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Hydrological Control of Greenhouse Gas Fluxes in a Sierra Nevada Subalpine Meadow

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Abstract

Alpine and subalpine meadows are often hotspots of water availability and biodiversity in montane landscapes, but we know little about whether these attributes also make meadows hotspots of greenhouse gas (GHG) emission. Furthermore, many of these meadows will likely become drier during the growing season in the future because of less precipitation, earlier timing of snowmelt, and increased evapotranspiration associated with climatic warming. To evaluate the potential effects of soil drying on GHG emission, we studied a soil moisture gradient in a Sierra Nevada subalpine meadow in California. Our objectives were: (1) to assess the strength of hydrological control for soil carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) fluxes both earlier and later in the growing season; and (2) to quantify the contribution of CH_4 and N_2O to net GHG emission. The replicated gradient spanned 50 m, from the wet middle to dry edge of the meadow, and soil volumetric water content was measured 0 to 12 cm deep. Fluxes of CO_2, CH_4, and N_2O were measured using static chambers at 10 m intervals across the gradient. We found that the wet side of the gradient was not a CH_4 or N_2O source on either sampling date. Net CH_4 emission from soil was rare and CH_4 uptake was prevalent, particularly on the dry side of the gradient. Soil N_2O fluxes shifted from net uptake at the middle of the meadow to net emission at the edge, but only earlier in the growing season. Of the three GHGs, CO_2 fluxes showed the most temporal variation but surprisingly varied little across the hydrological gradient. Other environmental factors—including plant species richness and soil carbon concentration—appeared more important than soil moisture in explaining CO_2 fluxes. Therefore, the strength of near-surface hydrological control increased in the following order: $CO_2 < N_2O < CH_4$. Our results suggest that non-CO_2 greenhouse gases will need proper accounting during the snow-free season in order to more accurately predict the effects of future soil drying on GHG emissions in heterogeneous montane landscapes.

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Introduction

Greenhouse gas (GHG) emissions from terrestrial ecosystems—which influence the global heat balance of the planet—often reflect changes in water availability across the landscape (Smith et al., 2003). Wet montane meadows, for example, can emit more carbon dioxide (CO_2) than surrounding drier upland forests (Riveros-Iregui and McGlynn, 2009). Wet montane meadows store carbon through high rates of plant production during the growing season followed by an extended cold season with low rates of microbial decomposition (Kato et al., 2004, 2006; Hu et al., 2010). Despite their relatively small area (e.g., 3% of Sierra Nevada in California; Keeler-Wolf et al., 2012), meadows could be significant sources of CO_2, methane (CH_4), and nitrous oxide (N_2O) because of high organic matter content and relatively low water limitation during the snow-free period (i.e., subsurface water sources and high field capacities due to high organic matter content). Many high-elevation ecosystems are likely on the cusp of hydrological and biogeochemical changes resulting from less precipitation (Seager et al., 2007), earlier timing of snowmelt (Mote et al., 2005; Stewart et al., 2005), and increased evapotranspiration due to climatic warming (Harte et al., 1995; Barnett et al., 2005; Fu et al., 2012). By better understanding current hydrological controls of GHG fluxes in high-elevation meadows, we can more accurately predict the effects of future soil drying on GHG emissions in heterogeneous montane landscapes.

Predicting the magnitude of CO_2 emission and the direction of CH_4 and N_2O fluxes in montane meadows is not straightforward. Most studies do not measure all three major GHGs together at the same site. Thus, it remains unclear how soil moisture in montane meadows influences the relative contribution of non-CO_2 GHGs to net radiative forcing (Jiang et al., 2010). Soil CH_4 and N_2O fluxes vary from net production to net consumption, depending on soil moisture, oxygen concentration, temperature, pH, nitrogen content, and microbial community structure (Mosier et al., 1993; Torn and Harte, 1996; Filippa et al., 2009; Lin et al., 2009; Hu et al., 2010; Jiang et al., 2010; Giles et al., 2012). By not accounting for CH_4 and N_2O—which have much higher warming potentials per mole than CO_2—we could be ignoring an important component of the GHG budget of montane meadows.

We may also be ignoring GHG-specific responses to drying. Can we assume, for example, that areas with dry surface soil also emit less CO_2? And does wet surface soil necessarily express net CH_4 emission? Meadow CO_2 fluxes often show large spatial variation and can be limited by too little water, too much water (i.e., slower anaerobic metabolism and reduced diffusional transport from deep soil), cold temperatures, and availability of labile carbon (Fisk et al., 1998; Saleska et al., 1999; Kato et al., 2004; Pacific et al., 2008, 2009; Saito et al., 2009; Suh et al., 2009; Jiang et al., 2010). There is also evidence that plant root respiration (as estimated by root biomass) can be more important than microcli-

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mate in explaining meadow CO_2 fluxes (Geng et al., 2012). Plant cover and diversity may also affect CH_4 and N_2O fluxes by altering carbon and nitrogen availability (Niklaus et al., 2006). Net CH_4 emission is favored in wetter soils (Mosier et al., 1993; Whalen, 2005), but the extent of CH_4 consumption in drier meadow soils is unclear. Net N_2O emission can also relate positively to soil moisture (Mosier et al., 1993; Fisk et al., 1998; Filippa et al., 2009) or show no relation to commonly measured environmental variables (Jiang et al., 2010). Thus, the controls on each GHG are apparently different, but because multiple GHGs have not been studied at many sites, we do not know how broadly these controls apply.

