Elevated CO_2 and warming effects on CH_4 uptake in a semiarid grassland below optimum soil moisture

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[1] Semiarid rangelands are a significant global sink for methane (CH_4), but this sink strength may be altered by climate change. Methane uptake is sensitive to soil moisture showing a hump-shaped relationship with a distinct optimum soil moisture level. Both CO_2 and temperature affect soil moisture, but the direction of CH_4 uptake response may depend on if the system is below or above the soil moisture optimum. Most climate change studies on CH_4 uptake have been conducted in mesic environments with soil moisture levels typically above optimum, but little is known about responses in drier systems with suboptimal soil water. We studied effects of atmospheric CO_2 (ambient versus 600 ppm), and temperature (ambient versus 1.5/3.0°C warmer day/night) on CH_4 uptake during two growing seasons in a full factorial semiarid grassland field experiment in Wyoming, United States. We observed typical hump-shaped relationships between CH_4 uptake and water filled pore space. Averaged over a range of soil moisture conditions, CH_4 uptake was not affected by elevated CO_2, but significantly decreased with warming in both seasons (25% in the first and 13% in the second season). Warming showed the strongest reduction and elevated CO_2 showed the strongest increase in CH_4 uptake when soils were below optimum moisture, indicating that these effects are particularly strong when soils are dry. Thus, directional effects of elevated CO_2 and warming on CH_4 uptake in semiarid grasslands can be opposite to their effects in mesic ecosystems because semiarid grasslands are often below optimum soil moisture for methane uptake.

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1. Introduction

[2] Semiarid grasslands account for approximately 11% of the global land surface [*Bailey*, 1979] and have been shown to be important sinks of CH_4 on a global scale, removing between 0.5 and 5.6 Tg of CH_4 from the atmosphere each year [*Mosier et al.*, 1991]. Natural seasonal variation in soil moisture strongly modulates biological activity in semiarid grasslands [*Huxman et al.*, 2004; *Potts et al.*, 2006]. Both empirical and modeling studies suggest that changes in soil moisture caused by atmospheric CO_2 enrichment and warming also strongly affect biological activity in these grasslands [*Melillo et al.*, 1993; *Morgan et al.*, 2004; *Liu et al.*, 2009]. The CH_4 sink strength of semiarid grasslands may also be sensitive to changes in soil moisture caused by climate change, but there is still much uncertainty about how CH_4 uptake in semiarid grasslands is affected by climate change factors such as atmospheric CO_2 enrichment and warming.

[3] The rate of CH_4 uptake is sensitive to soil moisture and typically shows a hump-shaped relationship with soil moisture [*Torn and Harte*, 1996; *Bowden et al.*, 1998; *Del Grosso et al.*, 2000]. At high soil moisture contents the CH_4 uptake rate is limited by diffusivity of CH_4 into the soil, while very low moisture contents limit biological activity of methanotrophs [*von Fischer et al.*, 2009] (Figure 1). Soil moisture often increases under elevated CO_2 [*Niklaus et al.*, 1998; *Nelson et al.*, 2004] because of increased plant stomatal closure and increased plant water use efficiency [*Morgan et al.*, 2004], but decreases with warming [*Harte et al.*, 1995; *Dermody et al.*, 2007]. Thus opposing effects of elevated CO_2 and warming on soil moisture may also have opposing effects on CH_4 uptake. Further, the direction of the effects of elevated CO_2 and warming on CH_4 uptake may depend on if soil moisture conditions are dry causing limitation for methanotroph activity or wet causing limitation of diffusivity (Figure 1).

[4] In several field studies atmospheric CO_2 enrichment decreased CH_4 uptake [*Ineson et al.*, 1998; *Ambus and Robertson*, 1999; *Phillips et al.*, 2001; *McLain et al.*, 2002;

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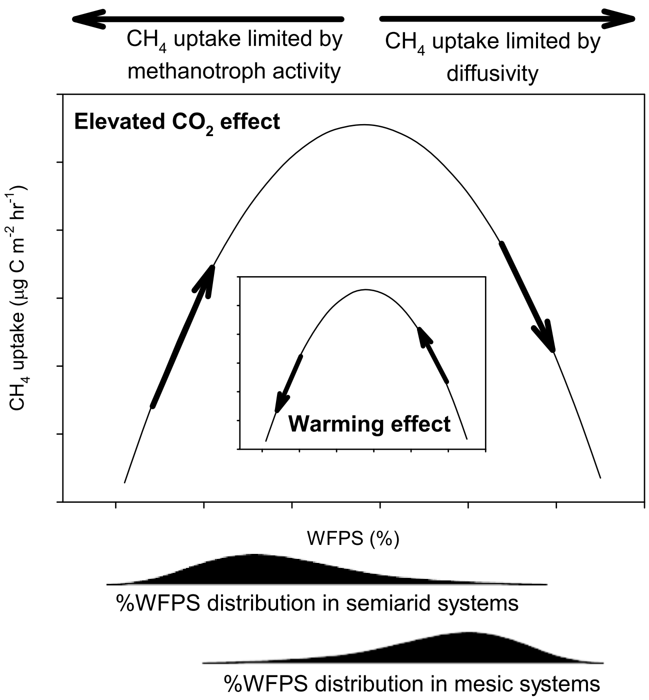

Figure 1. The relationship between CH_4 uptake and % water filled pore space (%WFPS), and how elevated CO_2 and warming affect CH_4 uptake mediated by their effects on soil moisture. Increased %WFPS under elevated CO_2 would increase CH_4 uptake when %WFPS is below optimum (i.e., when CH_4 uptake is limited by methanotroph activity) and decrease CH_4 uptake when WFPS is above optimum (i.e., when CH_4 uptake is limited by diffusivity). Inset shows opposite warming effects on CH_4 uptake mediated by its effect on soil moisture. Hypothetical distributions of %WFPS occurrences in semiarid and mesic systems are shown below the graph.

