8 | -26 - -34 | $Tg\,CH_4\,yr^{-1}$ |

* Denman, K. L. *et al*. in *Climate Change 2007: The Physical Science Basis*, (eds Solomon, S. *et al*.) 499-587 (Cambridge Univ. Press, 2007). Tables 6 and 7.

**Supplementary Table 10.** The effect of increased atmospheric $CO_2$ on the $CH_4$ and $N_2O$ emissions compared to its effect on soil C storage, and to the expected $CO_2$-induced change in the terrestrial C sink during this century. Results from the meta-analyses are based on the response metric $U$, using either studies weighted by replication or unweighted studies. Results are expressed in Pg $CO_2$ equiv. $yr^{-1}$, if not indicated differently.

| **Terrestrial C sink - modelled[*] (1)** | years | | |
|---|---|---|---|
| | 1976-2000 | 2076-2100 | difference |
| | 3.52 | 10.30 | 6.78 |

| **Meta-analyses on the effect of elevated $CO_2$** | *Weighted by replication* | *Unweighted* |
|---|---|---|
| Soil C[**] (2) | 4.01 | 4.09 |
| Soil emissions of $CH_4$ and $N_2O$ (combined)[***] (3) | 1.12 | 1.38 |
| (3) as a % of (1) | 16.6 | 20.3 |
| (3) as a % of (2) | 28.0 | 33.6 |

[*] Thornton, P. E., Lamarque J. –F., Rosenbloom, N. A. & Mahowald, N. M. Influence of carbon-nitrogen cycle coupling on land model response to $CO_2$ fertilization and climate variability. *Glob. Biogeochem. Cy.* **21**, GB4018, doi:10.1029/2006GB002868 (2007). Table 3.
[**] Hungate, B. A. *et al.* Assessing the effect of elevated $CO_2$ on soil carbon: a comparison of four meta-analyses. *Glob. Change Biol.* **15**, 2020-2034 (2009).
[***] This study.

**Supplementary Table 11.** Summary of the results of the meta-analysis on the response of soil water content for upland soils to atmospheric $CO_2$ enrichment, using the response metric $\ln R$ (see Methods). Results are shown for the entire data set and for 6 different categories of studies. The meta-analysis was performed on studies weighted by replication, on unweighted studies, and on studies weighted by the inverse of the pooled variance.

| | | *Weighted by replication* | | | *Unweighted* | | | *Weighted by (1 / var)* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **n=** | **average** | **95% CI** | | **average** | **95% CI** | | **average** | **95% CI** | |
| | | | bootstrapping | | | bootstrapping | | | bootstrapping | |
| $\ln R$ | | | min. | max. | | min. | max. | | min. | max. |
| (%) | | | | | | | | | | |
| overall | 55 | 5.8 | 2.2 | 10.2 | 6.0 | 2.7 | 10.5 | 6.2 | 2.6 | 10.6 |
| *N fertilization (kg ha$^{-1}$ yr$^{-1}$)* | | | | | | | | | | |
| <30 | 28 | 8.5 | 3.4 | 15.6 | 8.9 | 2.8 | 15.5 | 7.1 | 2.5 | 12.2 |
| >30 | 27 | 2.0 | -0.7 | 4.8 | 2.8 | 0.4 | 5.9 | 2.7 | 0.8 | 5.1 |
| *Pot study* | | | | | | | | | | |
| no | 27 | 5.0 | 0.5 | 11.3 | 5.3 | 0.1 | 12.2 | 8.4 | 1.2 | 14.3 |
| yes | 28 | 7.2 | 3.3 | 12.3 | 7.1 | 3.5 | 11.7 | 5.5 | 2.0 | 11.1 |
| *Plant community* | | | | | | | | | | |
| natural | 18 | 7.2 | 2.2 | 15.8 | 8.1 | 1.8 | 17.7 | 13.3 | 2.4 | 18.1 |
| planted | 37 | 4.4 | 0.3 | 8.7 | 4.6 | 1.5 | 8.5 | 3.6 | 1.9 | 7.0 |