A hydrological gradient based on meadow topography is a way to assess the relative control of soil moisture on GHG fluxes. Topographic position relates to soil moisture, which may in turn relate to GHG fluxes, which thus aids in the modeling and upscaling of GHG emissions across montane landscapes (Fisk et al., 1998; Grayson and Western, 1998; Western et al., 1999; Riveros-Iregui and McGlynn, 2009; Pacific et al., 2011; Jeong et al., 2012). The depth of the groundwater table typically decreases from the middle to edges of meadows (Lowry et al., 2010), resulting in drier soils near the edges. Greenhouse gas emissions are expected to follow a similar pattern (Mosier et al., 1993)—decreasing from the middle to the edges—but few studies have attempted to quantify this spatial pattern.

The Sierra Nevada in California provides an ideal alpine setting to investigate hydrological control of meadow GHG fluxes during the growing season because of the abundance of montane meadows and the Mediterranean-type climate. Sierra Nevada meadows, as opposed to the Rocky Mountains for example, receive almost no precipitation after spring snowmelt and are therefore expected to provide a consistent topographic soil moisture gradient without the confounding effects of summer precipitation. Soil moisture can strongly control CO_2 emission in a Mediterranean-type climate (Correia et al., 2012), but, to date, no study has measured all three major GHGs simultaneously within the same Sierra Nevada meadow. A spring-fed wetland in the Sierra Nevada foothills was found to be a hotspot of CH_4 and N_2O emission compared to surrounding oak savanna (Oates et al., 2008). We therefore expected that the wetter portion of a subalpine meadow would also be a hotspot of CH_4 and N_2O emission.

We measured GHG fluxes across a soil moisture gradient from the middle to edge of a Sierra Nevada subalpine meadow in Yosemite National Park. To determine whether the effect of seasonal drying is similar to the effect of drying along the hydrological gradient, we measured GHG gas fluxes both earlier and later in the growing season. The gradient spanned from wet soils near field capacity at the middle of the meadow to considerably drier soils at the edge of the meadow. To identify the potential impacts of future soil drying, our first objective was to quantify the strength of hydrological control on different GHG fluxes. We hypothesized that the wetter portion of the meadow would be a hotspot of GHG emission compared to the drier edge. Our second objective was to determine the contribution of CH_4 and N_2O fluxes to net GHG emission in a subalpine meadow. We expected that CH_4 and N_2O fluxes would contribute most to net GHG emission in the wetter portion of the meadow.

Methods

SITE DESCRIPTION

A Sierra Nevada subalpine meadow (2860 m a.s.l.; 37.8997°N, 119.3397°W) was chosen based on trail access (~5 km north-northeast of Tuolumne Meadows in Yosemite National Park, California, U.S.A.) and minimal previous disturbance (i.e., no recreational camping or packstock use). The sampled portion of the meadow was at least 200 m from the trail and showed no signs of human disturbance. The middle of the meadow was slightly lower in elevation, surrounded by a higher and drier edge of the meadow that transitioned to coniferous forest approximately 50 m beyond where we sampled. The meadow was oriented east-west (slope < 5°) with Delaney Creek near the middle flowing west. The meadow was medium-sized (15.8 ha) compared to other meadows in Yosemite National Park, and dominated by small-statured plant species (<30 cm tall) including *Aster alpigenus*, *Calamagrostis breweri*, *Carex filifolia*, *Deschampsia cespitosa*, and *Vaccinium caespitosum*.

A weather station at Ellery Lake, California (WRCC, 2009), located 10 km northeast of the meadow at a similar elevation (2907 m a.s.l.), approximated the climate at our site. This area experiences a Mediterranean-type climate with less than 5% of annual precipitation falling during summer. The growing season lasts approximately 3 months (July until September), during which the groundwater table can fall from above the soil surface to more than 1.5 m below the soil surface (Lowry et al., 2010). The mean annual precipitation is 63.7 cm of water equivalent, with a mean annual cumulative snowfall of 544 cm. The mean maximum monthly snow depth (150 cm) typically occurs in March. The mean maximum air temperature in July is 19.8 °C, and the mean minimum air temperature in January is –11.8 °C (mean annual air temperature is ~3 °C). The mean air temperature in July and September, the months sampled, is 12.2 °C and 8.3 °C, respectively.

Soils within the meadow are classified as the Marmotland–Oxyaquic Dystrocryepts–Xeric Dystrocryepts complex. Marmotland, the dominant soil within the meadow (25%), is classified within the coarse-loamy, isotic, Vitrandic Dystrocryepts Soil Taxonomic family. The Marmotland soil series consists of very deep, moderately well drained or well drained soils that formed in alluvium or minor till derived from granitoid rock and volcanic ash. Occasionally, an organic litter layer (Oi, <1 cm thick) overlaid the mineral soil. The surficial mineral soil horizon (A1, 0–29 cm) has a fine sandy loam texture and is strongly acid (pH 5.1; USDA NRCS, 2007).

