Elevated CO_2 and Warming Effects on Soil Carbon Sequestration and Greenhouse Gas Exchange in Agroecosystems: A Review

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Abbreviations: C, carbon; CH_4, methane; CO_2, carbon dioxide; eCO_2, elevated atmospheric CO_2 concentration; FACE, free air CO_2 enrichment; GHG, greenhouse gas; HC, heating cable; IPCC, Intergovernmental Panel on Climate Change; IRH, infrared heater; MAP, mean annual precipitation; MAT, mean annual temperature; N, nitrogen; N_2O, nitrous oxide; OTC, open top chamber; PT, plastic tunnel; SACC, screen-aided CO_2 control

Concentrations of CO_2 and other greenhouse gases (GHGs) have been increasing dramatically in earth's atmosphere since the industrial revolution, and are expected to continue increasing from ~385 ppmv today to more than 600 ppmv by the end of this century (IPCC, 2007). Global surface temperatures are expected to rise between 1.1 to 5.4°C by 2100, depending on how fast greenhouse gas concentrations increase. Precipitation dynamics are also predicted to

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TABLE 27.1 Summary of Studies Reporting Elevated CO_2 Effects On Soil C, Soil Respiration, N_2O Emission, and CH_4 Exchange

				Reference			
Agroecosystem	**Site**	**Facility[1]**	**Other treatment**	**Soil C**	**Respiration**	**N_2O**	**CH_4**
N Fertilized Studies							
Sorghum (Sorghum AL)	Auburn AL, U.S.	OTC		Prior et al. 2004			
Sorghum (Sorghum AZ)	Maricopa AZ, U.S.	FACE	Low and high irrigation	Cheng et al. 2007		Welzmiller et al. 2008	
Cotton (Cotton AZ)	Maricopa AZ, U.S.	FACE	Low and high irrigation	Wood et al. 1994	Nakayama et al. 1994		
Wheat (Wheat AZ)	Maricopa AZ, U.S.	FACE		Leavitt et al. 1996, Prior et al. 1997			
Wheat (Wheat AZ)	Maricopa AZ, U.S.	FACE	Low and high N fertilization	Leavitt et al. 2001	Pendall et al. 2001		
Wheat (Wheat GE)	Hohenheim, Germany	FACE		Marhan et al. 2010			
Wheat (Wheat CH)	Beijing, China	FACE			Lam et al. 2011	Lam et al. 2011	Lam et al. 2011
Wheat (Wheat SE)	Ostad, Sweden	OTC				Pleijel et al. 1998	
Soybean (Soybean AL)	Auburn AL, U.S.	OTC		Prior et al. 2004			
Rice (Rice JA)	Iwate, Japan	FACE	Unwarmed and warmed				Inubushi et al. 2003, Tokida et al. 2010
Rice (Rice FL)	Gainesville FL, U.S.	PT	Unwarmed and warmed				Schrope et al. 1999
Rice (Rice PH)	Los Baños, Phillipines	OTC	Unwarmed and warmed, dry and wet season				Ziska et al. 1998
Wheat/sugar beet (Wheat/sugar GE)	Braunschweig, Germany	FACE		Giesemann and Weigel 2008			
Wheat/soybean (Wheat/soy MD)	Beltsville MD, U.S.	OTC	Low and high irrigation, low and high ozone	Islam et al. 2000			
Corn/soybean (Corn/soy IL)	Urbana IL, U.S.	FACE		Peralta and Wander 2008	Peralta and Wander 2008		
Sorghum/soybean (Sorghum/soy AL)	Auburn AL, U.S.	OTC	Conventional and Conservation tillage	Prior et al. 2005	Smith et al. 2010	Smith et al. 2010	Smith et al. 2010

Rice/wheat (Rice/wheat JI)	Jiangdu, Jiangsu, China	FACE	Low and high N fertilization	Zhong et al. 2009	Kou et al. 2007		
Rice/wheat (Rice/wheat WU)	Wuxi, Jiangsu, China	FACE	Low and high N fertilization	Juan et al. 2007			Xu et al. 2004, Zheng et al. 2006
White clover (White clover SW White clover bin SW)	Eschikon, Switzerland	FACE	Low and high N fertilization	Van Kessel et al. 2006, 2000	Baggs et al. 2003	Baggs et al. 2003	
Rye grass (Rye grass SW Rye grass bin SW)	Eschikon, Switzerland	FACE	Low and high N fertilization	Van Kessel et al. 2006, 2000	Ineson et al. 1998, Baggs et al. 2003	Ineson et al. 1998, Baggs et al. 2003	Ineson et al. 1998
White clover/rye grass (White clover/rye SW)	Eschikon, Switzerland	FACE	Low and high N fertilization	Van Kessel et al. 2006	Baggs et al. 2003	Baggs et al. 2003	
Rye grass (Rye grass FR)	France	PT	Low and high N fertilization		Casella et al. 1997		
Temperate grassland (Temperate grass GE)	Giessen, Germany	FACE		Jäger et al. 2003		Kammann et al. 2008	
Alpine grassland (Alpine grass SW)	Switzerland	OTC		Niklaus and Körner 1996			
Non-N Fertilized Studies							
Alpine grassland (Alpine grass SW)	Switzerland	OTC		Niklaus and Körner 1996			
Temperate grassland (Temperate grass SW)	Switzerland	SACC		Niklaus et al. 2001			
Temperate grassland (Temperate grass NZ)	Manawatu, New Zealand	FACE		Ross et al. 2004			
Temperate grassland (Temperate grass AU)	Tasmania, Australia	FACE	Unwarmed and warmed; C_3 and C_4 grasses	Pendall et al. 2011			
Annual grassland (Annual grass CA)	Stanford CA, U.S.	OTC	Two soil types	Hungate et al. 1997a	Luo et al. 1996, Hu et al. 2001	Hungate et al. 1997b	
Tall grass prairie (Tall grass prairie KS)	Manhattan KS, U.S.	OTC		Williams et al. 2000			
Short grass steppe (Short grass steppe CO)	Nunn CO, U.S.	OTC		Pendall et al. 2004	Mosier et al. 2002	Mosier et al. 2002	Mosier et al. 2002
Northern mixed grassland (Northern mixed grass WY)	Cheyenne WY, U.S.	FACE	Unwarmed and warmed	Unpublished results	Unpublished results	Unpublished results	Dijkstra et al. 2011 Unpublished results

[1] *FACE: Free Air CO_2 Enrichment; OTC: Open Top Chamber; PT: Plastic Tunnel; SACC: Screen-Aided CO_2 Control.*

change, although there is still considerable uncertainty in these projections. While some of the details of these events are unclear, most agree climate change has already affected agroecosystems worldwide, and will have even more profound effects as climate change accelerates (Solomon et al., 2009). Important feedback exists between the atmosphere and the soil (Heimann and Reichstein, 2008), and a clear understanding of how climate change and rising atmospheric CO_2 might affect soil C sequestration and greenhouse gas exchange in agroecosystems is urgently needed.

Our review will address the effects of warming and rising CO_2 on the GHG balance. Although precipitation can have strong effects on C sequestration and greenhouse gas exchange in agroecosystems, current projections about precipitation responses remain highly uncertain. Our review will focus on manipulative field experiments in which researchers alter the environment to evaluate ecosystem responses. These experiments include manipulations of atmospheric CO_2 through Open Top Chambers (OTC), Free Air Carbon dioxide Enrichment (FACE), or Screen-Aided CO_2 Control (SACC), manipulations of temperature using heating cables (HC) or infrared heaters (IRH), or a combination of atmospheric CO_2 and temperature. We assess important mechanisms and identify critical knowledge gaps regarding the effects of elevated CO_2 (eCO_2) and warming on C sequestration and greenhouse gas exchange in agroecosystems.