**Supplementary Table 12.** Summary of the results of the meta-analysis on root biomass response to atmospheric $CO_2$ enrichment, for studies included in data sets 1 and 2, using the response metric ln$R$ (see Methods). Results are shown for the entire data set and for 9 different categories of studies. The meta-analysis was performed on studies weighted by replication, on unweighted studies, and on studies weighted by the inverse of the pooled variance.

| ln*R* (%) | n= | Weighted by replication | | | Unweighted | | | Weighted by (1/var) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | average | 95% CI bootstrapping | | average | 95% CI bootstrapping | | average | 95% CI bootstrapping | |
| | | | min. | max. | | min. | max. | | min. | max. |
| overall | 84 | 18.6 | 11.0 | 25.9 | 22.9 | 14.6 | 34.7 | 22.1 | 15.2 | 30.8 |
| *N fertilization (kg ha$^{-1}$ yr$^{-1}$)* | | | | | | | | | | |
| <30 | 35 | 14.6 | 2.8 | 26.0 | 16.7 | 1.9 | 43.1 | 9.4 | 2.0 | 19.5 |
| >30 | 49 | 24.1 | 16.7 | 31.7 | 28.5 | 21.4 | 36.5 | 29.8 | 21.5 | 39.2 |
| *Pot study* | | | | | | | | | | |
| no | 39 | 14.2 | 3.7 | 24.1 | 13.7 | 2.4 | 24.0 | 21.9 | 9.4 | 37.6 |
| yes | 45 | 26.5 | 18.8 | 39.5 | 31.5 | 19.3 | 52.3 | 22.2 | 13.9 | 32.1 |
| *Plant community* | | | | | | | | | | |
| natural | 25 | 11.1 | -2.1 | 23.3 | 16.2 | -2.4 | 46.5 | 8.7 | -2.8 | 21.7 |
| planted | 59 | 26.6 | 20.8 | 33.0 | 27.3 | 20.7 | 34.8 | 26.4 | 18.3 | 35.1 |
| *Habitat* | | | | | | | | | | |
| wetland | 14 | 30.0 | 20.2 | 48.6 | 40.8 | 22.0 | 83.9 | 34.5 | 20.4 | 50.1 |
| upland | 53 | 6.2 | -3.9 | 16.1 | 9.4 | -0.5 | 20.9 | 15.8 | 8.1 | 26.0 |
| rice | 17 | 31.8 | 23.8 | 44.3 | 30.8 | 21.1 | 43.0 | 28.7 | 16.1 | 48.2 |

**Supplementary Table 13.** Overview of the average degree of $CO_2$ enrichment (p.p.m.v. above ambient) for studies in each of the data sets on $N_2O$ and $CH_4$ fluxes. The average was calculated for studies weighted by replication and for unweighted studies.

| Data set | average $CO_2$ enrichment (p.p.m.v.) | |
|---|---|---|
| | *Weighted by replication* | *Unweighted* |
| $N_2O$ | 237 | 250 |
| $CH_4$ - wetlands | 251 | 279 |
| $CH_4$ - rice paddies | 257 | 257 |
| $CH_4$ - upland soils | 254 | 263 |