HYDROLOGICAL GRADIENT LAYOUT

The meadow was surveyed in mid-July 2010 (as soon as Tioga Pass Road opened) to identify a suitable area with unidirectional variation in soil moisture. A 50 × 70 m sampling grid was marked on the northern half of the meadow, spanning from the lower and wetter middle to the higher and drier edge. To capture the hydrological gradient, the 50 m side of the grid was oriented north-south, from the middle toward the edge at 10m intervals. The 70 m side of the grid was oriented east-west marking the start of eight gradient transects spaced 10 m apart.

Soil volumetric water content (VWC) was measured immediately after gas flux sampling both early (28 July 2010) and late in the growing season (11 September 2010). Soil VWC was measured 5 cm to the south of each gas flux chamber and 0 to 12 cm below the soil surface using a portable time domain reflectometer (CD620 Hydrosense System, Campbell Scientific, Logan, Utah). The wet side of the gradient was near field capacity (~70% VWC) in July, which was approximately 3 weeks after snowmelt.

To assess non-moisture controls on GHG fluxes, we also measured midday soil temperature (both dates), plant species richness (July only), and soil chemistry (September only). Soil temperature was measured 5 cm to the south of each gas flux chamber and 6

cm below the soil surface (VWR Digital Dial Thermometer, VWR International, Radnor, Pennsylvania). Three temperature readings were recorded before, during, and after gas flux sampling, and then averaged. Plant species richness was measured to explain variation in gas fluxes potentially caused by differences in root respiration (presence/absence of plants) and resource utilization. Richness was determined by counting the number of different plant species present within the same 10.2-cm-diameter circular plots that were used to measure gas fluxes (0.0082 m^2). If there was no aboveground plant growth in a plot, then species richness was recorded as zero. A species richness of three was the maximum that occurred with replication; there was one plot with a species richness of four. Soil chemical measurements are described separately below.

GAS FLUX SAMPLING

Field fluxes of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) were measured between 13:00 and 17:00 on 28 July and 29 July 2010 (eight transects) and 11 September 2010 (four transects) using the static chamber technique (Hutchinson and Mosier, 1981; Hart, 2006). Every other transect was sampled in September because of logistical constraints; there were not enough people or daylight to sample all eight replicates during the same day.

Chamber tops were constructed from a 10.2-cm-diameter white PVC pipe closed at one end with a 4-cm-tall PVC cap equipped with a rubber septum and vent tube. The length (10 cm) and diameter (0.5 cm) of the vent tube were calculated to minimize chamber air mixing with outside air due to sample collection and perturbations from wind (i.e., the Venturi effect). Because of National Park Service regulations, the anchors for the chamber tops were not permanently installed at the site. Instead, to minimize artifacts of disturbance, the 14-cm-tall PVC anchors were inserted 4 cm into the soil at least 2 h before gas sampling began. Small flags were used to mark plot locations between sampling dates.

Headspace gas samples (18 mL) were collected from each chamber using a 20 mL polyethylene syringe with stopcock and 20-gauge needle. Gas samples were collected 0, 20, and 40 minutes after sealing the chamber top and applying a latex band as a secondary airtight seal between the chamber top and anchor. Gas samples were injected into 12 mL evacuated glass vials with rubber septa (Exetainer, Labco, Lampeter, Ceredigion, U.K.) until laboratory analysis (2 mL injection volume) on a gas chromatograph system (GC 2014 Greenhouse Gas Analyzer, Shimadzu Scientific Instruments, Columbia, Maryland) with Combi Pal AOC 5000 auto injector (CTC Analytics, Zwingen, Switzerland). The gas chromatograph used packed stainless steel columns (oven temperature = 80 °C) and was equipped with a flame ionization detector (FID) to measure CH_4 concentration, a thermal conductivity detector (TCD) to measure CO_2 concentration, and an electron capture detector (ECD) to measure N_2O concentration. The FID and TCD were set at 250 °C and 150 °C, respectively, and equipped with Hayesep D 80/100, Hayesep T 80/100, and Shimalite Q 100/180 columns (3.2 mm diameter). The ECD was set at 325 °C and equipped with Hayesep D 80/100, Hayesep N 80/100, and Porapak N 80/100 columns (1.6 mm diameter).