McLain and Ahmann, 2008], but no change in CH_4 uptake has also been observed [*Kang et al.*, 2001; *Mosier et al.*, 2002; *Kettunen et al.*, 2005]. A decrease in CH_4 uptake in response to elevated CO_2 has been related to an increase in soil moisture reducing diffusivity [*Ineson et al.*, 1998; *Ambus and Robertson*, 1999; *McLain et al.*, 2002], but also to increased production of CH_4 by methanogens or to changes in the methanotroph/methanogen community in the soil [*Phillips et al.*, 2001; *McLain and Ahmann*, 2008]. Experimental warming increased CH_4 uptake in some field studies, possibly due to a reduction in soil moisture increasing diffusivity [*Peterjohn et al.*, 1994; *Sjögersten and Wookey*, 2002], but not in others [*Christensen et al.*, 1997; *McHale et al.*, 1998; *Rustad and Fernandez*, 1998]. An increase in soil temperature could also directly stimulate methanotroph activity [*Castro et al.*, 1995; *Bowden et al.*, 1998]. Often, temporal variation in field measurements of CH_4 uptake correlates positively with temporal fluctuations in soil temperature [*van den Pol-van Dasselaar et al.*, 1998; *West et al.*, 1999; *Phillips et al.*, 2001], but it is not always clear how much this correlation is caused by direct or indirect temperature effects.

[5] Soil moisture contents in semiarid systems are often below optimum soil moisture [*Mosier et al.*, 2008], and as a result, semiarid systems may respond very differently to elevated CO_2 and warming than mesic sites where soil moisture contents may often be above this optimum (Figure 1). Most field studies that examined the effects on elevated CO_2 or warming on CH_4 fluxes were done in temperate/boreal forests, and (sub)arctic ecosystems where soil moisture contents may have been at or above optimum soil moisture, and thus where CH_4 uptake may have been limited by CH_4 diffusivity [*Peterjohn et al.*, 1994; *Christensen et al.*, 1997; *McHale et al.*, 1998; *Rustad and Fernandez*, 1998; *Ambus and Robertson*, 1999; *Phillips et al.*, 2001; *McLain et al.*, 2002; *Sjögersten and Wookey*, 2002]. One exception is a study by *Mosier et al.* [2002] who studied the effects of elevated CO_2 using open top chambers on CH_4 uptake in a semiarid grassland in Colorado, United States. Five years of elevated CO_2 did not significantly alter CH_4 uptake in this system. However, CH_4 uptake tended to be greater under elevated CO_2 than under ambient CO_2, suggesting that greater soil water savings under elevated CO_2 reduced soil moisture limitation on methanotroph activity.

[6] To better understand the response of dry grassland CH_4 uptake to climate change factors, we examined the effects of elevated CO_2 and warming on CH_4 uptake during the growing season in a semiarid grassland in Wyoming, United States. We hypothesized that elevated CO_2 and warming effects on CH_4 uptake in this semiarid grassland are mediated by their effects on soil moisture. Because CH_4 uptake in this semiarid grassland is often below optimum soil moisture thereby limiting methanotroph activity, we expected that increased soil moisture under elevated CO_2 would increase CH_4 uptake, and that decreased soil moisture with warming would decrease CH_4 uptake during these dry periods.

2. Materials and Methods

2.1. Site Description and Experimental Design

[7] We did our study in the Prairie Heating And CO_2 Enrichment (PHACE) experiment located at the USDA-ARS High Plains Grasslands Research Station, Wyoming, United States (41°11′ latitude, 104°54′ longitude). Mean annual precipitation is 384 mm and mean air temperatures are 17.5°C in July and −2.5°C in January. The vegetation is of a northern mixed-grass prairie dominated by *Pascopyrum smithii*, *Hesperostipa comata* (C_3 grasses) and *Bouteloua gracilis* (C_4 grass). These 3 species comprise approximately 80% of the total aboveground biomass. Other species include *Carex eleocharis* (sedge), *Artemisia frigida* (subshrub), and *Sphaeralcea coccinea* (forb). The site has not been grazed since 2004. Soils are of the Ascalon (north side) and Altvan series (south side, fine-loamy, mixed, mesic Aridic Argiustoll). The well-drained soils have a pH of 7.0 (top 20 cm).

[8] Site preparation of the PHACE experiment started in 2005. Twenty-five circular plots (12 on the north side, 18 on the south side) were established by installing a 60 cm deep, 3.7 m diameter plastic perimeter barrier around each experimental plot. A steel flange buried to 25 cm into the soil divided each plot in half. One half of the plot (randomly assigned to the north or south part of the plot) was disturbed and planted with invasive weeds, while in the other half native vegetation was maintained. Our study was done on the side with the native vegetation. The CO_2 and warming treatments were established in 20 plots ("core plots") in a full

factorial design (2 levels of CO_2 * 2 levels of warming * 5 replicates). Ten plots received an elevated atmospheric CO_2 concentration of 600 ppm using free-air CO_2 enrichment technology [*Miglietta et al.*, 2001]. The CO_2 was injected into the plot from a plastic pipe, perforated with 300 μm laser-drilled holes, surrounding the plot (diameter 3.4 m). Plots were treated with CO_2 only during the day and during the growing season (April–November), and started in April 2006. The canopy of 5 ambient CO_2 and 5 elevated CO_2 plots were warmed 1.5°C above ambient temperature during the day and 3°C above ambient temperature during the night with 1000 W ceramic infrared heaters. Each plot was heated by six heaters installed on a triangular frame 1.5 m above the ground. Heaters were controlled by a proportional-integral-derivative feedback loop [*Kimball et al.*, 2008]. The heating treatment was year-round and started in April 2007. The 5 plots not used for the CO_2 and warming were irrigated with 20 mm four times during the growing season of 2007 (total of 80 mm yr^{-1}) and three times during the growing season of 2008 (total of 60 mm yr^{-1}). We included this treatment to better understand the relationship between CH_4 uptake and soil water. Because 2006 was a dry year, all 25 plots received 20 mm irrigations eight times during the course of the season (total of 160 mm) to facilitate establishment in the adjacent invasive species experiment.