**Supplementary Figures**
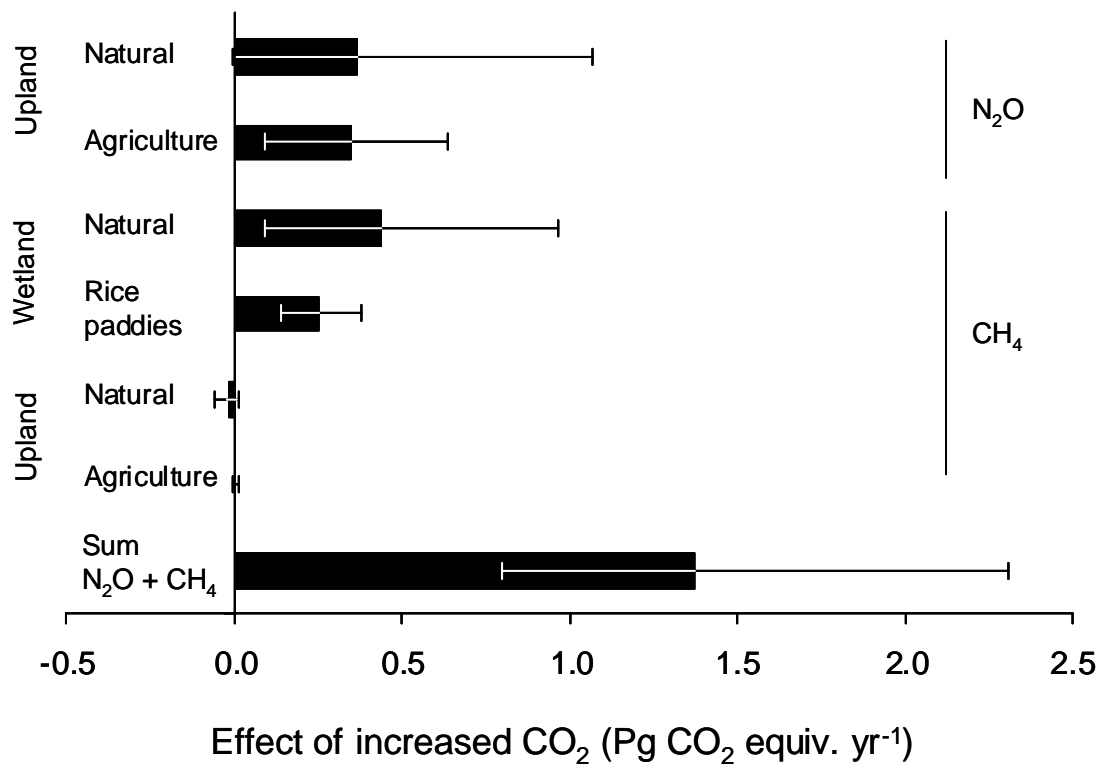


**Supplementary Figure 1.** The effect of rising atmospheric $CO_2$ on GHG emissions, expressed on the global scale. For $N_2O$ fluxes, the results for natural and agricultural soils were based on 35 and 19 observations, respectively. For $CH_4$ fluxes, the results for natural wetlands, rice paddies, natural upland soils and agricultural upland soils were based on 16, 21, 10 and 8 observations, respectively. Results were calculated