METHODS

In our review we focused on manipulative field experiments, while we excluded growth chamber and greenhouse studies, studies conducted in arctic and subarctic environments, and studies conducted in systems with no direct agronomic benefit (e.g. forests). In most experiments, CO_2 concentrations were manipulated above present-day ambient concentrations (~375–385 ppmv) to enriched levels (470–720 ppmv). Temperature increases ranged between 1 and 5°C above ambient, consistent with IPCC projections for the end of the 21st century (IPCC, 2007). We reviewed a total of 32 eCO_2 and 13 warming studies (Tables 27.1 and 27.2).

The eCO_2 and warming effects on soil C, soil respiration, and N_2O emission were separated in N fertilized and non-N fertilized studies with the expectation that eCO_2 and warming effects on these properties largely depend on soil N availability. For instance, in other meta-analyses a significant increase in soil C under eCO_2 required N fertilization (Van Groenigen et al., 2006; Hungate et al., 2009). We further separated eCO_2 and warming effects on CH_4 exchange conducted in dry land sites (non-rice) where the net CH_4 efflux is predominantly negative (i.e. net CH_4 uptake in soils), and in rice paddy field studies where the net CH_4 efflux is much larger and always positive (i.e. net CH_4 production in soils). When other treatments were included, eCO_2 and warming effects were averaged across those other treatments (e.g. irrigation, ozone).

We calculated the effect of eCO_2 and warming on soil C as the absolute change in soil C (in $\mathrm{g\,C\,kg^{-1}}$ soil) divided by the number of years of treatment. We used absolute changes rather than relative changes because absolute changes provide more biogeochemical significance (Hungate et al., 2009). The absolute changes were calculated for the shallowest soil depths reported, which ranged between 0–5 and 0–26 cm among studies. The number of years of treatment effects on soil C ranged between 2 and 10 years. We calculated the effect of CO_2 and warming on soil respiration, N_2O, and CH_4 flux rates as the absolute change in the average flux rates measured during the growing season (in $\mathrm{kg\,C\,ha^{-1}\,d^{-1}}$, $\mathrm{g\,N\,ha^{-1}\,d^{-1}}$, and $\mathrm{g\,C\,ha^{-1}\,d^{-1}}$ for CO_2, N_2O, and CH_4, respectively). When flux rates were measured in multiple years, we averaged the flux rates across years. All flux rates were measured using static chambers.

Because the effect of eCO_2 on soil C, soil respiration, N_2O, and CH_4 flux rates were highly variable among studies, we tested whether this variability could be explained by climate factors or soil properties of the study site. For the climate factors we chose mean annual temperature

TABLE 27.2 Summary of Studies Reporting Warming Effects On Soil C, Soil Respiration, N_2O Emission, and CH_4 Exchange

			Other	Reference			
Agroecosystem	**Site**	**Facility[1]**	**treatment**	**Soil C**	**Respiration**	**N_2O**	**CH_4**
N Fertilized Studies							
Wheat (Wheat GE)	München, Germany	HC				Kamp et al. 1998	
Wheat (Wheat UK)	York, U.K.	HC			Hartley et al. 2007		
Corn (Corn UK)	York, U.K.	HC			Hartley et al. 2007		
Rice (Rice JA)	Iwate, Japan	HC	Ambient and elevated CO_2				Tokida et al. 2010
Rice (Rice FL)	Gainesville FL, U.S.	TGC	Ambient and elevated CO_2				Schrope et al. 1999
Rice (Rice PH)	Los Baños, Phillipines	OTC	Ambient and elevated CO_2				Ziska et al. 1998
Rye grass (Rye grass FR)	France	PT	Low and high N fertilization		Casella et al. 1997		
Non-N Fertilized Studies							
Alpine grassland (Alpine grass TI)	Tibet, China	IRH	No grazing and grazing			Hu et al. 2010	
Temperate grassland (Temperate grass CH)	Inner Mongolia, China	IRH	No irrigation and irrigation; day, night, and diurnal warming		Liu et al. 2009, Xia et al. 2009		
Temperate grassland (Temperate grass UK)	Scotland, U.K.	HC			Briones et al. 2009		
Temperate grassland (Temperate grass AU)	Tasmania, Australia	IRH	Ambient and elevated CO_2; C_3 and C_4 grasses	Pendall et al. 2011			
Tall grass prairie (Tall grass OK)	OK, U.S.	IRH	No clipping and clipping	Luo et al. 2009	Zhou et al. 2007		
Northern mixed grassland (Northern mixed grass WY)	Cheyenne WY, U.S.	IRH	Ambient and elevated CO_2	Unpublished results	Unpublished results	Unpublished results	Unpublished results

[1] *HC: Heating Cable; IRH: Infrared Heater; PT: Plastic Tunnel.*

(MAT) and mean annual precipitation (MAP) of the site where the studies were conducted and for soil properties we chose %clay and pH. We chose these climate and soil factors because they can have significant effects on plant growth and biological activity in the soil (Epstein et al., 1997; Guo et al., 2006; Fierer et al., 2009) and therefore we expected that they could significantly influence eCO_2 and warming effects on soil C and GHG flux rates among sites. These parameters are also frequently reported in the literature. We used %clay when reported in the study, but often only the textural class was reported. In that case we used the average %clay of the two boundaries of the textural class according to the textural triangle. For instance, if it was reported that the study was conducted in a sandy clay loam with a clay content between 20 and 35% according to the textural triangle, we designated that soil with the average clay content of 27.5%. We related CO_2 effects on soil C and GHG flux rates to each of MAT, MAP, %clay, and pH using linear regression. With the linear regressions, we put more weight on studies that were conducted over a longer time period, because we assumed that studies over longer time periods provide more reliable data. We weighted the absolute rate of change in soil C by the treatment length (in years) after which soil C was measured and weighted the absolute change GHG flux rates by the duration of the measurements (in years; Wu et al., 2011). Some studies were conducted at the same location and soil type, but in different years (e.g. the wheat, sorghum, and cotton studies at Maricopa, AZ). In those cases eCO_2 effects and treatment length/duration of measurements were averaged across the different studies conducted at the same site. We only constructed relationships when there were data available for four or more sites. All linear regressions were performed with JMP (version 8.0.1; SAS Institute, Cary, NC, USA).