In July, concentrations of CO_2 ranged from an average of 476 parts per million (ppm) at the start of flux measurements to 2847 ppm after 40 min (429–1299 ppm in September). The range of CH_4 concentrations was 2.2–1.7 ppm in July and 2.2–1.8 ppm in September. The range of N_2O concentrations was 0.34–0.33 ppm in July and 0.45–0.43 ppm in September. Carbon dioxide and CH_4 fluxes were linear during the 40-min sampling period (mean r^2 = 0.99 and 0.97, respectively), and N_2O fluxes were approximately linear (mean r^2 = 0.54). It is possible that N_2O was more sensitive than the other gases to the pressure perturbation of sealing the chamber top (Curiel Yuste et al., 2007), or the disturbance of installing the anchors 2 h prior. For the roughly one-third of chambers where N_2O flux was clearly not linear, fitting with parabolic or exponential curves greatly improved the r^2 value (≥0.95) but did not improve our ability to determine an hourly N_2O flux rate. To minimize error propagation caused by regression (particularly for N_2O), we calculated the flux rate for all three gases by subtracting the known initial concentration from the known final concentration after 40 min. Net CO_2, CH_4, and N_2O fluxes were expressed as mg C m^{-2} h^{-1}, μg C m^{-2} h^{-1}, and μg N m^{-2} h^{-1}, respectively. Positive rates indicate net emission (from soil to atmosphere), and negative rates indicate net uptake (from atmosphere to soil).

LABORATORY SOIL CHEMICAL ANALYSES

Soil samples (0 to 12 cm) were collected from all eight transects immediately after gas sampling in September using an Oakfield soil probe (2 cm diameter). We did not collect soil in July to minimize potential disturbance effects on future gas flux measurements. After field collection, soils were transported cold (4 °C) to the laboratory at the University of California, Merced, and stored until processed (within 72 h of initial sampling). Field-moist soils were first sieved (2 mm mesh) and homogenized. Gravimetric water content was determined by oven-drying the sieved soil for 24 h at 105 °C. Oven-dried soils were analyzed for C and N (g kg^{-1} soil) using an elemental combustion system (ECS 4010 CHNSO Analyzer, Costech Analytical Technologies, Valencia, California).

Ammonium and NO_3^- concentrations were determined by extracting 5 g of field-moist soil with 25 mL of 2 M potassium chloride (KCl), filtered through Whatman No. 1 filter paper (preleached with deionized water), followed by flow injection analysis (QuikChem 8500, Lachat Instruments, Hach Company, Loveland, Colorado). Ammonium and NO_3^- were determined by colorimetric methods on separate manifolds, the former using phenolate (method #12-107-06-1-B) and the latter using a cadmium-copper reduction column (method #12-107-04-1-B). The concentrations of NH_4^+ and NO_3^- were expressed as mg N kg^{-1} dry soil.

DATA ANALYSES

Means and standard errors of soil VWC, temperature, CO_2 flux, CH_4 flux, and N_2O flux were calculated for each date and distance along the hydrological gradient. A one-way analysis of variance (ANOVA) was used to test for differences between dates at an alpha level of 0.05 (JMP 8.0.2 software, SAS Institute, Cary, North Carolina). Linear regression was used to test relations between GHG fluxes, position in the meadow, soil microclimate, and chemistry.

Radiative forcing calculations were based on CH_4 and N_2O being 25 and 298 times stronger per mole, respectively, than CO_2 as a greenhouse gas during the next 100 years (Forster et al., 2007). Hourly fluxes of CO_2, CH_4, and N_2O in each chamber were converted to g CO_2-equivalents m^{-2} d^{-1}. In the cases of CH_4 and N_2O consumption, values of CO_2-equivalents were negative. We totaled the CO_2-equivalents for each sampled chamber, and then averaged across all chambers to determine the mean rate of GHG emission from the meadow on each date. Because our intent was not to construct an annual GHG budget—and because we know little about

diurnal and weekly variation in GHG fluxes at this meadow—we refrained from temporal upscaling.

Results

SOIL MICROCLIMATE

Near-surface soils in the meadow were 2.2 °C warmer in July compared to September (Table 1). Soil VWC did not show a statistically significant difference from July to September, but VWC tended to decrease more in soils that were wetter in July. On both dates, ranges of soil VWC (~60%) and temperature (~10 °C) across the meadow were similar, and soils near the edge of the meadow were 23% drier (by volume) compared to the middle of the meadow (Fig. 1, part a). There was a negative correlation between soil temperature and VWC, particularly in September (Table 2). The distribution of soil VWC was normal in July and skewed in September (i.e., more locations with dry soil and fewer locations with wet soil). Soil gravimetric and volumetric water contents in September were positively correlated ($P = 0.0007$; $R^2_{adj} = 0.39$; GWC = 0.58VWC + 0.34). The correlation may have been stronger if we would have included rock fragments >2 mm in the gravimetric calculation, or if we would have measured VWC in September at all 48 plots instead of 24 plots.

CARBON DIOXIDE FLUX

Average CO_2 emission across all plots was three times greater in July than in September (Table 1). However, soil CO_2 emission did not vary significantly across the hydrological gradient (Fig. 1, part b). July CO_2 flux was not significantly explained by VWC or temperature, whereas September CO_2 flux showed a strong positive correlation with both VWC and temperature (Table 2). Plant species richness was the best predictor of July CO_2 flux ($F = 5.18$; $P = 0.0039$ in one-way ANOVA; Fig. 2). September CO_2 flux was positively related to soil C and N concentration, but showed no correlation with extractable NH_4^+ or NO_3^- concentrations (Table 2).