using the response metric $U$ for unweighted studies (that is, by using weighting function $W_U$). Error bars, 95% confidence intervals.
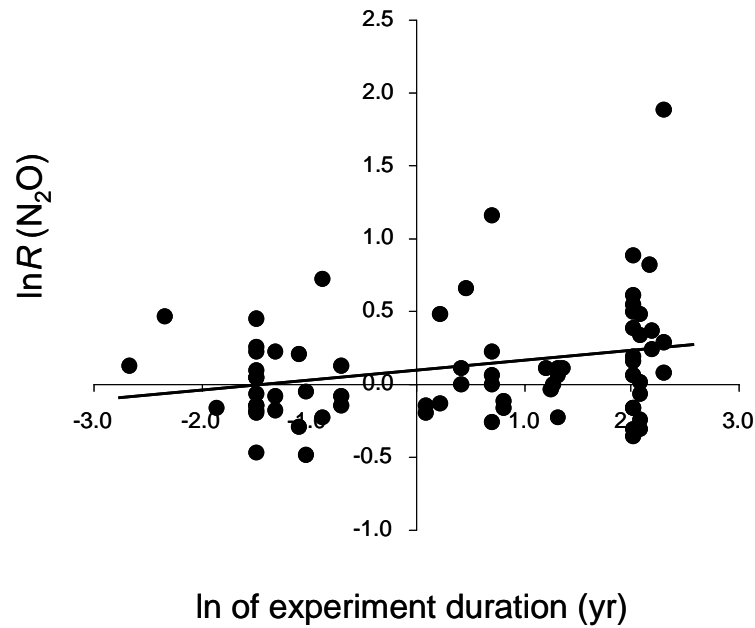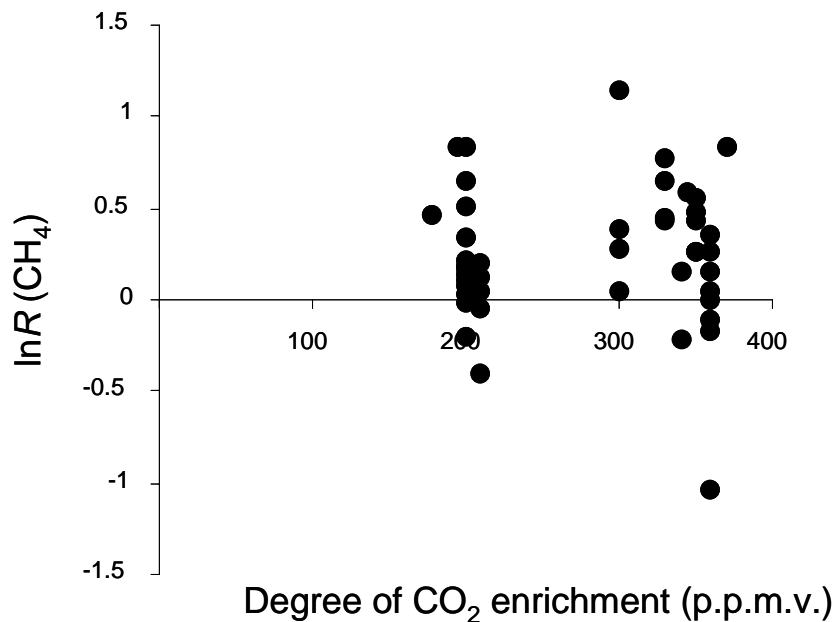
**Supplementary Figure 2.** Effect of increased atmospheric $CO_2$ on soil emissions of $N_2O$ (ln$R$) vs. the natural log of experiment duration in years. ln$R$ is significantly correlated with the length of the experiment ($r^2=0.06$, p=0.01).
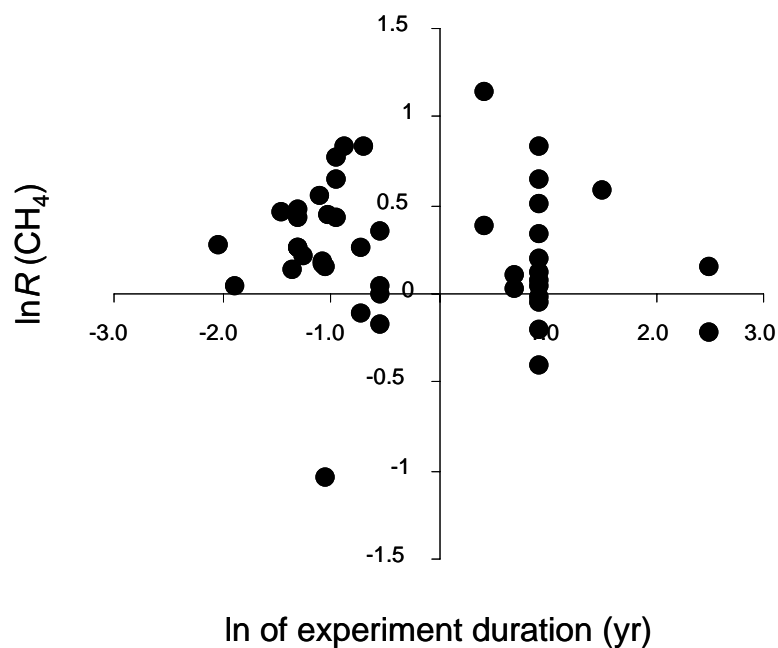