THE EFFECT OF eCO_2 ON SOIL C

We found 27 studies (19 N fertilized and 8 non-N fertilized studies) where the effect of eCO_2 on soil C was reported (Figure 27.1). In 74% of the studies (79% of the N fertilized and 63% of

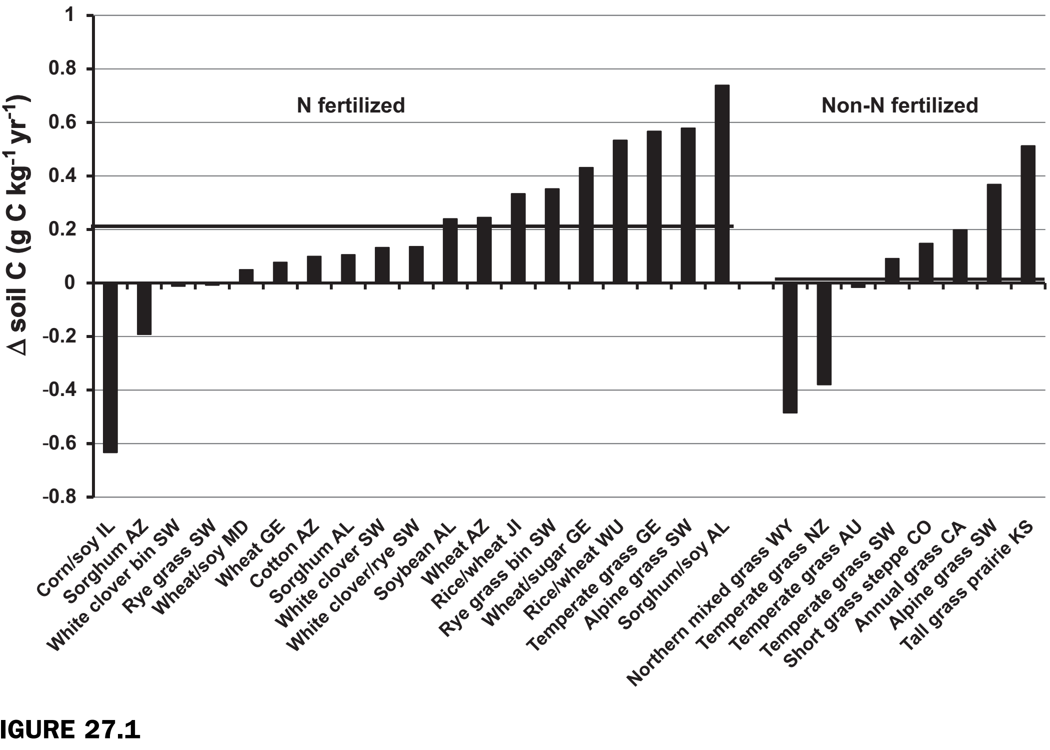

FIGURE 27.1

The rate of change in soil C in response to eCO_2 among different studies. Horizontal bold lines represent averaged values for N fertilized and non-N fertilized studies.

the non-N fertilized studies) a positive effect of eCO_2 on soil C was found, although only in a few occasions were these positive effects statistically significant (e.g. Williams et al., 2000; Prior et al., 2004, 2005; Zhong et al., 2009). While the positive effects of CO_2 enrichment on plant production are generally observed in the initial treatment year (Kimball et al., 2002), detection of significant changes in soil C may take many years of CO_2 enrichment due to the high amount of C present in soils and the relatively small amounts that accrue on an annual basis (Conant and Paustian, 2002; Smith, 2004). On average soil C increased by $0.205\ g\ kg^{-1}\ yr^{-1}$ in the N fertilized studies and by $0.008\ g\ kg^{-1}\ yr^{-1}$ in the non-N fertilized studies. If we assume that in all studies the soil had a bulk density of $1.3\ g\ cm^{-3}$ and that the change in soil C occurred in the top 20 cm, this would correspond to an average rate of soil C increase of 1460 and $57\ g\ ha^{-1}\ d^{-1}$ in the N fertilized and non-N fertilized studies, respectively. A greater response in N fertilized studies was also found by Van Groenigen et al. (2006) in their meta-analysis, where they included greenhouse and growth chamber studies, and non-agronomic sites. Our results confirm the notion that soil C sequestration under eCO_2 is generally constrained by the availability of N and that N fertilization enhances the capacity to increase soil C under eCO_2 (Reich et al., 2006a; Van Groenigen et al., 2006).

Nitrogen fixation by legumes is often enhanced under eCO_2, especially with the addition of non-N nutrients (van Groenigen et al., 2006), and legume responses to CO_2 tend to be greater than non-legumes under conditions of low soil N (van Kessel et al., 2006). Yet no strong evidence was found of greater C sequestration under eCO_2 in studies with legumes. Soil C only slightly increased in plots of *Trifolium repens* (white clover) in the FACE experiment at Eschikon, Switzerland, the most extensive evaluation yet of legume CO_2 responses in a field setting (van Kessel et al., 2006), while soil C decreased under eCO_2 in a temperate pasture with legumes in New Zealand (Ross et al., 2004).

Although on average soil C sequestration in response to eCO_2 was higher in N fertilized than in non-N fertilized studies, within the N fertilized and non-N fertilized studies eCO_2 effects on soil C showed large variation (Figure 27.1). For example, the most negative response to eCO_2 was observed in an N fertilized study with a corn—soybean rotation in Illinois (Peralta and Wander, 2008) and the most positive response was observed in an N fertilized study with a sorghum—soybean rotation in Alabama (Prior et al., 2005). Both these extreme responses were larger than any of the responses observed in the non-N fertilized studies. We tested whether this variability in soil C response among sites could be explained by site differences in climate and soil type. When we related the absolute rate of change in soil C in response to eCO_2 to climate and soil parameters, only %clay in the fertilized sites exhibited a relationship, with marginal significance ($P = 0.08$, Table 27.3). Soil C sequestration in response to eCO_2 tended to decrease with increased clay content (Figure 27.2). Although only marginally significant, this result is remarkable (and any marginal or significant relationships discussed further on) given that all these studies were done using different methods under a variety of conditions. A possible explanation for the decrease in soil C sequestration with increased clay content in response to eCO_2 is that rhizosphere priming effects on soil organic matter decomposition under eCO_2 may be stronger in more clayey soils. Rhizosphere priming, where microbial decomposition of relative recalcitrant soil organic matter is enhanced because of microbial stimulation by energy-rich root exudates, may increase under eCO_2 (Cheng, 1999), particularly in soils with greater clay content (Dijkstra and Cheng, 2007). Thus, an eCO_2-induced increase in rhizosphere priming in more clayey soils may result in less C sequestration, or even cause a net loss of soil C as was observed in the silty clay loam in Illinois, U.S. (Peralta and Wander, 2008).

THE EFFECT OF eCO_2 ON SOIL RESPIRATION

Soil respiration increased with eCO_2 in 12 of the 13 studies reviewed (Figure 27.3). A decrease in soil respiration under eCO_2 was observed in a study with rye grass in Switzerland (Ineson

TABLE 27.3 Summary of Regression Analyses Explaining Variation in Soil C, Soil Respiration, N_2O Emission and CH_4 Exchange in Response to eCO_2

A. Soil C

	All sites			Fertilized sites			Non-fertilized sites		
	*n**	*Corr. C.*	*P*	*n*	*Corr. C.*	*P*	*n*	*Corr. C.*	*P*
MAT	19	0.26	0.26	11	0.22	0.51	8	0.30	0.46
MAP	20	0.28	0.23	11	0.12	0.73	9	0.36	0.34
pH	20	−0.21	0.38	11	−0.20	0.56	9	−0.18	0.65
% Clay	22	−0.19	0.39	13	−0.51	*0.08*	9	0.11	0.79

B. Soil Respiration

	All sites			Fertilized sites		
	n	*Corr. C.*	*P*	*n*	*Corr. C.*	*P*
MAT	9	0.56	0.13	6	0.29	0.60
MAP	8	0.46	0.22	5	0.15	0.80
pH	8	−0.71	*0.06*	5	−0.82	0.06
% Clay	10	0.71	*0.03*	7	0.50	0.33

