Effects of elevated carbon dioxide and increased temperature on methane and nitrous oxide fluxes: evidence from field experiments

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Climate change could alter terrestrial ecosystems, which are important sources and sinks of the potent greenhouse gases (GHGs) nitrous oxide (N_2O) and methane (CH_4), in ways that either stimulate or decrease the magnitude and duration of global warming. Using manipulative field experiments, we assessed how N_2O and CH_4 soil fluxes responded to a rise in atmospheric carbon dioxide (CO_2) concentration and to increased air temperature. Nitrous oxide and CH_4 responses varied greatly among studied ecosystems. Elevated CO_2 often stimulated N_2O emissions in fertilized systems and CH_4 emissions in wetlands, peatlands, and rice paddy fields; both effects were stronger in clayey soils than in sandy upland soils. Elevated temperature, however, impacted N_2O and CH_4 emissions inconsistently. Thus, the effects of elevated CO_2 concentrations on N_2O and CH_4 emissions may further enhance global warming, but it remains unclear whether increased temperature generates positive or negative feedbacks on these GHGs in terrestrial ecosystems.

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Global warming is caused by increased atmospheric concentrations of the greenhouse gases (GHGs) carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4). Terrestrial ecosystems are important sources and sinks of these GHGs, all of which are produced and consumed through biological processes including photosynthesis, decomposition, nitrification, denitrification, methanogenesis, and CH_4 oxidation (eg Schlesinger 1997). Increased atmospheric CO_2 concentration and elevated air/soil temperatures (hereafter elevated CO_2 and temperature; please note also that, unless stated otherwise, the following text refers to terrestrial ecosystems) can directly and indirectly alter these processes. Depending on the direction and magnitude of the alteration, elevated CO_2 and temperature could either accelerate or decelerate the rate of global warming.

In a nutshell:

- Net emissions of nitrous oxide (N_2O) and methane (CH_4) from terrestrial ecosystems could increase or decrease in response to climate change, thereby either accelerating or decelerating global warming
- Field experiments examining the effects of climate change on N_2O and CH_4 emissions provide important information that may help improve long-term predictions with process-based models
- A rise in atmospheric carbon dioxide concentration often increased N_2O emissions in fertilized systems and CH_4 emissions in wetlands, peatlands, and rice paddy fields; such increases may enhance global warming
- Conversely, responses of N_2O and CH_4 emissions to elevated temperatures have been inconsistent in many ecosystems

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The effects of elevated CO_2 and temperature on N_2O and CH_4 fluxes in terrestrial ecosystems have been studied less frequently than the effects on CO_2 exchange. This is not surprising given that CO_2 exchange rates are usually orders of magnitude greater than the exchange rates of N_2O and CH_4 (Schlesinger 1997). However, N_2O and CH_4 have higher global warming potentials (GWPs) than that of CO_2. Thus, although CO_2 is – per molecule – the most important GHG, N_2O and CH_4 are more efficient in warming the atmosphere (the GWPs of N_2O and CH_4 are 298 and 25 times that of CO_2, respectively, over a 100-year period; Forster *et al.* 2007). Global warming is therefore more sensitive to changes in the exchange of N_2O and CH_4 relative to that of CO_2.

Process-based ecosystem models applied at regional and continental scales have recently estimated that net N_2O and CH_4 emissions increased during the past 40 years and could further increase in the future because of elevated CO_2 and temperatures (Xu *et al.* 2010, 2012; Tian *et al.* 2012). Although important for long-term and large-scale predictions of climate-change feedbacks, modeling efforts still leave a lot of uncertainty, mostly due to our limited understanding of the underlying mechanisms governing N_2O and CH_4 fluxes in different ecosystems (Tian *et al.* 2012).

Controlled field experiments that manipulate atmospheric CO_2 levels and temperatures allow for a systematic evaluation of ecosystem responses. Experimental manipulations of CO_2 and temperature cause secondary changes in other environmental factors – such as soil temperature and moisture, and soil carbon (C) and nitrogen (N) availability – and also affect plant growth, microbial growth, and community composition (Pendall *et al.* 2004; Engel *et al.* 2009; Morgan *et al.* 2011). Elevated CO_2 and temperature effects on N_2O and CH_4 fluxes can therefore be investigated in a holistic way that incorporates all of these changes. Furthermore, manipulative field experiments allow for single, combined, and interactive effects of elevated CO_2 and temperature to be investigated. However, these field manipulations are usually performed with step increases in CO_2 concentration and temperature that may cause different effects than would gradual increases (Klironomos *et al.* 2005). Given the large monetary costs associated with maintaining such treatments in the field, these experiments usually do not extend for more than 5 years, which leaves much uncertainty concerning the long-term effects of these treatments. Despite these limitations, manipulative field experiments provide important information about the effects of elevated CO_2 and temperature on N_2O and CH_4 fluxes under realistic conditions that may help improve long-term predictions with process-based models.