METHANE FLUX

Net uptake of atmospheric CH_4 by soil predominated on both sampling dates (Table 1). Only 3 of the 48 plots (6%) showed net CH_4 emission in July, and only 1 of the 24 plots (4%) in September. The remaining plots showed net CH_4 uptake. Soil VWC and position on the hydrological gradient were the best predictors of CH_4 flux (Table 2; Fig. 1, part c). Drier soils near the edge of the meadow consumed roughly five times more CH_4 than wetter soils near the middle of the meadow. Methane flux was not correlated with soil temperature in July, but was positively correlated with temperature in September when VWC and temperature strongly covaried. There was no correlation between September CH_4 flux and soil concentrations of C, N, NH_4^+, or NO_3^- (Table 2).

NITROUS OXIDE FLUX

Soil N_2O fluxes did not vary significantly between July and September, and mean N_2O uptake occurred on both dates (Table 1). In July, N_2O uptake occurred more often in wetter soils near the middle of the meadow, while N_2O emission occurred more often in drier soils near the edge of the meadow (Table 2, Fig. 1, part d). In September, N_2O flux did not show this pattern of hydrological control. Soil N_2O flux was also positively related to temperature in July but showed no relationship with temperature in September. There was no correlation between September N_2O flux and soil concentrations of C, N, NH_4^+, or NO_3^- (Table 2).

TABLE 1

Soil chemistry, microclimate, and midday fluxes of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) along a 50-m hydrological gradient in a Sierra Nevada subalpine meadow early (July) and late (September) in the growing season.

Measurement	Date	Mean	S.E.	C.V.	Range	*F*-ratio	*P*-value
Total carbon (g kg^{-1})	Sept	50.4	3.4	0.33	24–87	n.a.	n.a.
Total nitrogen (g kg^{-1})	Sept	3.1	0.2	0.32	1.6–6.0	n.a.	n.a.
Extractable ammonium (mg N kg^{-1})	Sept	2.11	0.39	0.91	0.51–8.37	n.a.	n.a.
Extractable nitrate (mg N kg^{-1})	Sept	0.40	0.15	1.82	<0.01–2.96	n.a.	n.a.
Volumetric water content (%)	July	35.2	2.4	0.47	7–69	3.46	0.067
	Sept	27.2	3.7	0.67	1–60	n.a.	n.a.
Temperature (°C)	July	15.5	0.4	0.16	12–22	14.47	0.0003*
	Sept	13.3	0.5	0.17	9–18	n.a.	n.a.
Carbon dioxide flux (mg C m^{-2} h^{-1})	July	159.8	7.3	0.31	62–267	98.91	<0.0001*
	Sept	52.7	4.7	0.43	22–93	n.a.	n.a.
Methane flux (μg C m^{-2} h^{-1})	July	–31.3	2.9	0.65	–78 to 9	3.54	0.064
	Sept	–22.6	3.0	0.64	–58 to 6	n.a.	n.a.
Nitrous oxide flux (μg N m^{-2} h^{-1})	July	–0.6	1.6	17.95	–29 to 34	0.97	0.33
	Sept	–3.0	1.2	2.05	–20 to 12	n.a.	n.a.

Notes: Soil chemistry and volumetric water content were measured 0 to 12 cm deep, and soil temperature was measured 6 cm deep; positive gas fluxes indicate net emission from the soil to the atmosphere, and negative fluxes indicate net uptake from the atmosphere to the soil; S.E. is the standard error, and C.V. is the coefficient of variation (standard deviation divided by mean). *Indicates significant difference between sampling dates in a one-way ANOVA at an alpha level of 0.05; n.a. indicates not applicable.