C. N_2O Emission

	All sites			Fertilized sites		
	n	*Corr. C.*	*P*	*n*	*Corr. C.*	*P*
MAT	8	0.63	*0.09*	6	0.51	0.24
MAP	7	0.06	0.86	5	−0.16	0.85
pH	7	−0.10	0.90	5	0.36	0.50
% Clay	9	0.62	*0.09*	7	0.60	0.21

D. CH_4 Exchange

	Non-rice		
	n	*Corr. C.*	*P*
MAT	5	−0.15	0.85
MAP	4	0.66	0.32
pH	4	0.24	0.76
% Clay	5	0.87	0.07

**n: number of sites included in the regression; Corr. C.: Pearson's correlation coefficient; P: P-value of linear regression.*

et al., 1998). Because root respiration was included in all studies, it is not surprising that soil respiration increased under eCO_2 in most studies. Elevated CO_2 generally increases plant productivity in agroecosystems (Kimball et al., 2002), and thus the increase in soil respiration under eCO_2 may largely have been driven by an increase in root production. The effect of eCO_2 on soil respiration was on average 6.4 and 1.9 kg C ha^{-1} d^{-1} in N fertilized and non-N fertilized studies respectively. Again, the greater eCO_2 effect on soil respiration in N fertilized studies may have been caused by an increase in root productivity and respiration that often occurs under eCO_2 with N additions (Van Groenigen et al., 2006).

Of the two climate and two soil parameters that we tested, both soil pH and %clay explained most of the variability in eCO_2 effects on soil respiration, although only the relationship with % clay was significant ($P = 0.03$, Table 27.3). When we included both N fertilized and non-N fertilized sites in the regression, the increase in soil respiration in response to eCO_2 increased with increased clay content, explaining 45% of the variability, and decreased with increased soil pH, explaining 48% of the variability (Figure 27.4). As was argued for the relationship between

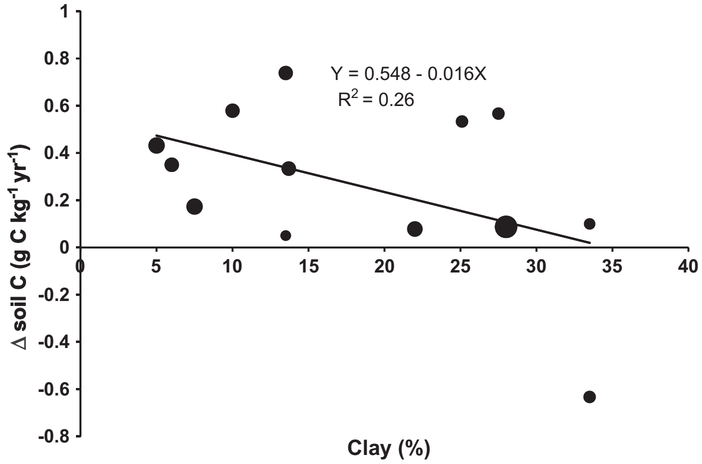

FIGURE 27.2
The rate of change in soil C in response to eCO_2 in the N fertilized studies as a function of the soil clay content. The size of the dots indicate the weight used in the regression (i.e. bigger dots have more weight).

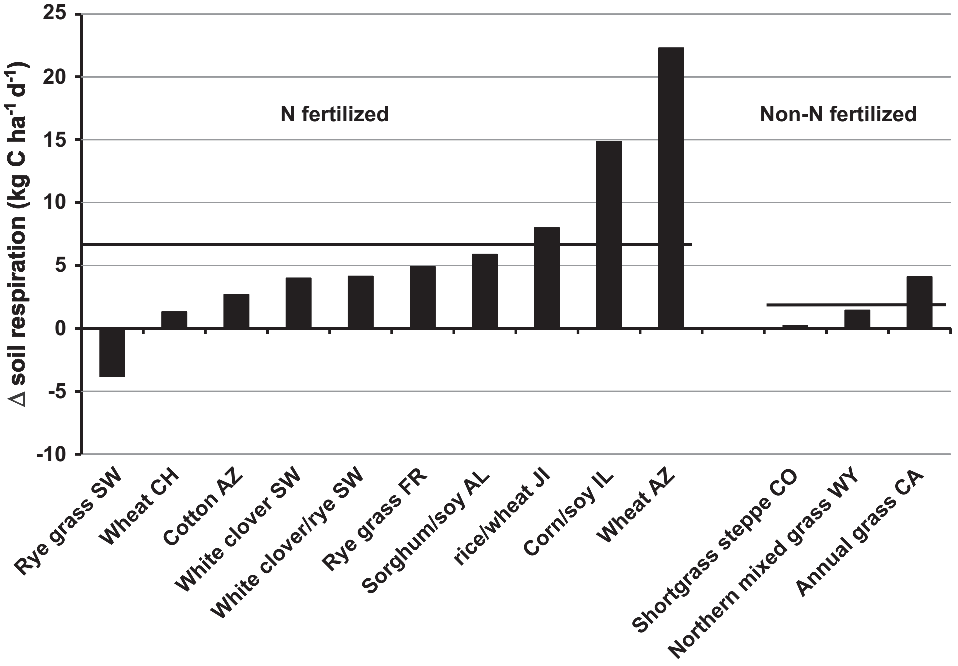

FIGURE 27.3
The change in soil respiration in response to eCO_2 among different studies. Horizontal bold lines represent averaged values for N fertilized and non-N fertilized studies.

clay content and eCO_2 effects on soil C, an increase in rhizosphere priming under eCO_2 may have resulted in larger eCO_2 effects on soil respiration with increased clay content. The negative relationship with soil pH is less clear. Microbial community composition and enzyme activity are often strongly affected by soil pH (Sinsabaugh et al., 2008; Fierer et al., 2009) that can be altered by changes in substrate inputs (Aciego Pietri and Brookes, 2009). It is, however, unclear to what degree the negative relationship that we observed between soil pH and soil respiration in response to eCO_2 was caused by changes in microbial or plant respiration.

THE EFFECT OF eCO_2 ON N_2O EMISSION

Of the 8 N fertilized studies that we found, the N_2O emission increased under eCO_2 in 6 studies. The average increase in N fertilized studies was 9.3 g N ha^{-1} d^{-1}, while in the 3 non-N fertilized studies eCO_2 had hardly any effect on N_2O emission with an average decrease of

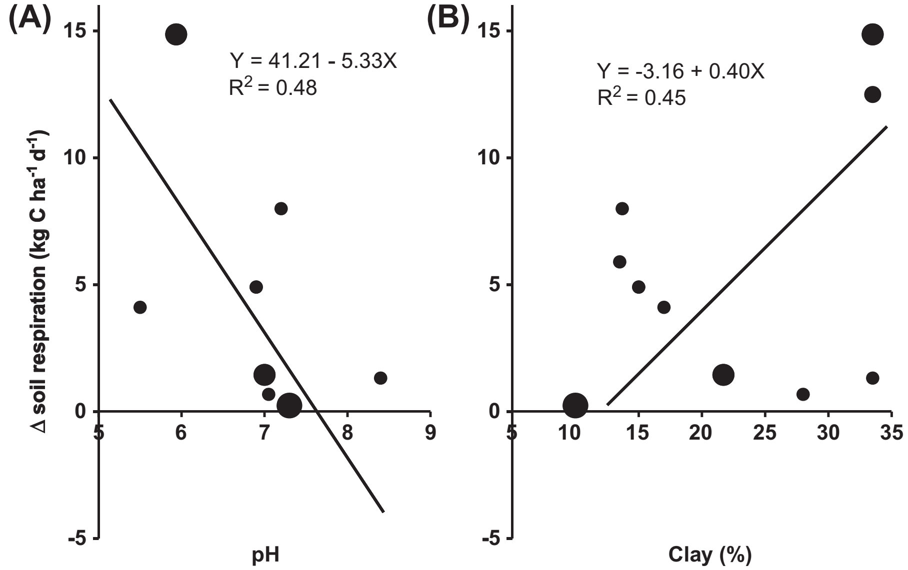

FIGURE 27.4
The change in soil respiration in response to eCO_2 as a function of (A) soil pH and (B) clay content. The size of the dots indicate the weight used in the regression (i.e. bigger dots have more weight).