2.2. Measurements

[9] In 2005 EnviroSMART soil moisture probes were installed to 80 cm soil depth, one probe at each plot. Volumetric soil moisture was monitored at 10, 20, 40, 60, and 80 cm soil depth. In 2005 thermocouples were installed at 3 and 10 cm soil depth in each plot. Soil moisture and temperature data were logged every hour, starting in July 2006. Water filled pore space (WFPS) in the top 15 cm of the soil was calculated based on soil moisture measured at 10 cm soil depth and bulk densities measured at 0–5 and 5–15 cm soil depth in 2005.

[10] In March 2007 we pounded polyvinyl chloride (PVC) circular chamber bases (height, 10 cm; diameter, 20 cm) 8 cm into the ground, one base in each plot. From April to October in 2007 and 2008 we measured CH_4 fluxes approximately once every 2 weeks (total of 16 measurements in 2007 and 14 measurements in 2008) using a vented closed chamber technique [*Hutchinson and Mosier*, 1981]. Leakage of CH_4 in or out of this system is considered to be small, and thus CH_4 fluxes measured are representative of the area covered by the base. Midmornings of each sampling day a vented closed PVC chamber (height, 10 cm; diameter, 20 cm) was placed on the base in each plot, sealed off with a rubber band, and 30 ml gas samples were taken from the headspace at 0, 15, 30, and 45 min after chamber placement. Gas samples were analyzed for CH_4 on a gas chromatograph equipped with a flame ionization detector. Methane fluxes were calculated using linear regressions using the CH_4 concentrations measured in the four samples taken at 15 min intervals. We calculated cumulative CH_4 uptake during the growing season of 2007 and 2008 by multiplying the average CH_4 uptake rate between two measuring dates by the time interval between two measuring dates, and by adding the preceding CH_4 uptake. We did not measure CH_4 uptake before the treatments started to test for preexisting differences among treatments. However, because the CO_2, warming, and irrigation treatments were replicated 5 times randomly assigned at our site (2 replicates on the north side and 3 on the south side), we are confident that we strongly reduced potential treatment effects caused by spatial variability of the study site.

2.3. Statistical Analyses

[11] We used repeated measures analysis of variance (repeated measures ANOVA) to test for main effects of CO_2 (ambient versus elevated), warming (no warming versus warming, both between-subjects factors), date (within-subjects factor), and their interactions on WFPS in the top 15 cm of the soil (on weekly averages) and on CH_4 uptake rates from April to October in 2007 and 2008. For the same variables we used a separate repeated measures ANOVA to test for irrigation effects (5 irrigated plots versus 5 plots under ambient CO_2 and no warming, between-subjects factor), date, and their interaction. We used ANOVA to test for main effects of CO_2, warming, and their interaction (20 core plots only), and for irrigation effects separately, on cumulative CH_4 uptake during the growing season of 2007 and 2008. We used quadratic regression analyses to examine relationships between average daily CH_4 uptake rates and WFPS in the top 15 cm of the soil and soil temperature at 3 and 10 cm soil depth. We further tested to what extent CO_2, warming, and irrigation effects on CH_4 uptake measured on each date in both years could be explained by their effects on soil moisture. We first averaged CH_4 uptake for each date (average of the 5 replicates for each treatment). We then used the average CH_4 uptake for each date as replicates in analyses of covariance (ANCOVAs) thereby removing the date effect, since we were no longer interested in *when* treatment effects occurred, but in how much of the treatment effects on CH_4 uptake could be explained by treatment-induced changes in soil moisture with WFPS as the covariate. Because CH_4 uptake showed a hump-shaped relationship with WFPS, we included a quadratic term of the covariate in the ANCOVAs. We also compared CO_2 and warming treatment effects in the ANCOVAs with their effects in ANOVAs without WFPS as the covariate. We included the random effect of soil type (north versus south, block effect) in all ANOVAs and ANCOVAs. Note that we tested the irrigation effect separately with ANOVAs and ANCOVAs using the 5 ambient CO_2 and ambient temperature plots without irrigation and the 5 ambient CO_2 and ambient temperature plots with irrigation. We log-transformed data when necessary to reduce heteroscedasticity. All statistical analyses were done with JMP (version 4.0.4).

3. Results

[12] Growing season precipitation in 2007 was close to average (from 1 April to 31 October, 315 mm fell compared to 310 mm on average from 1951 to 2008), while in 2008 it was slightly above average (354 mm). From 1 April to 31 October 2007 and 2008, WFPS to 15 cm soil depth was significantly higher under elevated than under ambient CO_2 ($P = 0.003$ in 2007 and in 2008, repeated measures ANOVA, Figures 2a and 2b). Warming significantly reduced WFPS in both years ($P = 0.02$ in 2007 and $P = 0.005$ in 2008). We observed no significant CO_2*warming interactions on WFPS in either year ($P > 0.1$). Irrigation events caused spikes in