Here, we summarize results from manipulative field experiments conducted in different terrestrial ecosystems and assess how elevated CO_2 and temperature affected soil fluxes of N_2O and CH_4. Although precipitation has a major effect on N_2O and CH_4 fluxes (eg Borken *et al.* 2000; Goldberg and Gebauer 2009), current projections about precipitation regimes in response to climate change remain uncertain (Meehl *et al.* 2007). Meta-analysis is often applied to summarize results from independent experiments where effect sizes of individual experiments are standardized by log response ratios or differences between treatment and control groups divided by the within-group standard deviation (Hedges *et al.* 1999). However, we focus on reporting absolute effects of elevated CO_2 and temperature from individual studies, which allows us to (1) assess the biogeochemical importance of elevated CO_2 and temperature effects on N_2O and CH_4 fluxes, and (2) relate the variability in responses among studies to site-specific soil characteristics (eg soil texture and pH).

Methods

We reviewed 41 peer-reviewed publications that reported effects on N_2O and/or CH_4 fluxes from elevated CO_2 and/or temperature treatments from 45 field sites that encompass a wide range of ecosystems (WebTable 1). Most field studies manipulating atmospheric CO_2 used open-top chamber (OTC) or free air carbon dioxide enrichment technology. Researchers manipulated the temperatures of field plots passively, using OTC or area covers or actively using heating cables buried in the soil or else infrared heaters installed above the canopy. Atmospheric CO_2 levels in elevated treatments ranged between 470 and 700 parts per million, and "warming" treatments resulted in temperature increases of between 1° and 5°C above ambient soil, canopy, or air temperatures. These atmospheric CO_2 and temperature increases are consistent with Intergovernmental Panel on Climate Change projections for the middle or end of the 21st century (Meehl *et al.* 2007).

We report effects of elevated CO_2 and temperature on N_2O and CH_4 fluxes as the change in the average flux rates in CO_2 or temperature treatments as compared with ambient control treatments during the time frame of measurement. Effects that increased or decreased emissions into the atmosphere are presented as positive or negative values, respectively. In studies where other treatments were included (eg irrigation, plant species, ozone), we averaged results across those treatments. In elevated CO_2 studies that included N fertilization, elevated CO_2 effects on N_2O fluxes were reported for each level of N fertilization. All fluxes reported here are expressed in milligrams of CO_2 equivalents per square meter per day (mg $CO_2eq\ m^{-2}\ d^{-1}$) to allow for comparison between N_2O and CH_4 flux responses.

Because elevated CO_2 and temperature effects on N_2O and CH_4 flux rates were highly variable among studies, we tested whether this variability could be explained by soil properties at each study site. We chose clay content and pH because these two factors (1) can have important effects on biological activity and N_2O and CH_4 fluxes (Stehfest and Bouwman 2006; Fierer *et al.* 2009) and (2) are frequently reported in the literature. We related site-specific clay content and pH to site-specific changes in N_2O and CH_4 fluxes in response to elevated CO_2 and temperature. At some sites, N_2O and CH_4 fluxes were reported in more than one study during different time periods; in those cases, the fluxes were averaged across the different studies and weighted by the time period of measurement. Using JMP (version 8.0.1; SAS Institute, Cary, North Carolina), we ran linear and non-linear regressions where flux measurements conducted over longer time periods were more heavily weighted (Dijkstra and Morgan 2012).

Results

Effects of elevated CO_2 on N_2O fluxes

Elevated CO_2 levels had highly variable effects on N_2O fluxes (Figure 1). The largest increases in N_2O emissions in response to CO_2 treatments were observed in N-fertilized studies (up to 5058 mg $CO_2eq\ m^{-2}\ d^{-1}$) and were frequently significant (Figure 1a). In contrast, the effects of elevated CO_2 on N_2O were consistently non-significant in non-fertilized studies (Figure 1b). In a meta-analysis that included growth chamber and greenhouse studies, van Groenigen *et al.* (2011) concluded that elevated CO_2