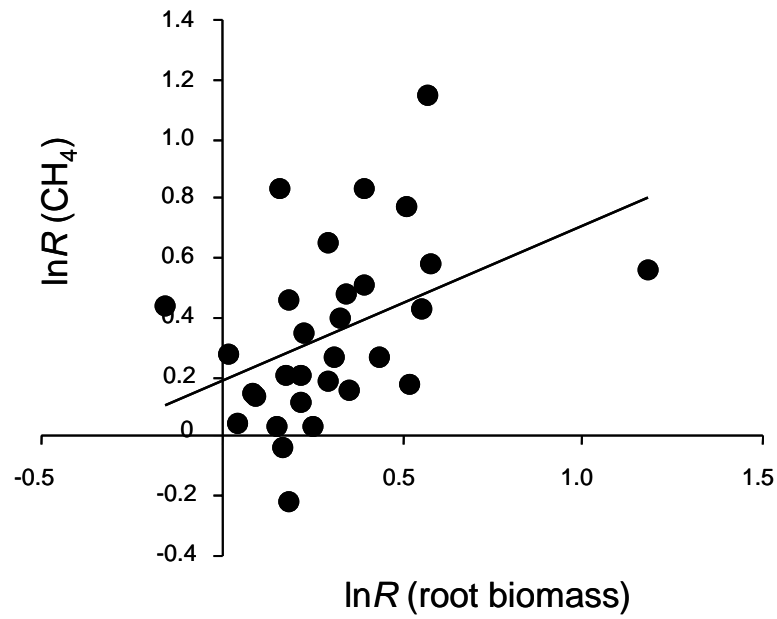**Supplementary Figure 3.** Effect of increased atmospheric $CO_2$ on soil emissions of $CH_4$ from wetlands and rice (ln$R$) vs. the natural log of experiment duration in years. ln$R$ is not significantly correlated with the length of the experiment ($r^2=0.03$, p=0.30).
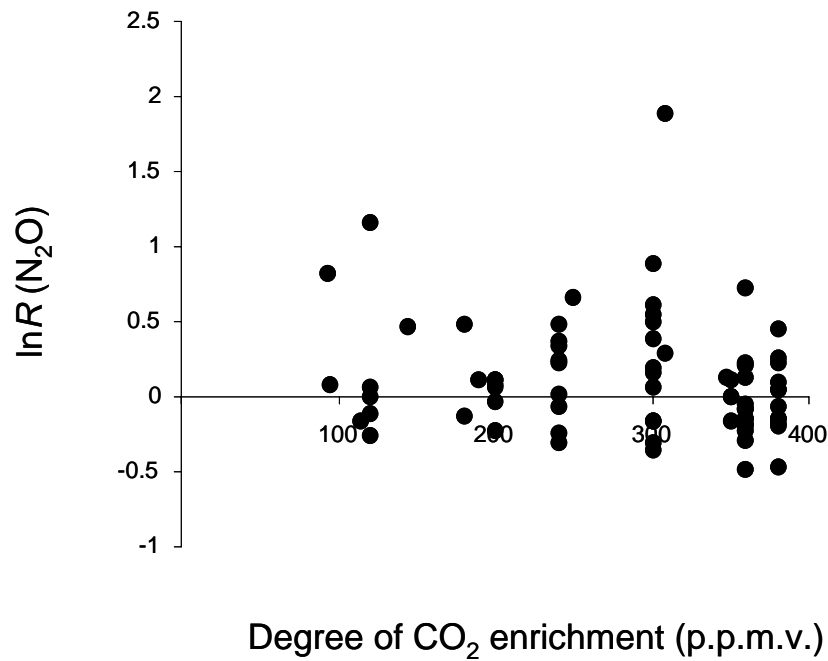
**Supplementary Figure 4.** Effect of increased atmospheric $CO_2$ on soil emissions of $N_2O$ (ln$R$) vs. the degree of $CO_2$ enrichment. ln$R$ is not significantly correlated with degree of $CO_2$ enrichment ($r^2$=0.03, p=0.20).



**Supplementary Figure 5.** Effect of increased atmospheric $CO_2$ on soil emissions of $CH_4$ from wetlands and rice (ln$R$) vs. the degree of $CO_2$ enrichment. ln$R$ is not significantly correlated with degree of $CO_2$ enrichment ($r^2$=0.00, p=0.93).

**Supplementary Figure 6.** The effect of increased atmospheric $CO_2$ on soil emissions of $CH_4$ from wetlands and rice (ln$R$) vs. its effect on root biomass (ln$R$). The effect sizes were significantly correlated with each other ($r^2$=0.17, p=0.02).