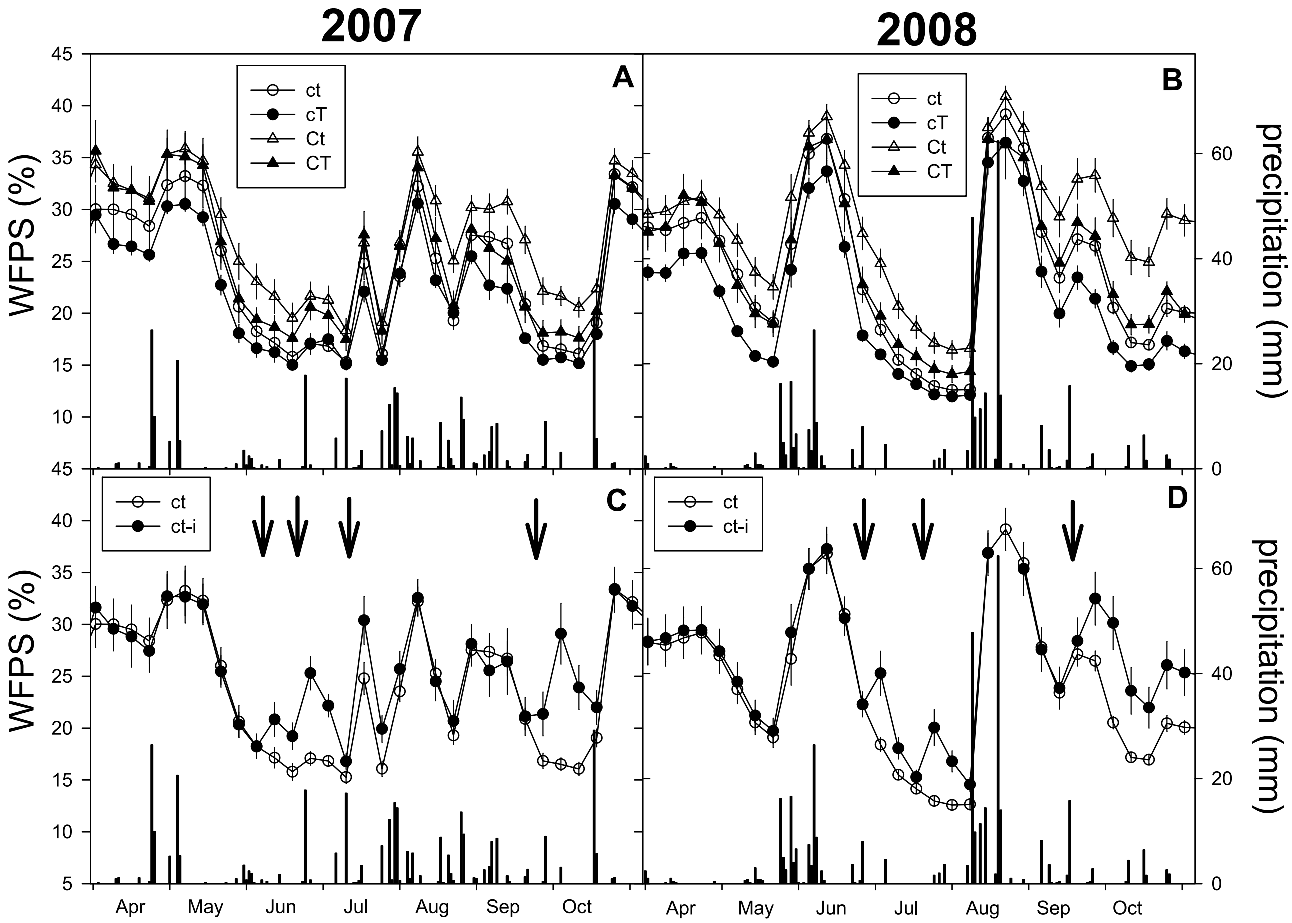

Figure 2. Water filled pore space (WFPS, left-hand axis) to 15 cm soil depth in 2007 and 2008 averaged by (a and b) elevated CO_2 treatment (ct, ambient CO_2 and ambient temperature; cT, ambient CO_2 and elevated temperature; Ct, elevated CO_2 and ambient temperature; CT, elevated CO_2 and elevated temperature) and by (c and d) irrigation treatment (ct-i, ambient CO_2 and ambient temperature, but irrigated). Each data point is a weekly average of the hourly logged data. Bars in each panel show daily precipitation (right-hand axis). Arrows in Figures 2c and 2d indicate the time when 20 mm water events occurred. Error bars indicate 1 SE.

WFPS relative to the ambient plots, but otherwise were similar in WFPS (Figures 2c and 2d).

[13] In this ecosystem methane was a net sink throughout the growing season of 2007 and 2008. We did not observe significant CO_2*warming or CO_2*warming*date interaction effects on CH_4 uptake rates in the repeated measures ANOVA. We therefore present CO_2 effects averaged across the warming treatment and warming effects averaged across the CO_2 treatment. Elevated CO_2 did not significantly affect CH_4 uptake rates in 2007 or in 2008 ($P > 0.1$, Figures 3a and 3b). However, CO_2*date interaction effects were highly significant in both years ($P < 0.0001$) with CH_4 uptake rates sometimes higher (midsummer of 2007 and 2008) and sometimes lower (late summer 2008) under elevated than under ambient CO_2. Possibly, positive CO_2 effects during midsummer when soils were relatively moist, may have canceled out negative CO_2 effects later in the season when soils were much drier. Warming significantly reduced CH_4 uptake rates in both years ($P < 0.05$, Figures 3c and 3d). This reduction occurred throughout most of the growing season, but was particularly large during the middle of the growing season causing significant warming*date interactions in both years ($P < 0.01$). The irrigation treatment had only a marginally significant effect on CH_4 uptake rates in 2008 ($P = 0.06$, Figures 3e and 3f). The CH_4 uptake rates increased after irrigation events in midsummer, but decreased after irrigation events in late summer. Thus, not surprisingly, the irrigation*date interactions were significant in both years ($P < 0.01$).

[14] Similar to CH_4 uptake rates, elevated CO_2 had no effect on the cumulative amount of CH_4 taken up during the growing season (Table 1). Apparently, opposing effects of CO_2 on CH_4 uptake rates during different times of the growing season canceled each other out. On the other hand, warming significantly reduced the cumulative amount of CH_4 uptake by 25% in 2007 and by 13% in 2008. The cumulative amount of CH_4 uptake increased by 20% in 2007 and decreased by 20% in 2008 in response to irrigation, although the irrigation effect in 2007 was not significant.