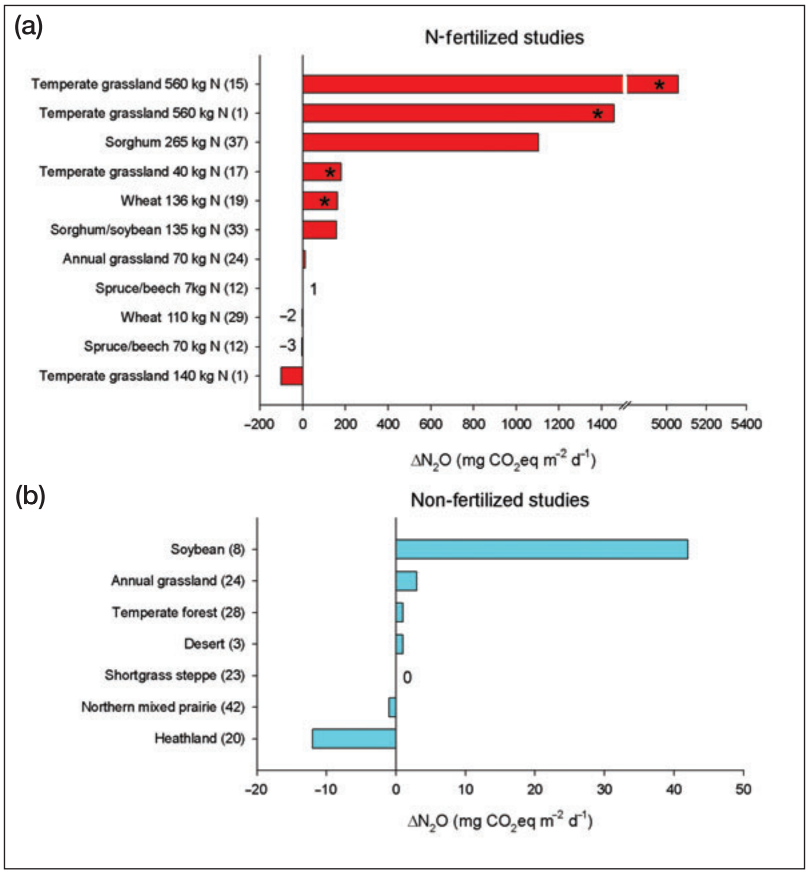

Figure 1. *Effects of elevated CO_2 on N_2O emissions in (a) N-fertilized and (b) non-fertilized studies. Effects of elevated CO_2 are expressed in mg CO_2eq m^{-2} d^{-1} (ΔN_2O = absolute difference in the N_2O flux between elevated and ambient CO_2). Bars with asterisks indicate that the effect of elevated CO_2 was significant ($P < 0.05$). When N addition was included as a treatment, effects of elevated CO_2 are shown for each N-addition level, while amounts of N fertilizer (in kg N ha^{-1} yr^{-1}) are included on the y axis. If other treatments were included in the study, effects of elevated CO_2 were calculated across those treatments. Numbers in parentheses after the ecosystem type and fertilizer amount refer to reference numbers in WebTable 1.*

significantly increased N_2O emissions by 19%. Our results suggest that emissions-related effects of elevated CO_2, in combination with N fertilization, may be intensified. Indeed, the three largest increases in N_2O emissions under elevated CO_2 occurred in studies with the highest N-fertilization rates (ranging from 265 to 560 kg N ha^{-1} yr^{-1}; Figure 1a).

Nitrous oxide fluxes were often measured during the growing season, which includes high-emission periods after N-fertilizer applications as compared with periods of lower emissions during the winter (Stehfest and Bouwman 2006). If CO_2 effects on N_2O fluxes were smaller during the winter than during the growing season, then CO_2 effects – when considered over the course of a given year – are lower than reported here.

Increased N_2O emissions can result from elevated CO_2 because of the effects of the latter on soil moisture, labile C, or both (Ineson *et al.* 1998; Kammann *et al.* 2008; Niboyet *et al.* 2011). Elevated CO_2 often increases soil moisture as a result of reduced plant stomatal conductance and leaf transpiration, which increases plant water-use efficiency (Morgan *et al.* 2011). Furthermore, elevated CO_2 often increases labile C input as a result of the increased belowground plant-C allocation (Rogers *et al.* 1994; Milchunas *et al.* 2005). Higher soil moisture levels can create anaerobic conditions that are conducive to denitrification and N_2O emissions, and labile C input is an important energy source for denitrifiers (Firestone 1982). The fact that CO_2-induced increases in N_2O emissions only occur with N-fertilization suggests that N_2O production is also often limited by inorganic N availability in terrestrial ecosystems. Indeed, without N fertilization, increased plant demand for N under elevated CO_2 could reduce N availability for nitrifiers and denitrifiers, thereby constraining elevated CO_2 effects on N_2O emissions (Hungate *et al.* 1997; Mosier *et al.* 2002). Thus, elevated CO_2 conditions increase N_2O emissions only when N fertilizer is applied in excess of plant N demand.