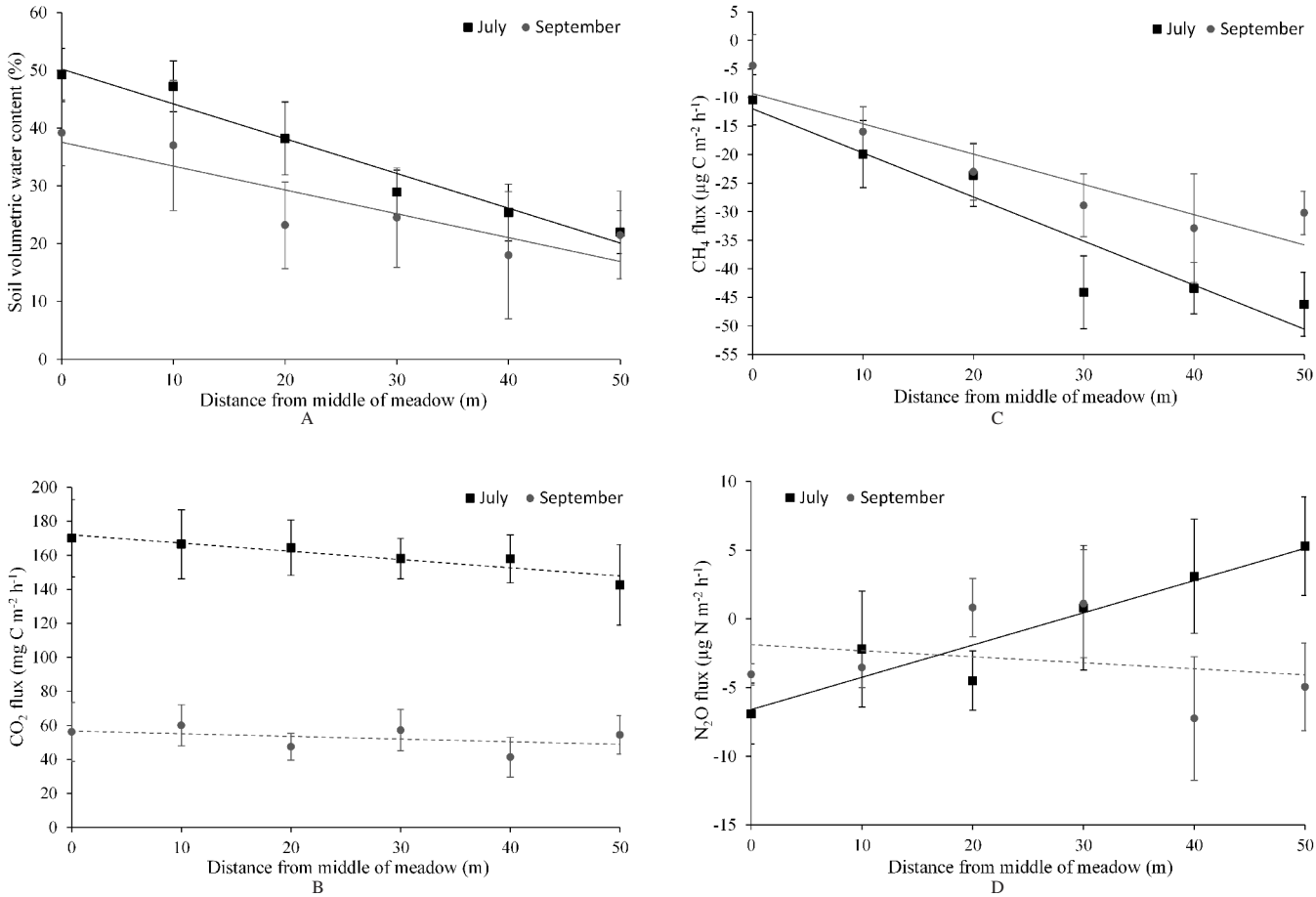

FIGURE 1. Variation in (a) soil moisture 0–12 cm deep and fluxes of (b) carbon dioxide (CO_2), (c) methane (CH_4), and (d) nitrous oxide (N_2O) along a 50-m hydrological gradient in a Sierra Nevada subalpine meadow. The gradient extended from the wet middle (0 m) to dry edge (50 m) of the meadow. Soil moisture and gas fluxes (mean ± standard error) were measured in July (black line; n = 8) and September (gray line; n = 4). The solid line indicates that the slope of the linear fit differed from zero at an alpha level of 0.05, and the dashed line indicates that the slope did not differ from zero. Negative fluxes indicate net uptake from the atmosphere to the soil, and positive fluxes indicate net emission from the soil to the atmosphere.

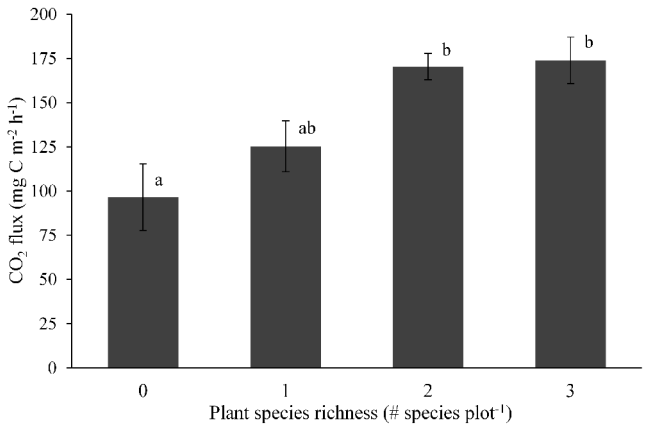

FIGURE 2. Variation in soil CO_2 emission in July associated with plant species richness. Bars show means and standard errors. Letters indicate significant differences in Tukey's HSD test at an alpha level 0.05. There were 4, 7, 24, and 11 observations for plant species richness of 0, 1, 2, and 3, respectively.

RADIATIVE FORCING

An accounting of CO_2, CH_4, and N_2O fluxes in terms of CO_2-equivalents showed that average GHG emission was three times greater in July than in September (Table 3). This difference was primarily due to reduced CO_2 emission in September because CO_2 was responsible for over 98.5% of net GHG emission. Net GHG emission did not vary significantly with soil VWC in July ($F = 3.04$; $P = 0.088$; $R^2_{adj} = 0.04$; $y = 0.067x + 11.69$), but net GHG emission and soil VWC were positively correlated in September ($F = 26.18$; $P < 0.0001$; $R^2_{adj} = 0.52$; $y = 0.082x + 2.35$; Fig. 3). Methane uptake contributed more to GHG emissions reduction in September than in July. Soil N_2O fluxes increased net GHG emission in July (by a maximum of 4%), but reduced GHG emission in September (by a maximum of 11%). The "cooling effect" of CH_4 uptake increased with drying (linear fit: $F = 48.02$; $P < 0.0001$; $R^2_{adj} = 0.40$; $y = 0.014x - 0.77$) and was greatest in soils drier than 10% VWC (Fig. 4), or ~6% GWC.