[15] Although we found the usual hump-shaped relationship, the shape and optimum soil moisture level was affected by the CO_2 and warming treatments, suggesting that treat-

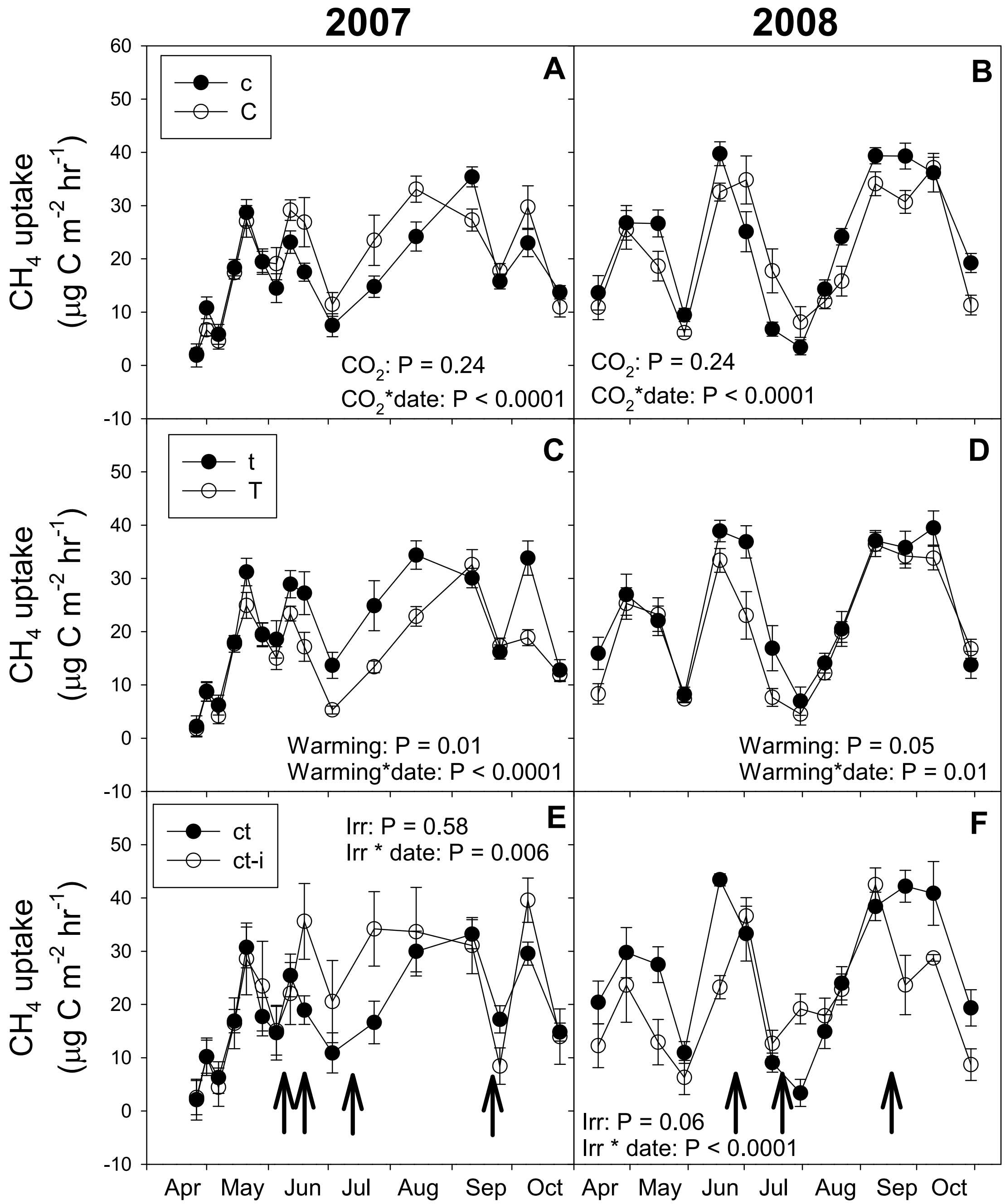

Figure 3. Methane uptake rates during the growing season of 2007 and 2008 averaged by (a and b) CO_2 treatment (c, ambient CO_2; C, elevated CO_2), by (c and d) warming treatment (t, ambient temperature; T, elevated temperature), and by (e and f) irrigation treatment (ct, ambient CO_2 and ambient temperature without irrigation; ct-i, ambient CO_2 and ambient temperature with irrigation). Arrows in Figures 3e and 3f indicate the time when 20 mm water events occurred. Error bars indicate 1 SE.

ment effects cannot solely be explained by their effects on WFPS. The CH_4 uptake rates measured in 2007 and 2008 showed a significant hump-shaped relationship with WFPS with an optimum %WFPS around 24%. This relationship with WFPS moved to the right under elevated CO_2 (averaged across warming treatment, Figure 4a) and moved downward with warming (averaged across the CO_2 treatment, Figure 4b). When we used WFPS as a covariate in the ANCOVA, then the warming treatment effect remained significant, while there was a significant CO_2*WFPS^2 interaction (Table 2). This suggests that other effects than changes in WFPS caused by the CO_2 and warming treatments were involved in altering CH_4 uptake. On the other hand, the hump-shaped relationship between CH_4 uptake and WFPS was very similar between the irrigated and nonirrigated plots (Figure 4c), and there were no significant interactions with WFPS in the ANCOVA (Table 2). Soil temperature at 10 cm soil depth showed a similar hump-shaped relationship with

Table 1. Average Cumulative Amount (±SE) of CH_4 Uptake During the Growing Season of 2007 and 2008[a]

Treatment	2007 (181 Days) (mg C m^{-2})	2008 (199 Days) (mg C m^{-2})
Ct	92 ± 9	127 ± 4
cT	75 ± 5	105 ± 6
Ct	113 ± 12	112 ± 12
CT	79 ± 9	102 ± 10
ct-i	111 ± 22	103 ± 10
ANOVA P values[b]		
CO_2	0.13	0.23
Warming	0.006	0.05
CO_2*warming	0.28	0.39
Irrigation	0.44	0.04

[a]Here ct, ambient CO_2 and ambient temperature; cT, ambient CO_2 and elevated temperature; Ct, elevated CO_2 and ambient temperature; CT, elevated CO_2 and elevated temperature; ct-i, ambient CO_2 and ambient temperature, but irrigated.