The wide variability in N_2O emissions observed in response to elevated CO_2 in fertilized systems could be partially explained by site-specific differences in soil clay content. Sites differed in their clay content by between 6% and 34%, and a significant positive relationship (r^2 = 0.78, P = 0.002) was detected between elevated CO_2 effects on N_2O emissions and soil clay content in N-fertilized systems (Figure 2a). This positive relationship suggests that elevated CO_2 increased N_2O emissions more in clayey than in sandy soils. Although this relationship was derived from a small sample size (n = 9), it is notable, given that each study site differed in many aspects besides soil texture (eg species, management type, climate, methods). We observed no relationship between soil pH and CO_2 effects on N_2O emissions.

Effects of elevated CO_2 on CH_4 fluxes

Elevated CO_2 effects on CH_4 fluxes were highly variable in upland soils (Figure 3a). Soils in upland studies were predominantly net sinks for CH_4 (through CH_4 oxidation by methanotrophic bacteria). Thus, increases and decreases in CH_4 uptake are shown as negative and positive effects, respectively, in Figure 3a. Significantly elevated CO_2 effects, all of which were positive (ie decreased CH_4 uptake), were observed in only three studies. An increase in soil moisture under elevated CO_2 may have either reduced CH_4 diffusion into the soil (thereby reducing the amount of CH_4 oxidation by methanotrophs) or increased

CH_4 production by methanogens (Phillips *et al.* 2001).

Elevated CO_2 often increased CH_4 emissions in wetlands, peatlands, and rice paddy fields (Figure 3, b and c). Significant increases in CH_4 emissions in response to elevated CO_2 were observed in one marsh and in four rice paddy studies; these increases were much larger than those observed in uplands. The anoxic conditions in wetlands, peatlands, and rice paddies promote the production of CH_4 by methanogenic bacteria. Increased CH_4 production in these systems, when subjected to elevated CO_2 conditions, has been attributed to increased C input into the soil (Ziska *et al.* 1998; Tokida *et al.* 2010). As with denitrifiers producing N_2O, methanogens require organic C to produce CH_4, and elevated CO_2 may fuel methanogens with greater inputs of belowground C to increase CH_4 production.

In terms of CO_2eq, the effects of elevated CO_2 on CH_4 production in rice paddies were of similar magnitude to the effects of elevated CO_2 on N_2O emissions in the high-N-fertilized systems. Considering that most rice paddies are also fertilized with N, N_2O emissions in response to elevated CO_2 conditions may be substantial in these systems. However, none of the rice paddy studies reported any effects of elevated CO_2 on N_2O emissions. Nevertheless, rice paddy fields appear to be one of the more sensitive ecosystems in terms of how non-CO_2 GHG emissions respond to elevated CO_2.

Similar to the effects of elevated CO_2 on N_2O emissions, the effect of elevated CO_2 on net CH_4 emissions in upland soils increased with clay content (r^2 = 0.60, P = 0.04; Figure 2b) but was not related to soil pH. As with the relationship for N_2O, the associated number of data points was small (n = 7). Greater sample sizes are therefore necessary to test the robustness of these relationships.

Soil texture largely determines the water-holding capacity and pore-size distribution in soils. Clayey soils have more micropores than sandy soils, and are therefore able to hold water more strongly; thus, anoxic conditions conducive to N_2O and CH_4 production may be more easily created and maintained in clayey soils (Stehfest and Bouwman 2006). Any changes in soil moisture caused by elevated CO_2 may therefore alter N_2O and CH_4 production to a greater degree in clayey soils than in sandy soils. Similarly, increased soil moisture may also decrease the diffusivity of CH_4 into soils more rapidly in clayey than in sandy soils (Thorbjørn *et al.* 2008). As such, clayey soils may be more sensitive to elevated CO_2 in terms of N_2O and CH_4 production.

Effects of increased temperature on N_2O fluxes

As with elevated CO_2, increased temperatures affected N_2O emission fluxes variably, ranging from a decrease of 111 mg CO_2eq m^{-2} d^{-1} to an increase of 56 mg CO_2eq m^{-2} d^{-1} (Figure 4). Significant positive and negative effects of warming were observed in both N-fertilized and non-fertilized settings. The effects of elevated temperature on N_2O emissions were inconsistent and remained relatively small, even in the presence of N fertilization, when compared with those of elevated CO_2.