0.5 g N ha^{-1} d^{-1} (Figure 27.5). With a global warming potential 298 times greater than CO_2 (IPCC, 2007), N_2O emission in N fertilized studies correspond on average to 1188 g C-CO_2 equivalents ha^{-1} d^{-1}. This is slightly less than the average rate that we calculated for C sequestration in the top 20 cm of the soil in N fertilized studies in response to eCO_2 (see above). This suggests that, although N fertilization has the potential to increase soil C under eCO_2 (Van Groenigen et al., 2006), these soil C gains can potentially be almost completely offset by increased N_2O emissions under eCO_2 when N fertilizer is applied.

In the N fertilized studies N_2O emission in response to eCO_2 showed large variation between a decrease of 0.2 g N ha^{-1} d^{-1} in white clover in Switzerland (Baggs et al., 2003) and an increase of 38 g N ha^{-1} d^{-1} in rye grass at the same site in Switzerland (Ineson et al., 1998). This large variation is to a great extent caused by the timing and frequency of measurements after the N fertilizer application. For instance, Ineson et al. (1998) observed some of the

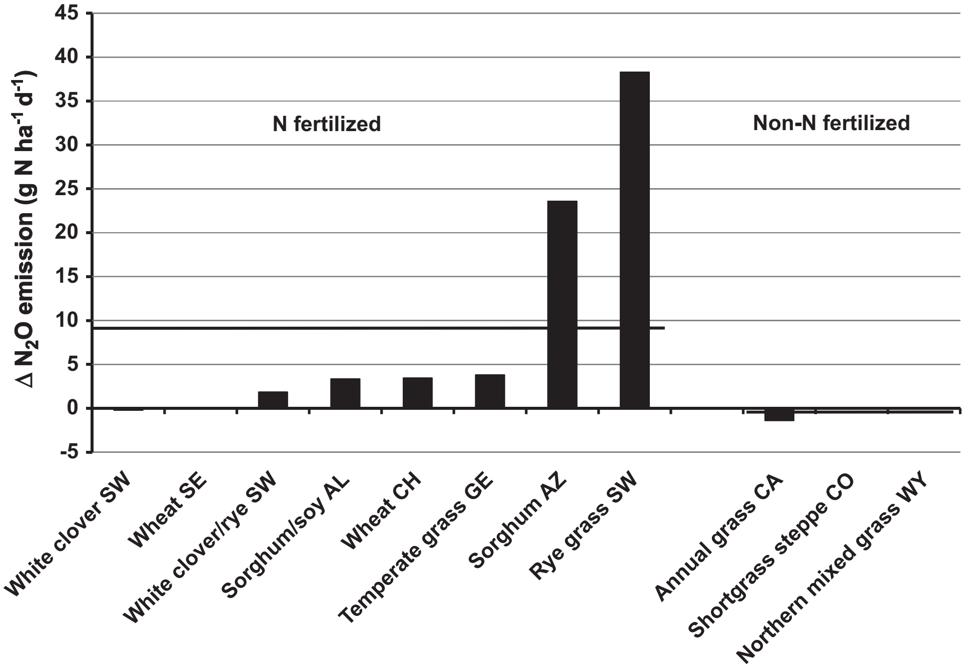

FIGURE 27.5
The change in N_2O emission in response to eCO_2 among different studies. Horizontal bold lines represent averaged values for N fertilized and non-N fertilized studies.

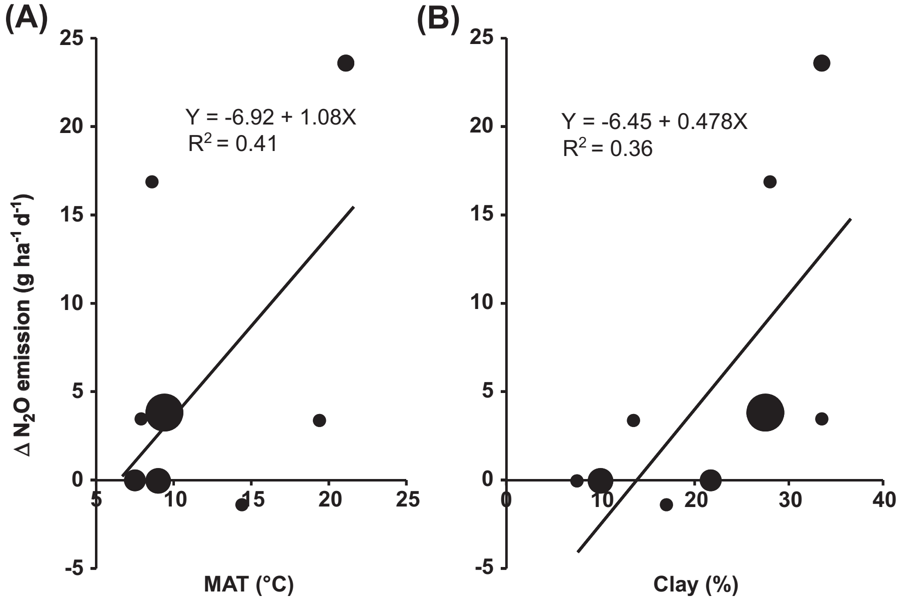

FIGURE 27.6
The change in N_2O emission in response to eCO_2 as a function of (A) mean annual temperature (MAT) and (B) clay content. The size of the dots indicate the weight used in the regression (i.e. bigger dots have more weight).

highest N_2O emissions ever recorded directly after N fertilizer application in grassland systems. Because of these high rates of N_2O emission, eCO_2 effects on N_2O emissions can also be high directly after N application (Ineson et al., 1998; Welzmiller et al., 2008). On the other hand, Kammann et al. (2008) measured the effect of eCO_2 on N_2O emissions during 9 years in a temperate grassland in Germany (the longest study conducted on the effect of eCO_2 on N_2O emission) and observed the greatest eCO_2 effects during vegetative growth periods in the summer when soil mineral N concentrations were low, while eCO_2 had no effect on N_2O emission directly after the N application in the spring. Regardless of the timing and frequency of measurements in relation to N fertilizer application, the majority of N fertilized studies showed an increase in N_2O emission in response to eCO_2. It has been suggested that the increase in N_2O emission under eCO_2 in some of these N fertilized studies was caused by an increase in labile C substrates fueling denitrification (Ineson et al., 1998; Kammann et al., 2008).

In contrast, no eCO_2 effect, or even a slight reduction in N_2O emissions, was observed in the 3 non-N fertilized studies. Possibly, eCO_2 increased plant N uptake and reduced soil N availability in these unfertilized systems where available soil N was already low, causing no or reduced effects on N_2O emission (Hungate et al., 1997b; Mosier et al., 2002).