## Supplementary Notes 1

*References Data sets 1-4*

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GLOBAL CHANGE

# Indirect feedbacks to rising CO₂

**There have been many studies on the effects of enriched levels of atmospheric carbon dioxide on soils. A meta-analysis shows that emissions of other greenhouse gases increase under high-CO₂ conditions. SEE LETTER P.214**

## ALEXANDER KNOHL & EDZO VELDKAMP

Human activities have caused atmospheric concentrations of carbon dioxide, a major greenhouse gas, to increase at an accelerating pace. Starting at around 280 parts per million (p.p.m.) in pre-industrial times, they have now exceeded 390 p.p.m., and are expected to reach 600–800 p.p.m. by the end of the century[1]. On page 214 of this issue[2], van Groenigen and colleagues add to our awareness of the complex consequences of this trend, in terms of the effect that it will have on emissions of other greenhouse gases from various ecosystems.

In producing global warming, CO₂ is responsible for the largest part of the anthropogenic impact on Earth's energy balance. It is, of course, also an essential nutrient for plant metabolism. Numerous CO₂-enrichment experiments over the past two decades have demonstrated the positive effect of elevated CO₂ on plant growth — increased biomass and increased carbon storage in soils[3]. The vegetation response to elevated CO₂ might be constrained by various interactions with water and nutrients such as nitrogen[4,5]. However, experiments and model projections suggest that accelerated plant growth due to CO₂ fertilization could draw down some of this gas from the atmosphere, and hence could weaken future rates of CO₂ increase and lessen the severity of climate change[6].

Van Groenigen et al.[2] present evidence that rising levels of CO₂ are not only resulting in an increased carbon sink in terrestrial ecosystems, but could also cause increased emissions of other, much more potent, greenhouse gases such as methane (CH₄) and nitrous oxide (N₂O) from soils. Methane is produced by anaerobic methanogenic microorganisms that thrive in wetlands, including rice paddies, where labile (biologically accessible) carbon is available and diffusion of oxygen into the soil is severely restricted. Nitrous oxide is mainly produced in soils by aerobic nitrifying and anaerobic denitrifying bacteria. The interaction between nitrogen availability and soil water content controls the rate of N₂O production. The respective global-warming potentials of CH₄ and N₂O are 25 and 298 times greater than that of CO₂, and thus they influence Earth's energy balance even though they occur in much smaller concentrations.

Van Groenigen and colleagues collected information from 49 published studies that reported the effect of atmospheric CO₂ enrichment on CH₄ and N₂O fluxes from soils. Using a meta-analysis, they show that elevated CO₂ stimulated N₂O emissions by 18.8%, and that CH₄ emissions from wetlands increased by 13.2% and from rice paddies by as much as 43.4%. Notably, they also suggest the mechanisms that are probably responsible for these observed increases in greenhouse-gas emissions (Fig. 1).