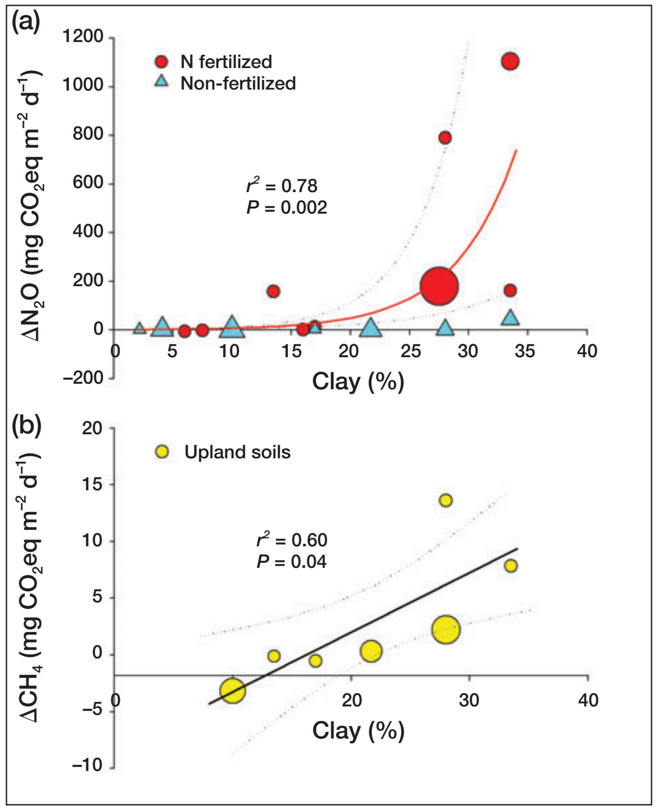

Figure 2. *The effect of elevated atmospheric CO_2 concentration on (a) N_2O and (b) CH_4 fluxes as a function of clay content. Each data point represents the result of one study or several studies at a specific site and soil clay content. For N_2O, results were separated for sites with (red circles) or without (blue triangles) N fertilization. For CH_4, only upland sites were included in the relationship. The size of the data points represents the weight (duration of measurement) used in the regression. Dotted lines represent 95% confidence bands.*

There are several possible reasons for this outcome. First, elevated temperatures affect multiple processes, some of which may offset N_2O emissions and result in an overall small net effect. For instance, increases in soil temperature can directly stimulate nitrifiers and denitrifiers that produce N_2O, but more rapid soil drying associated with warmer conditions would have the opposite effect (McHale *et al.* 1998; Bijoor *et al.* 2008). Temperature increases could also stimulate plant growth and N uptake, thereby reducing the chance of N being lost as N_2O. On the other hand, warming could boost N_2O emissions as a result of increased microbial activity and N supply through increased N mineralization. Second, warming often has no effect on, or sometimes even decreases, belowground C input (Dieleman *et al.* 2012). If N_2O is mainly produced by denitrifiers that are C-limited, then warming conditions would have little effect. Third, in the field experiments, soil, air, or canopy temperatures were increased by 1–5°C. Unlike elevated CO_2 manipulations,