TABLE 2

Relation between greenhouse gas fluxes (CO_2, CH_4, and N_2O), soil microclimate, and chemistry in a subalpine meadow early (July) and late (September) in the growing season.

Predictor	Response variable	Date	ddf	Slope	R^2adj	*F*-ratio	*P*-value
VWC (%)	Temperature	July	46	–0.05	0.11	7.10	0.011*
		Sept	22	–0.10	0.61	36.97	<0.0001*
	CO_2 flux	July	45	0.78	0.04	3.12	0.084
		Sept	22	0.93	0.52	26.32	<0.0001*
	CH_4 flux	Jul	46	0.92	0.56	59.63	<0.0001*
		Sept	22	0.51	0.39	15.57	0.0007*
	N_2O flux	July	46	–0.21	0.08	5.28	0.026*
		Sept	22	–0.01	–0.04	0.04	0.84
Temperature (°C)	CO_2 flux	July	45	4.17	0.02	1.97	0.17
		Sept	22	–6.82	0.42	17.97	0.0003*
	CH_4 flux	July	46	–0.32	–0.02	0.07	0.80
		Sept	22	–4.07	0.38	14.98	0.0008*
	N_2O flux	July	46	1.25	0.06	3.82	0.057
		Sept	22	0.28	–0.03	0.25	0.63
Total C (g kg^{-1})	CO_2 flux	Sept	22	0.58	0.14	4.83	0.039*
	CH_4 flux	Sept	22	0.28	0.07	2.61	0.12
	N_2O flux	Sept	22	–0.02	–0.042	0.07	0.79
Total N (g kg^{-1})	CO_2 flux	Sept	22	9.06	0.12	4.16	0.054*
	CH_4 flux	Sept	22	4.26	0.05	2.11	0.16
	N_2O flux	Sept	22	–0.38	–0.041	0.09	0.77
Ammonium (mg kg^{-1})	CO_2 flux	Sept	22	0.64	–0.042	0.06	0.80
	CH_4 flux	Sept	22	1.27	–0.016	0.63	0.44
	N_2O flux	Sept	22	–0.48	–0.022	0.51	0.48
Nitrate (mg kg^{-1})	CO_2 flux	Sept	22	5.79	–0.0097	0.79	0.39
	CH_4 flux	Sept	22	3.38	–0.015	0.66	0.43
	N_2O flux	Sept	22	0.99	–0.031	0.31	0.58

Notes: Soil volumetric water content (VWC) was measured 0 to 12 cm deep and temperature was measured 6 cm deep. R^2adj is the adjusted coefficient of determination; ddf indicates the denominator degrees of freedom for the linear regression test; *indicates significant linear regression between predictor (*x*) and response variable (*y*) at an alpha level of 0.05.

TABLE 3

Net greenhouse gas (GHG) emission and relative contribution of methane (CH_4) and nitrous oxide (N_2O) fluxes to radiative forcing in a subalpine meadow.

Metric	Date	Mean	S.E.	Range	*F*-ratio	*P*-value
Net GHG emission (g CO_2e m^{-2} d^{-1})	July	14.03	0.64	5.5–23.3	100.66	<0.0001*
	Sept	4.58	0.41	1.9–8.2		
CH_4 contribution to GHG emission (%)	July	–0.21	0.03	–1.0 to 0.1	15.64	0.0002*
	Sept	–0.55	0.11	–2.2 to 0.1		
N_2O contribution to GHG emission (%)	July	0.11	0.16	–1.6 to 4.3	6.13	0.016*
	Sept	–0.96	0.52	–10.6 to 3.1		

Notes: Fluxes of CH_4 and N_2O were transformed to CO_2 equivalents (CO_2e) by multiplying by radiative forcing factors of 25 and 298, respectively; CO_2e_{total} per plot was averaged across all plots in the meadow to calculate net GHG emission for each date; the contribution of CH_4 per plot was calculated as: $CO_2e_{methane}/CO_2e_{total} * 100\%$; the contribution of N_2O per plot was calculated as: $CO_2e_{nitrous\ oxide}/CO_2e_{total} * 100\%$; positive contribution indicates a warming effect and negative contribution indicates a cooling effect; * indicates significant difference between sampling dates at an alpha level of 0.05.