Their suggestion goes as follows. Elevated CO₂ led to reduced plant transpiration (the evaporation of water from plant surfaces, leaves in particular), which increased soil water content and promoted the existence of anaerobic microsites in soils. This, together with increasing biological activity, probably stimulated denitrification and consequently N₂O production. Also, the CO₂-induced increase in root biomass may have contributed by increasing the availability of labile carbon, a crucial energy source for denitrification. The CO₂-induced stimulation of CH₄ emissions from wetlands and rice paddies was probably the result of higher net plant production, leading to increasing carbon availability for substrate-limited methanogenic microorganisms. Extrapolating their
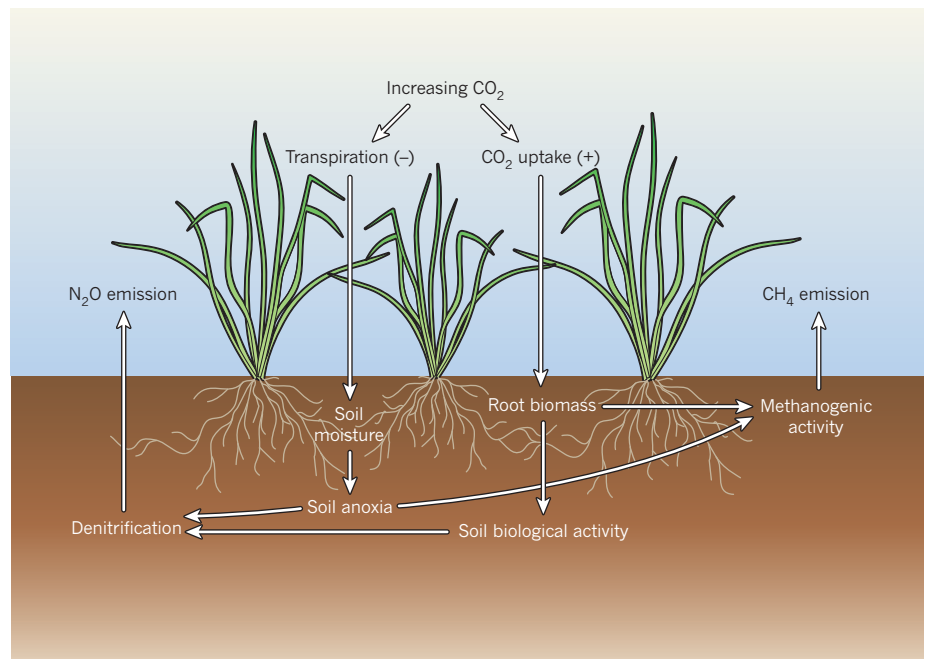


**Figure 1 | Proposed mechanisms of increased N₂O and CH₄ emissions from soils.** From their meta-analysis, van Groenigen et al.[2] estimate that rising levels of atmospheric CO₂ will result in more output of N₂O from upland soil (at a rate equivalent to 0.57 Pg CO₂ yr⁻¹) and of CH₄ from rice paddies and wetlands (equivalent to 0.56 Pg CO₂ yr⁻¹). They suggest that these increases are caused by reduced plant transpiration under conditions of elevated CO₂, resulting in increased soil moisture. Together with increased root biomass, this leads both to greater denitrification (and hence increased N₂O emission) and to more methanogenic activity (and hence increased CH₄ emission). The increase in these greenhouse gases will thus partially offset the predicted enhanced uptake of carbon by terrestrial ecosystems in a high-CO₂ world.

results to the global scale, van Groenigen et al.[2] estimate that the combined effect of stimulated $N_2O$ and $CH_4$ emissions could be equivalent to at least 1.12 Pg $CO_2$ $yr^{-1}$ (Pg = petagrams = $10^{15}$ grams). This is around 17% of the expected increase of the terrestrial $CO_2$ sink as a result of higher $CO_2$ concentrations.

Earlier studies have shown that long-term carbon sequestration in a $CO_2$-enriched atmosphere can be constrained by nitrogen availability[5,6]. Critics may wonder how these studies and van Groenigen and colleagues' analysis fit together, as it seems unlikely that denitrification would be stimulated by elevated $CO_2$ in nitrogen-limited ecosystems. This apparent discrepancy may be explained by the geographical bias in the present paper. The large majority of the 49 studies included in the meta-analysis were located in temperate regions, in areas — the United States, Europe, China and Japan — that are nowadays subject to considerable deposition of atmospheric nitrogen[7]. Some ecosystems included in the meta-analysis, such as agricultural areas receiving little or no fertilizer, and regions of natural vegetation, may thus have been subject to the input of considerable anthropogenic nitrogen through the atmosphere. Because nitrogen deposition is predicted to increase in the coming decades, the studies may therefore be more representative of future conditions, when nitrogen deposition will have become a global feature.