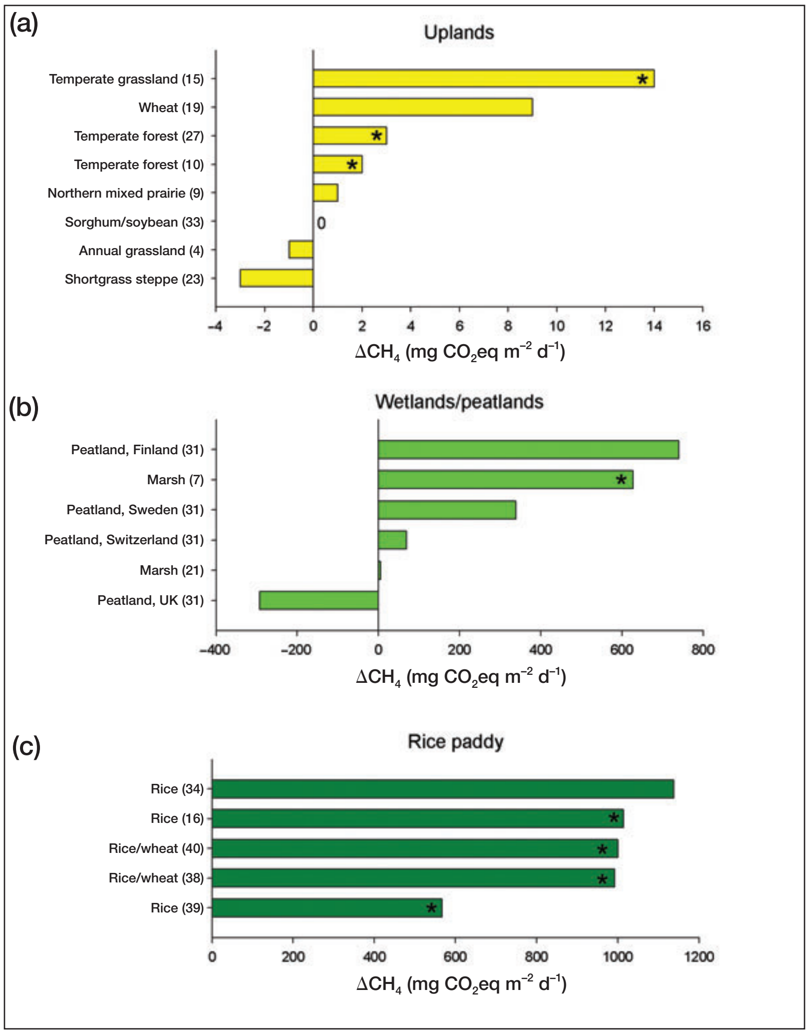

Figure 3. *Effects of elevated CO_2 on net CH_4 emissions in (a) uplands, (b) wetlands/peatlands, and (c) rice paddy fields. Effects of elevated CO_2 are expressed in mg CO_2eq m^{-2} d^{-1} (ΔCH_4 = absolute difference in the CH_4 flux between elevated and ambient CO_2). Bars with asterisks indicate that the effect of elevated CO_2 was significant ($P < 0.05$). If other treatments were included in the study, effects of elevated CO_2 were calculated across those treatments. Numbers in parentheses after the ecosystem type refer to reference numbers in WebTable 1.*

where the CO_2 concentration is often doubled, these temperature increases are relatively small for most sites where N_2O fluxes were reported and, as such, effects due to warming may also be minor. We observed no relationship between the N_2O flux in response to elevated temperatures and the soil clay content or pH at each site, possibly because of the complex effects of warming on N_2O.

Effects of increased temperature on CH_4 fluxes

Warming treatments increased net CH_4 uptake (ie resulted in a more negative CH_4 flux) in most upland studies and had variable effects on net CH_4 emissions in wetlands, peatlands, and rice paddy fields (Figure 5). The increase in CH_4 uptake observed with warming has been associated with the direct effects of higher soil temperatures on CH_4 oxidation and lower soil moisture content, which increases diffusivity of CH_4 into the soil (Peterjohn *et al.* 1994; Sjögersten and Wookey 2002). In contrast with elevated CO_2, we found no relationship between the effects of elevated temperature on CH_4 uptake and soil clay content. This absence of a significant relationship may be due to the much smaller range in clay content among sites that underwent warming treatments (between 15% and 22%) and those experiencing elevated CO_2 treatments. The wide variability in CH_4 emissions among elevated temperature studies conducted in peatlands and rice paddies could be attributed to the variable effects of warming on root biomass production and aerobic decomposition in these systems. In rice paddies subjected to warming treatments, increased CH_4 emissions were associated with increased root biomass production in one study (Tokida *et al.* 2010); however, in two other studies (Ziska *et al.* 1998; Yun *et al.* 2012), root biomass production and CH_4 emissions were unaffected by warming. In contrast, reduced CH_4 emissions with warming treatments conducted in a peatland in Sweden were associated with faster decomposition of plant material during aerobic soil conditions (Eriksson *et al.* 2010).

In peatlands at high latitudes, CH_4 emissions could further be affected by changes in the water table. As a result of climate warming, permafrost thawing could either decrease the water table (through increased drainage of melted water) or increase the water table (through thermokarst formation and flooding; Smith *et al.* 2005; Zona *et al.* 2009). For instance, a rise in the water table can promote anaerobic conditions in the soil and therefore increase CH_4 production by methanogens. Indeed, in an Alaskan peatland, an increase in the water table had a greater effect on CH_4 emissions than did direct warming (Turetsky *et al.* 2008).

Combined effects of elevated CO_2 and temperature

Although a considerable amount of data has been gathered regarding impacts of either elevated CO_2 or elevated temperature on N_2O and CH_4 emissions, little is known about their combined impacts. It is not known whether the combined effects will be equal to (additive), greater than (synergistic), or smaller than (antagonistic) the sum of single effects. Synergistic and antagonistic effects could occur when microbial processes resulting in N_2O and CH_4 emissions are simultaneously controlled by more than one driver. For example, greater C inputs under elevated CO_2 conditions and accelerated N mineralization associated with elevated temperatures could mitigate both C and N limitations for denitrification and result in synergistic effects on N_2O emissions. Likewise, antagonistic effects could occur when N limitation for denitrification (under elevated CO_2 conditions) shifts to water limitation (under elevated temperatures), so that when both factors are combined, N_2O emissions will still be constrained by one of the drivers. Combined effects could also be non-additive when one or more drivers exhibit non-linear relationships with GHG emissions (Zhou *et al.* 2008).