[b]Soil type effects were never significant (P > 0.1) and are not reported.

CH_4 uptake, while at 3 cm soil depth this relationship was not significant (Figure 5). Soil temperature was also significantly correlated to soil moisture (r = 0.51 and 0.48 for relationships with soil temperature at 3 and 10 cm soil depth, respectively, P < 0.0001 for both relationships).

[16] The CH_4 uptake responses to elevated CO_2 and warming depended on overall dryness or wetness of the soil. We plotted the average CH_4 uptake response to elevated CO_2 (averaged across the warming treatment), and the average CH_4 uptake response to warming (averaged across the CO_2 treatment) for each measuring date in 2007 and 2008 against the average %WFPS of all 20 core plots for each date (Figure 6). Methane uptake rates were mostly higher under elevated CO_2 than ambient CO_2 when soils were below optimum %WFPS (around 24%), and mostly lower under elevated CO_2 than under ambient CO_2 when soils were above optimum %WFPS (Figure 6a). The lower CH_4 uptake rates with warming particularly occurred when soils were below optimum %WFPS (Figure 6b). Exponential curves fitted the data better than linear relationships, suggesting that both CO_2 and warming treatment effects were more sensitive under drier soil conditions. Nonirrigated soils in this semiarid system were more frequently below than above optimum %WFPS (59% of the times measured below 24% WFPS, Figure 4d).

4. Discussion

[17] Throughout the growing seasons of 2007 and 2008, CH_4 was taken up by this semiarid grassland. Methane uptake rates ranged between 2 and 44 μg C m^{-2} h^{-1}, similar to rates measured in a semiarid grassland in Colorado, United States [*Mosier et al.*, 2002, 2008] and other ecosystems [*Christensen et al.*, 1997; *Ineson et al.*, 1998; *Phillips et al.*, 2001; *Sjögersten and Wookey*, 2002]. As expected, the relationship between CH_4 uptake and WFPS was hump-shaped with an optimum WFPS around 24%. This optimum %WFPS agrees well with optimum %WFPS values of fine-textured sites in semiarid grasslands of Colorado [*Mosier et al.*, 2008]. Often %WFPS was below the optimum, suggesting that soil water constraints on methanotroph activity are important during the growing season.

[18] Our results indicate that CH_4 uptake in a semiarid grassland responds differently to elevated CO_2 and warming than CH_4 uptake in mesic environments. While other field studies in mesic environments have shown a decrease in CH_4 uptake in response to elevated CO_2 [*Ineson et al.*,

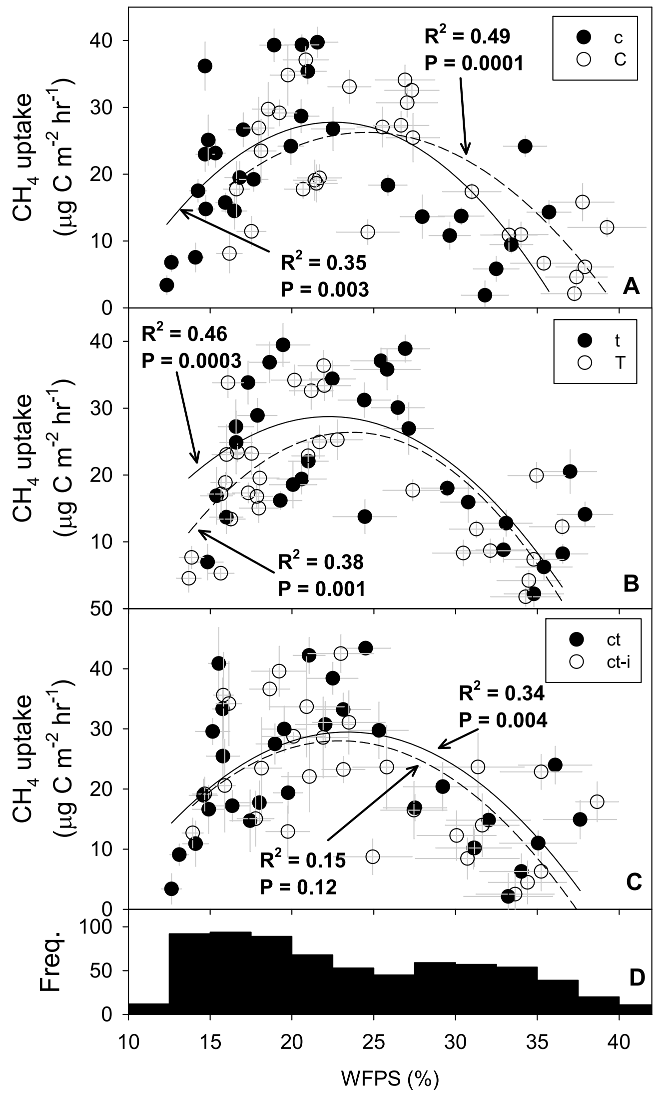

Figure 4. Methane uptake rate as a function of water filled pore space (WFPS) averaged by (a) CO_2 treatment (c and solid line, ambient CO_2; C and dashed line, elevated CO_2), by (b) warming treatment (t and solid line, ambient temperature; T and dashed line, elevated temperature), and by (c) irrigation treatment (ct and solid line, ambient CO_2 and ambient temperature without irrigation; ct-i and dashed line, ambient CO_2 and ambient temperature with irrigation), and (d) frequency distribution of %WFPS: at the time of CH_4 flux measurements in all nonirrigated plots. Each data point in Figures 4a–4c is the average CH_4 uptake and %WFPS in the ambient and elevated CO_2 plots (averaged across the warming treatment, Figure 4a), in the nonwarmed and warmed plots (averaged across the CO_2 treatment, Figure 4b), and in the ct and ct-i plots (Figure 4c) at each measuring date in 2007 and 2008. Regression R^2 and P values are based on these averaged values. Error bars are 1 SE.