Another striking point is the almost complete lack of studies in the tropics and subtropics, where the strongest increases in nitrogen deposition are expected to occur[7]. Some tropical ecosystems may react differently from temperate ecosystems to elevated $CO_2$ concentrations. Many intact tropical forests tend to cycle large quantities of nitrogen[8], and an increase in soil-moisture content may have strong effects on $N_2O$ emissions even without nitrogen deposition. Tropical grasslands are dominated by grasses using the $C_4$ photosynthetic pathway, which may improve their water-use efficiency to different extents from that of plants using the $C_3$ pathway. There is a clear need for field studies in these ecosystems, in order to improve our ability to evaluate the overall effect of elevated $CO_2$ on the budgets of greenhouse-gas emissions.

Obviously, the report by van Groenigen et al.[2] is not the end of the story, and future research may provide evidence of other feedbacks that have not yet been quantified or even hypothesized. Nevertheless, this study provides the first comprehensive analysis of available data that shows the importance of indirect feedbacks of elevated $CO_2$ on $CH_4$ and $N_2O$ emissions on a global scale. It is now up to the scientific community to include these feedbacks in global climate models and to fill in the large gaps in information that still exist. ∎

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REGENERATIVE MEDICINE

# Drawing breath after spinal injury

**New work on a rat model suggests that, after spinal-cord injury, restoration of sustained and robust respiratory function is possible using strategies that promote both neuronal plasticity and regeneration.** SEE ARTICLE P.196

**KATHERINE ZUKOR & ZHIGANG HE**

'Above C4, breathe no more.' This is the memory aid that reminds medical students that damage to the spinal cord above the fourth cervical vertebra (C4) — that is, the neck — can interrupt breathing. Injuries at the cervical level are the most common type of spinal-cord injury and account for more than half of all cases. Individuals who survive such injuries usually need ventilators to breathe, and so face a host of complications to their overall health and quality of life. A study by Alilain et al.[1] on page 196 of this issue offers hope that we may one day know how to treat this problem, so that patients with spinal-cord injuries above C4 can breathe on their own.

Breathing rate, rhythm and depth are controlled automatically by specialized regions of the brainstem[2] (Fig. 1a). The neurons in these regions send their axonal processes down the spinal cord to control the activity of other neurons in the phrenic motor nuclei (PMN) of the cervical spinal cord (C3–C6). The axons of the PMN neurons form the phrenic nerves, which, in turn, innervate the muscles of the diaphragm. Thus, contraction and relaxation of the diaphragm enable rhythmic breathing. When the spinal cord is injured above the C4 level, axons connecting the brainstem to the PMN are damaged, and breathing is disrupted. To make matters worse, axons in the adult spinal cord do not regenerate well, one of the main reasons being the inhibitory environment of the injured spinal cord[3].

Over the years, researchers have invoked many strategies to provide axons with a more supportive environment. These include either removing inhibitory molecules, such as chondroitin sulphate proteoglycans (CSPGs) in the extracellular matrix[4], or grafting in a piece of peripheral nerve that could serve as a bridge for axonal growth[5]. Combinations of these approaches have yielded encouraging results. For example, after a cervical spinal-cord injury (SCI) in rats, applying a peripheral nerve graft, together with injection of the enzyme chondroitinase ABC (chABC) to degrade CSPGs, allows spinal-cord axons to regenerate through the graft, re-enter the spinal cord and form synaptic connections with neurons on the opposite side of the injury[6].

Alilain et al.[1] applied a similar treatment strategy to recover respiratory function in rats after SCI. The authors made a partial injury at the C2 level to paralyse the diaphragm on one side of the animals' body (Fig. 1b). They then removed a piece of the rats' tibial nerve and grafted one end of it in the injury site at C2 and the other end in a small slit at the C4 level — near the PMN. Finally, they injected chABC at both ends of the graft, as well as in the PMN area, to degrade CSPGs (Fig. 1b).

Twelve weeks after injury, the group receiving this treatment had the highest percentage of recovered animals and the best quality of recovery in respiratory function compared with controls. Specifically, in many animals the paralysed half of the diaphragm muscle recovered nearly normal rhythmic electrical activity. Moreover, neurons from breathing centres of the brainstem grew axons into the graft. To demonstrate that recovery was largely due to axons that had regenerated through the graft and not just the rewiring of circuits in the portions of the spinal cord that were uninjured, Alilain et al. cut the graft; this treatment