In the few experimental studies where interactive effects of elevated CO_2 and temperature were examined, no significant interactive effects on fluxes of N_2O were found (Larsen *et al.* 2011; Niboyet *et al.* 2011) or CH_4 (Ziska *et al.* 1998; Blankinship *et al.* 2010; Tokida *et al.* 2010; Dijkstra *et al.* 2011). However, the lack of interactive effects from these experiments may be related to inadequate statistical power or to the length of time before interactive effects are expressed being longer than the duration of the experiments (Norby and Luo 2004). Modeling approaches, on the other hand, have revealed important interactive effects of climate change on heterotrophic respiration and other ecosystem processes (Luo *et al.* 2008; Zhou *et al.* 2008). Long-term field observations are needed to understand interactive effects of elevated CO_2 and temperature on N_2O and CH_4 fluxes.

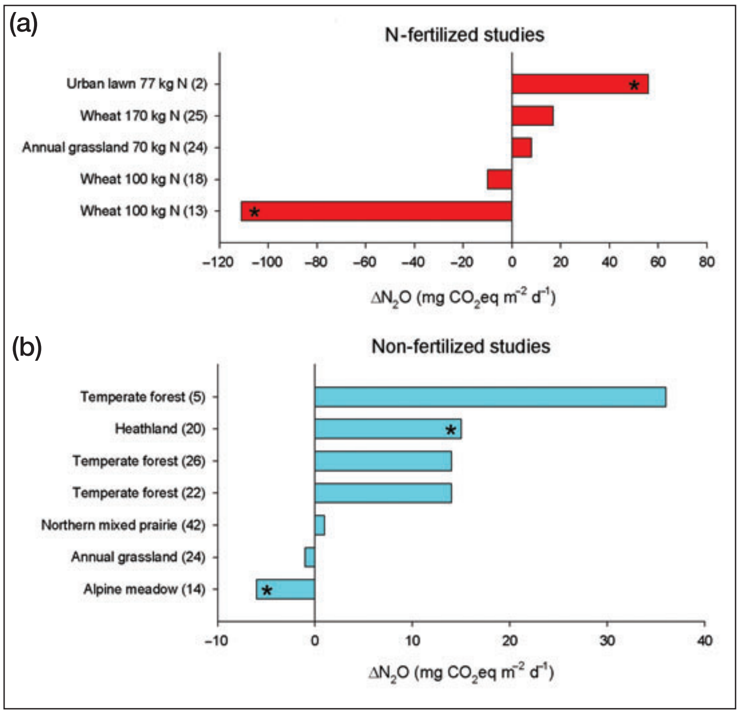

Figure 4. *Effects of elevated temperature on N_2O emissions in (a) N-fertilized and (b) non-fertilized studies. Effects of warming are expressed in mg CO_2eq m^{-2} d^{-1} (ΔN_2O = absolute difference in the N_2O flux between elevated and ambient temperature). Bars with asterisks indicate that the effect of elevated CO_2 was significant ($P < 0.05$). When N addition was included, effects of warming are shown for each N-addition level, while amounts of N fertilizer (in kg N ha^{-1} yr^{-1}) are included on the y axis. If other treatments were included in the study, effects of warming were calculated across those treatments. Numbers in parentheses after the ecosystem type and fertilizer amount refer to reference numbers in WebTable 1.*

Critical knowledge gaps

First, there is much uncertainty regarding the effects of elevated temperatures on CH_4 emissions in wetlands and peatlands. For peatlands at high latitudes in particular, CH_4 fluxes can be sensitive to warming as a result of permafrost thawing (Schuur and Abbott 2011); this affects geomorphic and hydrological processes (McGuire *et al.* 2010) and causes large-scale spatial and temporal variations in anaerobic and aerobic soil conditions. These complex effects are almost impossible to manipulate in small-scale field experiments, although attempts have been made (Turetsky *et al.* 2008). Clearly, additional field research is needed to better understand the complex effects of elevated temperatures on CH_4 emissions in high-latitude soils. Second, in tropical and sub-tropical systems, there is a noted absence of field experiments, yet N cycling and N_2O emissions in these systems can be extensive (Hedin *et al.* 2009); consequently, the effects of elevated CO_2 and temperature on N_2O emissions may also be important. Third, the effects of elevated CO_2 and temperature on N_2O fluxes in rice paddies, wetlands, or peatlands are unknown. However, N_2O emissions from – and the effects of elevated CO_2 and temperature on – these soils (particularly those with N fertilizer additions) could potentially be substantial, given that the soils are usually under anaerobic conditions. Finally, although N_2O and CH_4 fluxes under elevated CO_2 and temperature conditions are affected by plant *species* composition or presence (Verville *et al.* 1998; Billings *et al.* 2002; Eriksson *et al.* 2010), it is unclear how N_2O and CH_4 fluxes under these conditions will be affected by changes in plant *community* composition.