Table 2. ANOVA and ANCOVA P Values for Methane Uptake During the Growing Seasons of 2007 and 2008[a]

Model Effect[b]	ANOVA	ANCOVA
CO_2	0.90	0.63
Warming	**0.0001**	**<0.0001**
WFPS		**0.0003**
$WFPS^2$		**<0.0001**
CO_2*WFPS		0.20
CO_2*WFPS^2		**0.02**
Warming*WFPS		0.64
$Warming*WFPS^2$		0.28
Irrigation	0.73	0.85
WFPS		0.16
$WFPS^2$		**0.0003**
Irrigation*WFPS		0.17
$Irrigation*WFPS^2$		0.93

[a]P values are in bold when P < 0.05.
[b]Soil type effects were never significant (P > 0.1) and are not reported.

1998; *Ambus and Robertson*, 1999; *Phillips et al.*, 2001; *McLain et al.*, 2002; *McLain and Ahmann*, 2008], we found that on average CH_4 uptake was not affected by elevated CO_2. However, CH_4 uptake did decrease under elevated CO_2 when soils were above optimum %WFPS (i.e., when CH_4 uptake was limited by diffusivity, Figure 6a). In contrast, when soils were below optimum %WFPS (i.e., when CH_4 uptake was limited by methanotroph activity), then CH_4 uptake rates tended to be higher under elevated CO_2 than under ambient CO_2. Thus, the nonsignificant main effect of CO_2 on CH_4 uptake may have been a result of negative effects during times when soils were wet cancelling out positive effects during times when soils were dry. Warming significantly reduced CH_4 uptake in both years. These results also contrast other field studies where no or positive effects of warming on CH_4 uptake have been observed [*Peterjohn et al.*, 1994; *Christensen et al.*, 1997; *McHale et al.*, 1998; *Rustad and Fernandez*, 1998; *Sjögersten and Wookey*, 2002]. The reduction in CH_4 uptake with warming particularly occurred when soils were below the optimum %WFPS for CH_4 uptake (Figure 6b), conditions that frequently happen in semiarid grasslands, but that may not happen as frequently in mesic environments. These results clearly indicate that under dry soil conditions, which frequently occur in semiarid ecosystems, elevated CO_2 and warming effects on CH_4 uptake are very different from wet soil conditions as in mesic ecosystems. The exponential relationships in Figure 6 with steeper slopes at lower %WFPS further indicate that the CO_2 and warming treatment effects become more sensitive when soil conditions become drier.

[19] Elevated CO_2 and warming effects on CH_4 uptake were largely a result of their effects on soil moisture. A higher soil moisture or %WFPS under elevated CO_2 most likely increased CH_4 uptake when in general the soils were dry (i.e., when CH_4 uptake was limited by methanotroph activity), and decreased CH_4 uptake when in general the soils were wet (i.e., when CH_4 uptake was limited by diffusivity) due to the hump-shaped relationship between CH_4 uptake rate and WFPS (Figure 1). Likewise, a lower %WFPS in the warmed plots most likely decreased CH_4 uptake rates under generally dry soil conditions suggesting a positive feedback between methane flux and climate warming [*Torn and Harte*, 1996]. The importance of soil moisture for CH_4 uptake responses to CO_2 and warming is further illustrated by the irrigation effects on CH_4 uptake. In 2008, irrigation significantly reduced CH_4 uptake, which was largely driven by a reduction in CH_4 uptake after the irrigation event late in the season (September) and possibly from irrigation events in 2007 carried over into the spring of 2008 when soils were relatively wet (Figure 3f, i.e., when CH_4 uptake was limited by soil moisture effects on diffusivity). Likewise, the increase in CH_4 uptake in response to irrigation events in midsummer of 2007 and 2008 (Figures 3e and 3f) occurred when soils were dry, i.e., when CH_4 uptake was limited by soil moisture effects on methanotroph activity. Thus, irrigation effects on CH_4 uptake may to a large degree depend on the timing when irrigation events occur. Similarly, expected changes in precipitation patterns for this area (less winter snow and rainfall in the winter creating drier springs) [*Christensen et al.*, 2007;

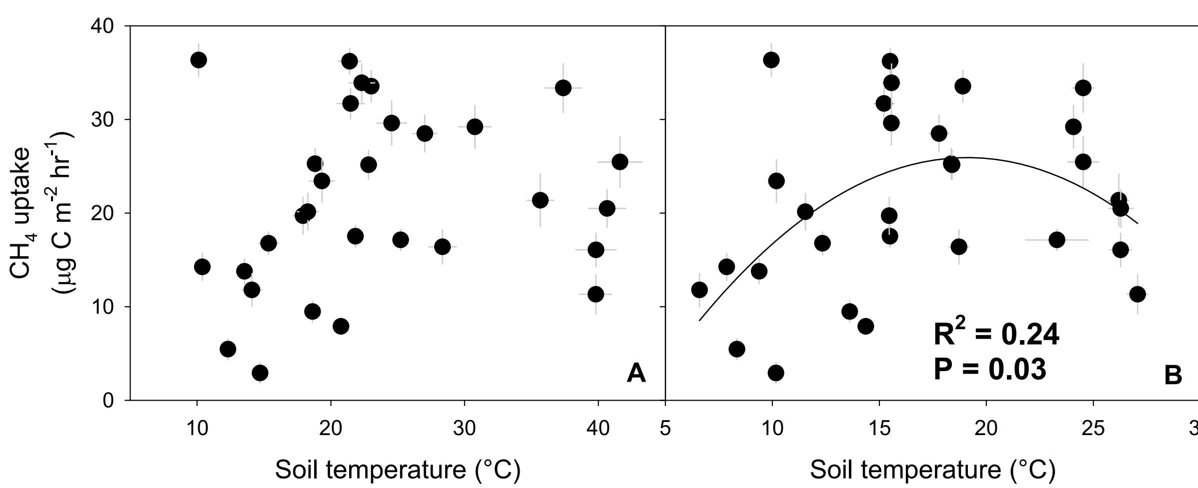

Figure 5. Methane uptake rate as a function of soil temperature at (a) 3 cm and (b) 10 cm soil depth. Each data point in each panel is the average CH_4 uptake and %WFPS of all 25 plots at each measuring date in 2007 and 2008. Regression R^2 and P values are based on these averaged values. Error bars are 1 SE.