Both MAT and %clay showed a positive relationship with N_2O emission in response to eCO_2, although both relationships were only marginally significant (Table 27.3, Figure 27.6). N_2O emissions are highly sensitive to temperature (Grant and Pattey, 2008), which could explain why N_2O emissions respond more to eCO_2 in combination with higher MAT. Further, an increase in soil moisture, because of decreased stomatal conductance under eCO_2 (Kimball and Idso, 1983; Morgan et al., 2004; Wand et al., 1999), can increase anaerobic conditions in the soil conducive to denitrification, particularly in clayey soils that have relatively more small pores than sandy soils. These results suggest that, apart from N fertilization, MAT and soil texture play important roles in the large variability in N_2O emission in response to eCO_2 among different sites.

THE EFFECT OF eCO_2 ON CH_4 EXCHANGE

In studies with rice, eCO_2 resulted in large increases in CH_4 emission in 3 out of 4 studies (Figure 27.7). The average increase in CH_4 emission in rice studies in response to eCO_2 was

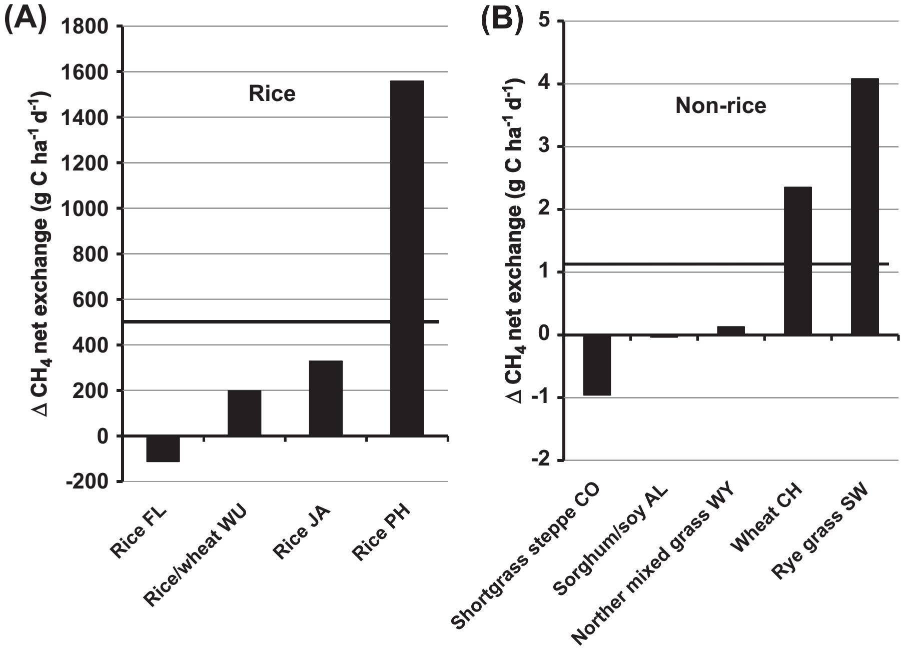

FIGURE 27.7
The change in CH_4 exchange in response to eCO_2 among different studies. Horizontal bold lines represent averaged values for (A) rice and (B) non-rice studies.

493 g C ha^{-1} d^{-1}. With a global warming potential 25 times greater than CO_2 (IPCC, 2007), this increase in CH_4 emission corresponds to an increase of 4482 g C-CO_2 equivalents ha^{-1} d^{-1} in response to eCO_2. Evidently, rice paddy fields show some of the greatest responses to eCO_2 in terms of GHG emissions (e.g. the average rate of C—CO_2 equivalents associated with CH_4 emission in rice is 3.8 times higher than the average rate associated with N_2O emission in N fertilized studies).

In the rice studies, we found no relationships between MAT, MAP, soil pH, or %clay with the rate of CH_4 emission in response to eCO_2. CH_4 emission in rice fields is to a large degree controlled by inputs of C substrates, and increased CH_4 emission under eCO_2 has been associated with increased plant residues, root productivity, and exudation (Inubushi et al., 2003; Xu et al., 2004; Tokida et al., 2010). The increase in CH_4 emission in response to eCO_2 through increased inputs of C substrates may simply have overwhelmed any soil or external climate effect. We should note that with only 4 studies, we had limited statistical power to do the regressions.

In most non-rice studies, soil is a net sink for CH_4, where it is oxidized by methanotrophic bacteria [an exception was the study by Smith et al. (2010) where soil was sometimes a CH_4 source in a sorghum—soybean rotation]. The effect of eCO_2 on CH_4 fluxes (where we used the same convention as in the rice studies, i.e. a positive flux indicates CH_4 emission, while a negative flux indicates CH_4 uptake) was mixed where both increases and decreases were observed with an average increase of 1.1 g C ha^{-1} d^{-1} among the 5 studies we evaluated (or on average a *reduction* in CH_4 uptake in response to eCO_2 because in most studies there was an overall net CH_4 uptake; Figure 27.7). The reduced transpiration and consequent higher soil water content that often occurs under eCO_2 can have opposite effects on CH_4 fluxes depending on whether methanotroph activity is limited by soil moisture (in most arid and semiarid environments) or by CH_4 diffusivity into the soil (in most mesic environments; Dijkstra et al., 2011). Note that responses of CH_4 fluxes to eCO_2 in non-rice or dry land systems are orders of magnitude smaller than in rice systems. Nevertheless, because a much larger proportion of the global area is covered by dry land systems than by rice paddy fields, small changes in CH_4 fluxes in dry land systems can still have a significant impact on the global CH_4 flux (Mosier et al., 1991).

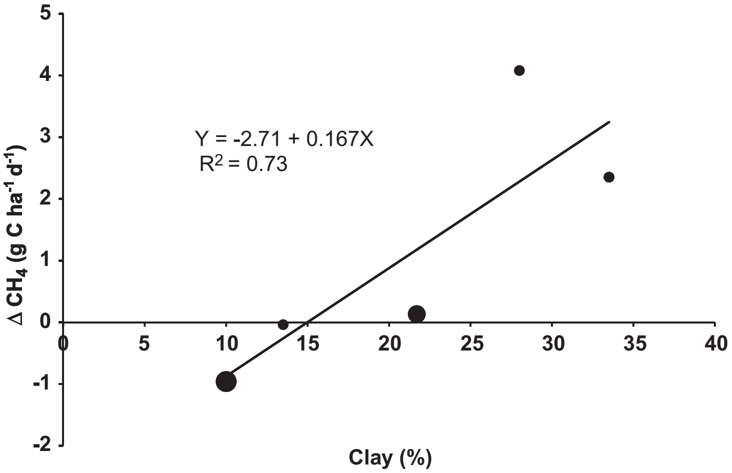

FIGURE 27.8

The change in CH_4 exchange in response to eCO_2 in non-rice studies as a function of soil clay content. The size of the dots indicate the weight used in the regression (i.e. bigger dots have more weight).

