G

oal warming is caused by increased atmospheric concentrations of the greenhouse gases (GHGs) carbon dioxide (CO₂), nitrous oxide (N₂O), and methane (CH₄). 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 CH₄ oxidation (e.g. Schlesinger 1997). Increased atmospheric CO₂ concentration and elevated air/soil temperatures (hereafter elevated CO₂ 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 CO₂ and temperature could either accelerate or decelerate the rate of global warming.

The effects of elevated CO₂ and temperature on N₂O and CH₄ fluxes in terrestrial ecosystems have been studied less frequently than the effects on CO₂ exchange. This is not surprising given that CO₂ exchange rates are usually orders of magnitude greater than the exchange rates of N₂O and CH₄ (Schlesinger 1997). However, N₂O and CH₄ have higher global warming potentials (GWPs) than that of CO₂. Thus, although CO₂ is – per molecule – the most important GHG, N₂O and CH₄ are more efficient in warming the atmosphere (the GWPs of N₂O and CH₄ are 298 and 25 times that of CO₂, respectively, over a 100-year period; Forster et al. 2007). Global warming is therefore more sensitive to changes in the exchange of N₂O and CH₄ relative to that of CO₂.

The effects of elevated CO₂ and temperature on N₂O and CH₄ fluxes in terrestrial ecosystems have been studied less frequently than the effects on CO₂ exchange. This is not surprising given that CO₂ exchange rates are usually orders of magnitude greater than the exchange rates of N₂O and CH₄ (Schlesinger 1997). However, N₂O and CH₄ have higher global warming potentials (GWPs) than that of CO₂. Thus, although CO₂ is – per molecule – the most important GHG, N₂O and CH₄ are more efficient in warming the atmosphere (the GWPs of N₂O and CH₄ are 298 and 25 times that of CO₂, respectively, over a 100-year period; Forster et al. 2007). Global warming is therefore more sensitive to changes in the exchange of N₂O and CH₄ relative to that of CO₂.

Process-based ecosystem models applied at regional and continental scales have recently estimated that net N₂O and CH₄ emissions increased during the past 40 years and could further increase in the future because of elevated CO₂ 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 N₂O and CH₄ fluxes in different ecosystems (Tian et al. 2012).

SPECIAL ISSUE

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 (N₂O) and methane (CH₄), in ways that either stimulate or decrease the magnitude and duration of global warming. Using manipulative field experiments, we assessed how N₂O and CH₄ soil fluxes responded to a rise in atmospheric carbon dioxide (CO₂) concentration and to increased air temperature. Nitrous oxide and CH₄ responses varied greatly among studied ecosystems. Elevated CO₂ often stimulated N₂O emissions in fertilized systems and CH₄ emissions in wetlands, peatlands, and rice paddy fields; both effects were stronger in clayey soils than in sandy upland soils. Elevated temperature, however, impacted N₂O and CH₄ emissions inconsistently. Thus, the effects of elevated CO₂ concentrations on N₂O and CH₄ emissions may further enhance global warming, but it remains unclear whether increased temperature generates positive or negative feedbacks on these GHGs in terrestrial ecosystems.

In a nutshell:

- Net emissions of nitrous oxide (N₂O) and methane (CH₄) 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 N₂O and CH₄ emissions provide important information that may help improve long-term predictions with process-based models
- A rise in atmospheric carbon dioxide concentration often increased N₂O emissions in fertilized systems and CH₄ emissions in wetlands, peatlands, and rice paddy fields; such increases may enhance global warming
- Conversely, responses of N₂O and CH₄ emissions to elevated temperatures have been inconsistent in many ecosystems

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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$_2$O 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 (Kliromanos 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$_2$O 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$_2$O and CH$_4$. Although precipitation has a major effect on N$_2$O 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$_2$O 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$_2$O 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$_2$O 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$_2$O 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$_2_{eq}$ m$^{-2}$ d$^{-1}$) to allow for comparison between N$_2$O and CH$_4$ flux responses.

Because elevated CO$_2$ and temperature effects on N$_2$O 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$_2$O 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$_2$O and CH$_4$ fluxes in response to elevated CO$_2$ and temperature. At some sites, N$_2$O 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$_2$O fluxes**

Elevated CO$_2$ levels had highly variable effects on N$_2$O fluxes (Figure 1). The largest increases in N$_2$O emissions in response to CO$_2$ treatments were observed in N-fertilized studies (up to 5058 mg CO$_2_{eq}$ m$^{-2}$ d$^{-1}$) and were frequently significant (Figure 1a). In contrast, the effects of elevated CO$_2$ on N$_2$O 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$_2$
significantly increased N\textsubscript{2}O emissions by 19%. Our results suggest that emissions-related effects of elevated CO\textsubscript{2}, in combination with N fertilization, may be intensified. Indeed, the three largest increases in N\textsubscript{2}O emissions under elevated CO\textsubscript{2} occurred in studies with the highest N-fertilization rates (ranging from 265 to 560 kg N ha\textsuperscript{-1} yr\textsuperscript{-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\textsubscript{2} effects on N\textsubscript{2}O fluxes were smaller during the winter than during the growing season, then CO\textsubscript{2} effects – when considered over the course of a given year – are lower than reported here.