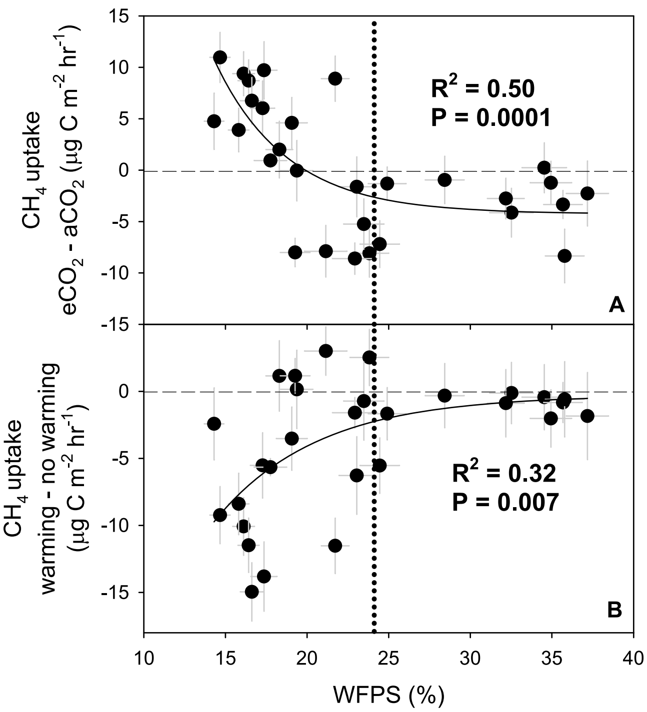

Figure 6. Methane uptake rate responses to (a) elevated CO_2 and (b) warming as a function of water filled pore space (WFPS). Each data point is the average CH_4 uptake response to elevated CO_2 (averaged across the warming treatment), and the average CH_4 uptake response to warming (averaged across the CO_2 treatment) for each measuring date in 2007 and 2008. The WFPS was calculated as the average %WFPS of all 20 core plots for each date. Regression R^2 and P values are based on these averaged values. Error bars are 1 SE. The vertical dotted line represents optimum %WFPS.

Overpeck and Udall, 2010] could potentially have large effects on CH_4 uptake both in magnitude and direction in these grasslands.

[20] We have little evidence that CH_4 uptake was constrained by soil temperature. When we related CH_4 uptake to soil temperature, we observed no relationship for the 3 cm soil temperatures, and a hump-shaped relationship for the 10 cm soil temperatures that was similar to, although much weaker than, the relationship between CH_4 uptake and soil moisture. Methane uptake decreased above 30°C at 3 cm soil depth and above 20°C at 10 cm soil depth. On the other hand, in a different study, the relationship between CH_4 uptake and soil temperature remained positively linear up to 35°C when soil moisture was not limiting [*Del Grosso et al.*, 2000]. It is likely that the curve-linear relationship between the 10 cm soil temperature and CH_4 uptake, and decrease in CH_4 uptake at high soil temperatures in our study was to a large extent caused by water limitation on methanotroph activity. There was a high degree of covariance between soil temperature and soil moisture, which made it difficult to separate temperature from moisture effects. Unfortunately, our study did not have a treatment with both warming and irrigation, which would have made it easier to separate soil moisture from soil temperature effects on CH_4 uptake. We note however, that the warming treatment caused a reduction in CH_4 uptake despite a significant increase in soil temperature [*Dijkstra et al.*, 2010], suggesting that, if the relationship between CH_4 uptake and soil moisture is positive, CH_4 uptake was not constrained by soil temperature in the warmed plots.

[21] We found limited support for other factors that may have contributed to the CO_2 and warming treatment effects on CH_4 uptake. The hump-shaped relationship between CH_4 uptake and WFPS under elevated CO_2 shifted slightly to the right (causing a significant CO_2*WFPS^2 interaction in the ANCOVA) and moved downward with warming (causing a significant warming effect after adjusting for WFPS effects in the ANCOVA), while the relationship between CH_4 uptake and WFPS was similar between irrigated and non-irrigated plots. These results could indicate that other factors than soil moisture (e.g., changes in soil NH_4^+, labile C, and/or microbial community composition) were responsible for the shifts caused by elevated CO_2 and warming. However, these shifts are relatively small compared to the large errors associated with each data point in Figure 4. Regardless, our results suggest that soil moisture is the most important factor for explaining the CO_2 and warming effects on CH_4 uptake in this semiarid system.

[22] We have shown that during dry soil conditions, CH_4 uptake in this semiarid grassland responded very differently to elevated CO_2 and warming compared to ecosystems with wetter soil conditions. While CH_4 uptake often decreases in response to elevated CO_2 and increases in response to warming under wetter soil conditions [*Peterjohn et al.*, 1994; *Ineson et al.*, 1998; *Ambus and Robertson*, 1999; *Phillips et al.*, 2001; *McLain et al.*, 2002; *Sjögersten and Wookey*, 2002; *McLain and Ahmann*, 2008], we observed the opposite during times when soil moisture was below the optimum soil moisture content for CH_4 uptake (Figure 6). Indeed, CH_4 uptake responses to elevated CO_2 and warming effects were more sensitive under dry soil conditions. Because the effect of elevated CO_2 on CH_4 uptake was opposite to the warming effect, our results also suggest that combined effects of elevated CO_2 and warming on CH_4 uptake could be less than when only one of these climate change factors is considered. Despite uncertainty about future changes in precipitation [*Christensen et al.*, 2007], recently some have suggested considerable drier conditions for western North America [*Overpeck and Udall*, 2010]. Our results suggest that under drier conditions CH_4 uptake in these grassland ecosystems, which occupy roughly 11% of the global land surface [*Bailey*, 1979], will be more sensitive to elevated CO_2 and warming.

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