As with the greenhouse gases CO_2 and N_2O, the CH_4 flux in response to eCO_2 was positively related to the clay content of the soil, explaining 73% of the variation (Table 27.3, Figure 27.8). Soil texture should influence CH_4 fluxes to the extent that methanotroph activity is limited by soil moisture or by CH_4 diffusivity. Since sandy soils have better aeration than clayey soils, CH_4 uptake is more likely to be limited by direct effects of soil moisture on methanotroph activity than by CH_4 diffusivity. Thus, a CO_2-induced increase in soil moisture would tend to increase CH_4 uptake (thus *decrease* the CH_4 flux in response to eCO_2) more in sandy soils (e.g. as observed by Mosier et al., 2002, in a sandy loam with only 10% clay). On the other hand, in clayey soils with poorer aeration, CH_4 uptake is more likely to be limited by CH_4 diffusivity, and a CO_2-induced increase in soil moisture might therefore decrease CH_4 uptake (or increase the CO_2 response) as observed in a clay loam by Lam et al. (2011). The positive relationship of CH_4 fluxes with clay content is based on only five observations, and it remains to be seen if this relationship will hold with more observations.

WARMING EFFECTS ON SOIL C, SOIL RESPIRATION, N_2O EMISSION AND CH_4 EXCHANGE

Little work has been done on the effects of warming on soil C sequestration and GHG fluxes in agroecosystems. We found only two published studies (Luo et al., 2009; Pendall et al., 2011) and one unpublished study (northern mixed grass prairie in Wyoming, U.S.), all in non-N fertilized grassland systems, reporting warming effects on soil C. Results are not consistent among those three studies, with an average decrease in soil C by $0.026\ \mathrm{g\,C\,kg^{-1}\,soil\,yr^{-1}}$ (Figure 27.9A). The effect of warming on soil C in all three studies is relatively small compared to the effect of eCO_2 in many studies (Figure 27.1). It is noteworthy that warming induced C loss only in Wyoming northern mixed-grass prairie, the driest of these three grasslands. Although warming has the potential to enhance biological activity and extend the length of growing season, it also desiccates, and in dry grasslands, such desiccation can lead to C loss (Zhang et al., 2010).

A little more work has been done evaluating the effects of warming on soil respiration, with more consistent results. In 6 of 7 studies, soil respiration increased with warming (Figure 27.9B). The exception was a study with ryegrass in France, where no change in soil respiration was observed (Casella and Soussana, 1997). On average soil respiration increased more in N fertilized ($6.8\ \mathrm{kg\,C\,ha^{-1}\,d^{-1}}$) than in non-N fertilized studies ($4.4\ \mathrm{kg\,C\,ha^{-1}\,d^{-1}}$), although the highest increase was observed in a non-N fertilized study (Briones et al., 2009). Warming often leads to increased rates of SOM decomposition, and likely led to increased soil respiration (Rustad et al., 2001), particularly when N is not limited. We related soil respiration

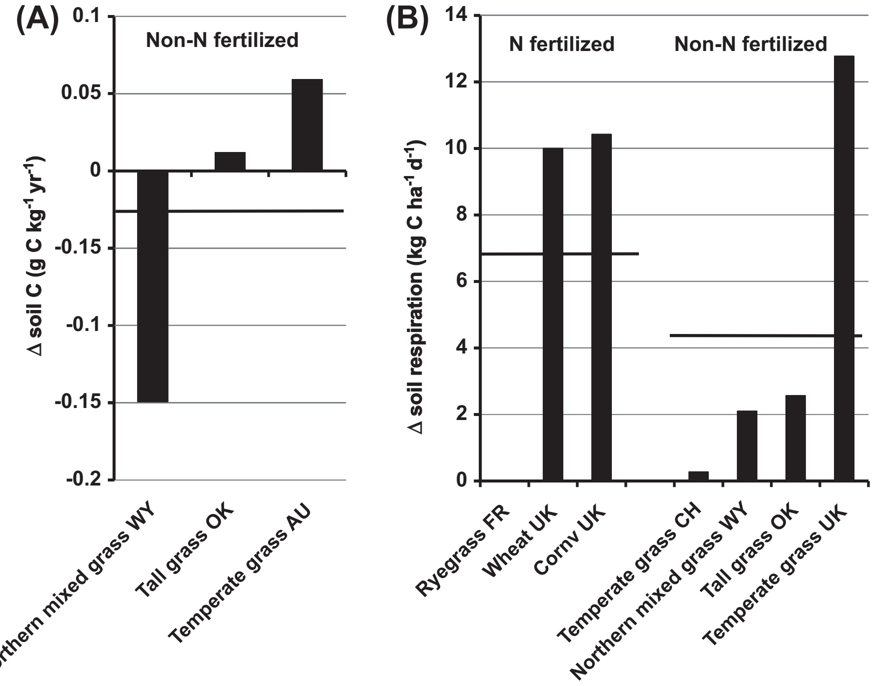

FIGURE 27.9

The rate of change in (A) soil C and (B) soil respiration in response to warming among different studies. Horizontal bold lines represent the averaged values for N fertilized and non-N fertilized studies.

rates in response to warming to climate and soil parameters, but observed no significant relationships (data not shown).

Little information is available on how warming affects N_2O and CH_4 fluxes. In the only N fertilized study we found, the N_2O emission decreased in response to warming (Kamp et al., 1998), while in the two non-N fertilized studies warming had very little effect on N_2O emission (Hu et al., 2010, and unpublished results from northern mixed grassland, Wyoming, U.S., Figure 27.10A). Warming had mixed effects on CH_4 emission in rice paddy fields where both decreased (Ziska et al., 1998) and increased emission rates (Tokida et al., 2010) were reported (Figure 27.10B). The only non-rice study conducted in a semiarid grassland showed that warming decreased CH_4 uptake (Figure 27.10C). It was argued that in this semiarid climate, methanotroph activity was mostly directly limited by a soil moisture and that the drying effect of warming therefore directly reduced methanotroph activity (Dijkstra et al., 2011). Because of the limited number of studies, we did not perform regressions with climate and soil parameters.

INTERACTIVE eCO_2 × WARMING EFFECTS ON SOIL C, SOIL RESPIRATION, N_2O EMISSION, AND CH_4 EXCHANGE

Few studies included both atmospheric CO_2 and temperature manipulations (Ziska et al., 1998; Schrope et al., 1999; Tokida et al., 2010; Dijkstra et al., 2011; Pendall et al., 2011). In only two studies were CO_2 × warming interactive effects on soil C investigated, both in non-N fertilized grassland systems. In both studies, soil C under eCO_2 decreased more in combination with warming than without warming (Table 27.4). In the northern mixed grassland soil respiration under eCO_2 also increased in combination with warming but slightly decreased without warming. These results suggest that eCO_2 effects on SOM decomposition rates may accelerate with increased temperature. However, we found little evidence for CO_2 × warming interactions on soil C from our regressions with MAT. Despite the relatively large numbers of studies included in this regression (19 studies, Table 27.3), we observed no significant relationship between soil C in response to eCO_2 and MAT, suggesting that eCO_2 effects on soil C sequestration did not depend on the temperature regime that the experiment was conducted