Increased N\textsubscript{2}O emissions can result from elevated CO\textsubscript{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\textsubscript{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\textsubscript{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\textsubscript{2}O emissions, and labile C input is an important energy source for denitrifiers (Firestone 1982). The fact that CO\textsubscript{2}-induced increases in N\textsubscript{2}O emissions only occur with N-fertilization suggests that N\textsubscript{2}O production is also often limited by inorganic N availability in terrestrial ecosystems. Indeed, without N fertilization, increased plant demand for N under elevated CO\textsubscript{2} could reduce N availability for nitrifiers and denitrifiers, thereby constraining elevated CO\textsubscript{2} effects on N\textsubscript{2}O emissions (Hungate et al. 1997; Mosier et al. 2002). Thus, elevated CO\textsubscript{2} conditions increase N\textsubscript{2}O emissions only when N fertilizer is applied in excess of plant N demand.

The wide variability in N\textsubscript{2}O emissions observed in response to elevated CO\textsubscript{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\textsubscript{2} effects on N\textsubscript{2}O emissions and soil clay content in N-fertilized systems (Figure 2a). This positive relationship suggests that elevated CO\textsubscript{2} increased N\textsubscript{2}O 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\textsubscript{2} effects on N\textsubscript{2}O emissions.

Effects of elevated CO\textsubscript{2} on CH\textsubscript{4} fluxes

Elevated CO\textsubscript{2} effects on CH\textsubscript{4} fluxes were highly variable in upland soils (Figure 3a). Soils in upland studies were predominantly net sinks for CH\textsubscript{4} (through CH\textsubscript{4} oxidation by methanotrophic bacteria). Thus, increases and decreases in CH\textsubscript{4} uptake are shown as negative and positive effects, respectively, in Figure 3a. Significantly elevated CO\textsubscript{2} effects, all of which were positive (ie increased CH\textsubscript{4} uptake), were observed in only three studies. An increase in soil moisture under elevated CO\textsubscript{2} may have either reduced CH\textsubscript{4} diffusion into the soil (thereby reducing the amount of CH\textsubscript{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$_2$O, 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$_2$eq, 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$_2$O emissions in the high-N-fertilized systems. Considering that most rice paddies are also fertilized with N, N$_2$O 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$_2$O 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$_2$O 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$_2$O, 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$_2$O 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$_2$O 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$_2$O and CH$_4$ production.

Effects of increased temperature on N$_2$O fluxes

As with elevated CO$_2$, increased temperatures affected N$_2$O emission fluxes variably, ranging from a decrease of 111 mg CO$_2$eq m$^{-2}$ d$^{-1}$ to an increase of 56 mg CO$_2$eq 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$_2$O emissions were inconsistent and remained relatively small, even in the presence of N fertilization, when compared with those of elevated CO$_2$.

There are several possible reasons for this outcome. First, elevated temperatures affect multiple processes, some of which may offset N$_2$O emissions and result in an overall small net effect. For instance, increases in soil temperature can directly stimulate nitrifiers and denitrifiers that produce N$_2$O, 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$_2$O. On the other hand, warming could boost N$_2$O 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$_2$O 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,
where the CO₂ concentration is often doubled, these temperature increases are relatively small for most sites where N₂O fluxes were reported and, as such, effects due to warming may also be minor. We observed no relationship between the N₂O 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 N₂O.

Effects of increased temperature on CH₄ fluxes

Warming treatments increased net CH₄ uptake (ie resulted in a more negative CH₄ flux) in most upland studies and had variable effects on net CH₄ emissions in wetlands, peatlands, and rice paddy fields (Figure 5). The increase in CH₄ uptake observed with warming has been associated with the direct effects of higher soil temperatures on CH₄ oxidation and lower soil moisture content, which increases diffusivity of CH₄ into the soil (Peterjohn et al. 1994; Sjögersten and Wookey 2002). In contrast with elevated CO₂, we found no relationship between the effects of elevated temperature on CH₄ 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 CO₂ treatments. The wide variability in CH₄ 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 CH₄ 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 CH₄ emissions were unaffected by warming. In contrast, reduced CH₄ 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, CH₄ 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 CH₄ production by methanogens. Indeed, in an Alaskan peatland, an increase in the water table had a greater effect on CH₄ emissions than did direct warming (Turetsky et al. 2008).

Combined effects of elevated CO₂ and temperature

Although a considerable amount of data has been gathered regarding impacts of either elevated CO₂ or elevated temperature on N₂O and CH₄ 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 N₂O and CH₄ emissions are simultaneously controlled by more than one driver. For example, greater C inputs under ele-
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$_2$O emissions in these systems can be extensive (Hedin et al. 2009); consequently, the effects of elevated CO$_2$ and temperature on N$_2$O emissions may also be important. Third, the effects of elevated CO$_2$ and temperature on N$_2$O fluxes in rice paddies, wetlands, or peatlands are unknown. However, N$_2$O 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$_2$O 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$_2$O and CH$_4$ fluxes under these conditions will be affected by changes in plant community composition.

Conclusions

The N$_2$O 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$_2$O and CH$_4$ are more sensitive in clayey than in sandy upland soils. Conversely, the effects of warming on N$_2$O and CH$_4$ fluxes were often less consistent than the effects of elevated CO$_2$. Methane emissions, and to a lesser degree N$_2$O emissions, showed similar sensitivity to warming as to elevated CO$_2$, but elevated temperature caused both
strong increases and decreases in CH$_4$ and N$_2$O 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$_2$O 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$_2$O and CH$_4$ emissions from these ecosystems will cause a negative or positive feedback.

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References


Climate-change effects on nitrous oxide and methane