Conclusions

The N_2O and CH_4 fluxes measured in different ecosystems showed various responses to elevated CO_2 and temperature. Nitrous oxide emissions in N-fertilized systems and CH_4 emissions in wetlands, peatlands, and rice paddies are particularly sensitive to, and may increase with, a rise in atmospheric CO_2 concentration. Our results also suggest that the effects of elevated CO_2 on N_2O and CH_4 are more sensitive in clayey than in sandy upland soils. Conversely, the effects of warming on N_2O and CH_4 fluxes were often less consistent than the effects of elevated CO_2. Methane emissions, and to a lesser degree N_2O emissions, showed similar sensitivity to warming as to elevated CO_2, but elevated temperature caused both

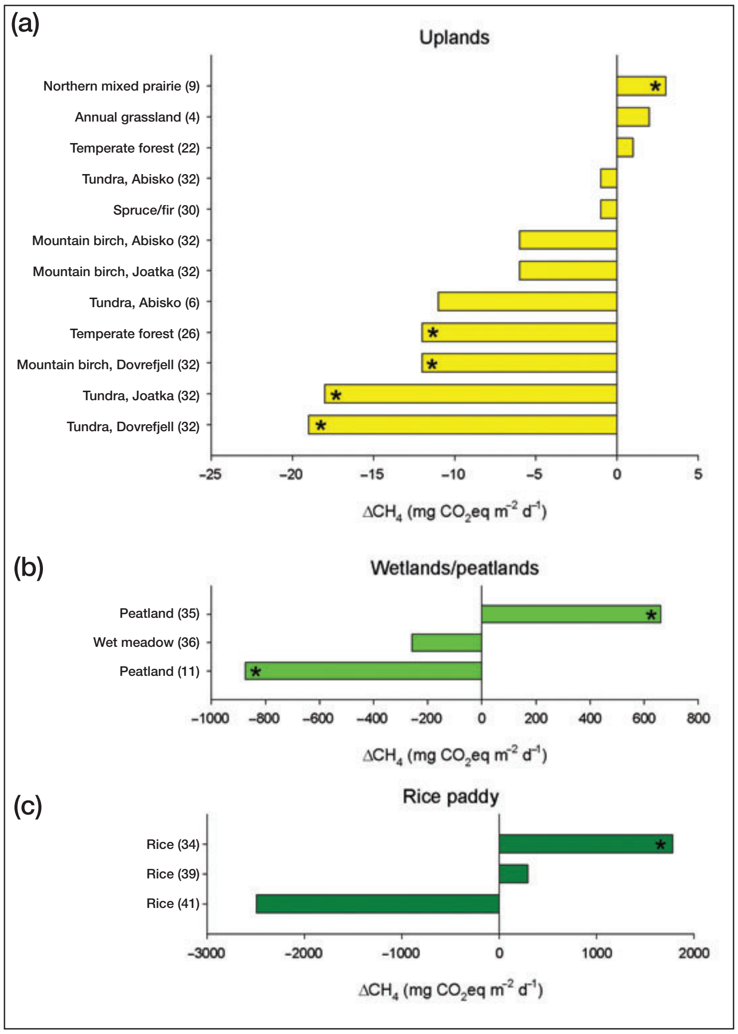

Figure 5. *Effects of elevated temperature on net CH_4 emissions in (a) uplands, (b) wetlands/peatlands, and (c) rice paddy fields. Effects of warming are expressed in mg CO_2eq m^{-2} d^{-1} (ΔCH_4 = absolute difference in the CH_4 flux between elevated and ambient temperature). Bars with asterisks indicate that the effect of warming was significant ($P < 0.05$). If other treatments were included in the study, effects of warming were calculated across those treatments. Numbers in parentheses after the ecosystem type refer to reference numbers in WebTable 1.*

strong increases and decreases in CH_4 and N_2O emissions in similar ecosystems. Warming showed more consistent increases in CH_4 uptake from upland soils, although these increases were small. However, because the global land area covered by upland systems is about 80 and 18 times as large as the global land area covered by rice paddies and natural wetlands, respectively (van Groenigen *et al.* 2011), increased CH_4 uptake associated with elevated temperature in uplands may play an important role in offsetting the warming due to other GHGs. On the basis of results from manipulative field experiments, we conclude that N_2O and CH_4 emissions from N-fertilized systems in uplands, wetlands, peatlands, and rice paddies are sensitive to a rise in atmospheric CO_2 concentration, thereby serving to enhance global climate change. However, it remains uncertain whether the effects of elevated temperature on N_2O and CH_4 emissions from these ecosystems will cause a negative or positive feedback.

Acknowledgements

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