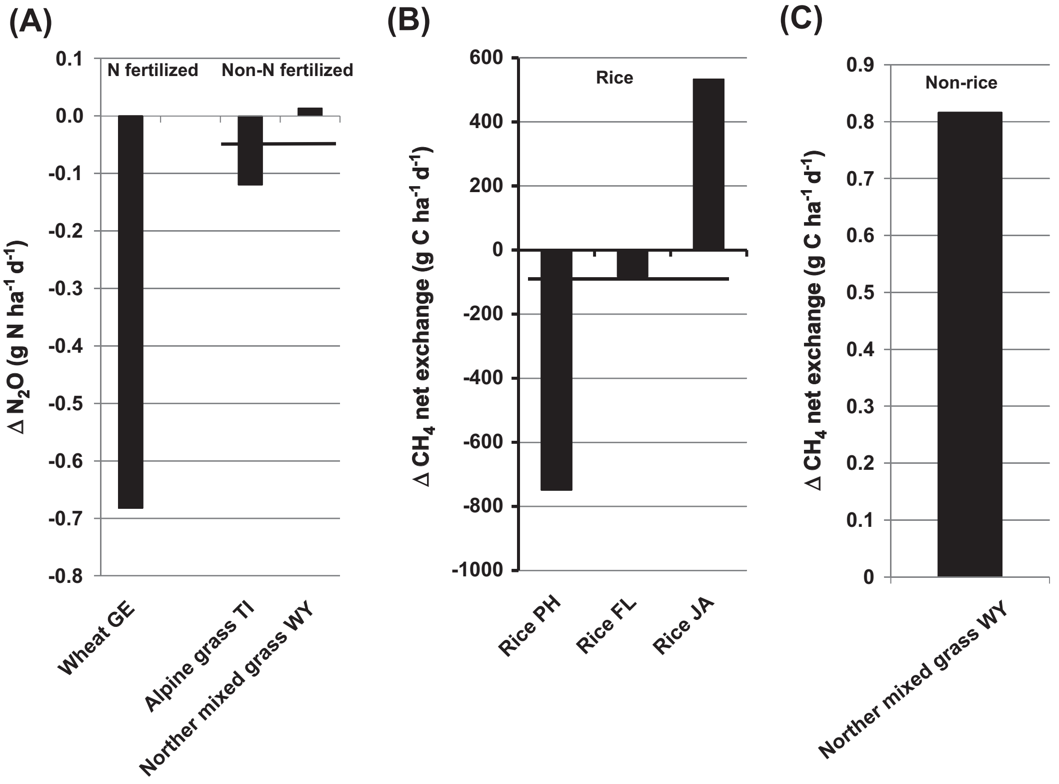

FIGURE 27.10

The change in (A) N_2O emission in N fertilized and non-N fertilized studies, (B) CH_4 exchange in rice studies, and (C) CH_4 exchange in non-rice studies in response to warming. Horizontal bold lines represent averaged values for non-N fertilized and rice studies.

TABLE 27.4 Interactive Effects of eCO_2 and Warming on Soil C, Soil Respiration, N_2O Emission, and Ch_4 Exchange

Agroecosystem	eCO_2 effect (% change from aCO_2)		Reference
	Low temperature	*High temperature*	
Soil C—Non-fertilized			
Temperate grass AU	12.5	−3.4	Pendall et al. 2011
Northern mixed grass WY	−2.8	−14.1	Unpublished results
Respiration—Non-fertilized			
Northern mixed grass WY	−2.0	13.6	Unpublished results
N_2O—Non-fertilized			
Northern mixed grass WY	−94.9	−21.6	Unpublished results
CH_4—Rice			
Rice FL	−84.2	−90.0	Schrope et al. 1999
Rice JA	22.1	29.1	Tokida et al. 2010
Rice PH	48.3	214.5	Ziska et al. 1998
CH_4—Non-rice			
Northern mixed grass WY	0.1	5.0	Dijkstra et al. 2011 Unpublished results

in. Although studies were done at locations that occupied a relatively large range of MAT between 7.5 and 21.1°C, we note that reported MAT values do not always reflect the actual temperature that occurred during the time-frame of the experiment. This may have contributed to finding no significant relationship with eCO_2 effects on soil C.

Only N_2O emission in response to eCO_2 showed a marginally significant relationship with MAT (Figure 27.6), suggesting a CO_2 × temperature interactive effect where eCO_2 effects are stronger with increased temperature. In the non-N fertilized northern mixed grassland study in Wyoming, the N_2O emission under eCO_2 decreased less with warming than without warming (Table 27.4). These results suggest that CO_2 × warming interactive effects may be important for N_2O emissions.

The increase in CH_4 emission under eCO_2 was much greater in combination with warming than without warming in a study with rice in the Philippines (Ziska et al., 1998), but no CO_2 × warming interactive effects on CH_4 exchange were observed in three other studies (Table 27.4). Clearly, more research is needed to identify clear patterns of eCO_2 × warming interactive effects on soil C sequestration and GHG emissions.

CONCLUSIONS

We reviewed studies conducted in agroecosystems to determine sensitivity of C cycling and GHG emissions to the effects of eCO_2 and warming. We found that eCO_2 had the potential to increase soil C, particularly in combination with N fertilization. Similar results were found in other reviews (Reich et al., 2006b; Van Groenigen et al., 2006; Hungate et al., 2009). However, we also found that the increase in soil C in combination with N fertilization did not come without a price. N_2O emissions also increased under eCO_2 with N fertilization, and indeed on average the CO_2-induced increase in N_2O emission in terms of its Global Warming Potential almost completely offset the average increase in soil C in N fertilized studies. Thus, particularly in N fertilized agroecosystems, one can come to the wrong conclusion about the effect of eCO_2 on the GHG balance expressed in CO_2 equivalents if N_2O emissions are not accounted for. A similar conclusion was reached by van Groenigen et al. (2011), who estimated that the Global Warming Potential caused by a CO_2-induced increase in N_2O and CH_4 emission in agricultural and non-agricultural lands could offset as much as 16.6% of the global increase in terrestrial C storage in response to eCO_2 by 2050.

Research is needed to determine whether or not practices like precision application of N fertilizers or use of nitrification inhibitors can be used to minimize N_2O emission but that can help capitalize on the potential for rising CO_2 to enhance C sequestration. Legumes have been suggested as a possible remedy to the N-limitation problem of plants exposed to eCO_2 (van Groenigen et al., 2006) and legumes tend to respond positively to eCO_2 (Newton et al., 1994; Teyssonneyre et al., 2002). However, lack of a significant positive effect of CO_2 on C sequestration in pastures with legumes (Ross et al., 2004; van Kessel et al., 2006) suggests that simply enhanced N fixation under increasingly higher CO_2 concentrations may not necessarily lead to greater C sequestration. More research is needed to evaluate how and under what conditions various mixtures of legumes and forage grasses in combination with non-N fertilization practices might lead to increased C sequestration under future CO_2-enriched atmospheres. Such research should consider appropriate combinations of legumes and non-legumes whose morphology and development might optimize the capture and cycling of N so as to minimize the release of N_2O.

We found that soil clay content is an important factor in explaining the large variability in GHG exchange among sites in response to eCO_2. We observed marginally significant to significant positive relationships between %clay and all three GHGs in response to eCO_2. Our results suggest that GHG exchange from clayey soils is more sensitive to eCO_2 than from sandy soils. The relationships we found between %clay and GHG exchange should be explored further to better understand the mechanisms involved and how widely applicable this relationship might be to scale up the effect of eCO_2 on GHG exchange in agroecosystems to regional or even global levels.

More research is needed about warming effects on soil C sequestration and GHG exchange. The limited studies that we found from agroecosystems often showed mixed warming effects, and no clear strong patterns emerged on how soil C and GHG exchange is affected by warming. Similarly, it remains unclear what the interactive effects of eCO_2 and warming are on soil C sequestration and GHG exchange in agroecosystems. While important challenges remain for agriculture to identify systems and practices that can mitigate global warming, future research with the objective to enhance C sequestration and mitigate GHG emissions will need to remain vigilant as climate change continues to increase in coming decades.

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