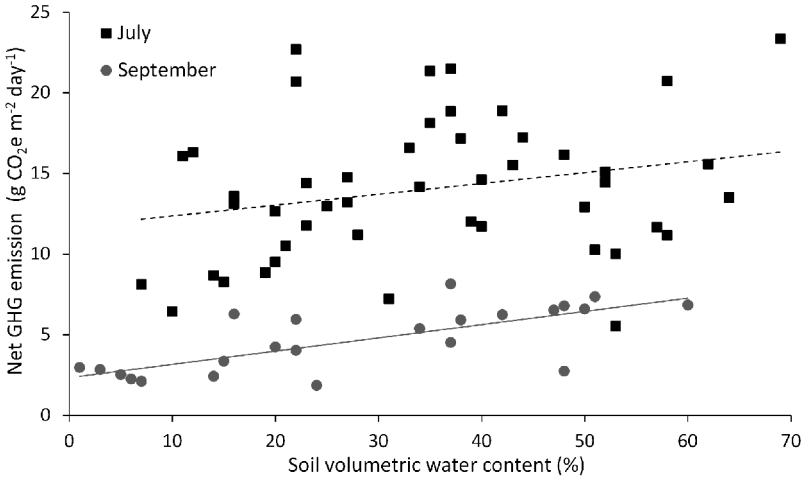

FIGURE 3. Relation between soil volumetric water content and net greenhouse gas (GHG) emission in July (solid line) and September (dashed line). Solid line indicates that the slope of the linear regression was significantly different from zero at an alpha level of 0.05, and dashed line indicates that the slope was not significantly different from zero. Net GHG emission in each plot was calculated as the net flux of carbon dioxide equivalents (CO_2e) based on the radiative forcing per mole of carbon dioxide (1), methane (25), and nitrous oxide (298).

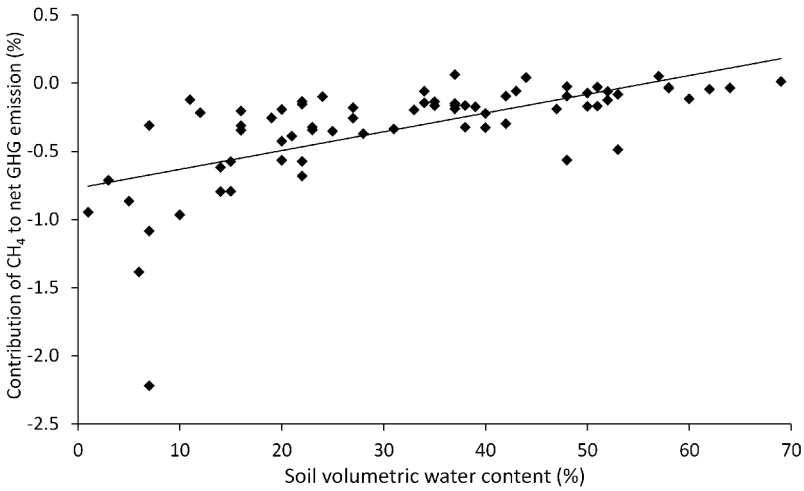

FIGURE 4. Relation between soil volumetric water content and the contribution of methane (CH_4) to net greenhouse gas (GHG) emission. The regression indicates a significant linear fit across sampling dates at an alpha level of 0.05. The contribution of CH_4 to net GHG emission in each plot was calculated as the CO_2-equivalents consumed or produced by soil as CH_4 ($CO_2e_{methane}$) divided by the total soil GHG emission including CO_2 and N_2O (CO_2e_{total}), and then multiplied by 100%. Negative values indicate a decrease in CO_2e_{total} and a net cooling effect.

Discussion

Our goal was to capture spatial variability of multiple GHG fluxes to infer their abiotic and biotic controls using a soil moisture gradient. Despite half as much water in surface soil at the edge of the meadow, CO_2 emission showed no obvious spatial pattern across the hydrological gradient on either date. Soil moisture was less important than we expected in explaining CO_2 fluxes. Soil CO_2 emission varied more in time than in space, likely because later in the growing season there was reduced plant root respiration, greater microbial C limitation, and colder temperatures (Jiang et al., 2010). Early in the growing season, soil CO_2 fluxes (but not CH_4 or N_2O fluxes) were best explained by a positive correlation with plant species richness. The plots with no aboveground plant growth (i.e., richness = 0) emitted the least amount of CO_2. This suggests that the abundance and resource utilization of plants were linked to spatial patterns of soil CO_2 emission. Root respiration, exudates, and priming of soil organic matter in the rhizosphere could drive this spatial pattern (Bird et al., 2011; Geng et al., 2012; Guenet et al., 2012). Drought conditions can increase the occurrence of bare ground in montane meadows (Debinski et al., 2010), and, in our study, bare ground was associated with roughly one-third less soil CO_2 emission. Root respiration, therefore, perhaps accounted for a maximum of 30% of soil respiration.

It was not until later in the dry season that CO_2 emission showed signs of water limitation. For example, CO_2 emission and soil moisture showed a strong positive correlation in September (mean VWC = 27%) but not in July (mean VWC = 35%). However, the large seasonal reduction in CO_2 emission even on the wet side of the hydrological gradient suggests that labile carbon was more limiting than water. And if microbial and plant respiration were water stressed in drier soils, then less CO_2 production in shallow soil was apparently compensated by greater CO_2 transport from deeper, wetter soil (Pacific et al., 2008). Whatever the mechanism, we found that topographic position within the meadow, and associated variation in near-surface soil moisture, had little influence on rates of CO_2 emission during the growing season.

We also find it surprising that, at least on our sampling dates, the wet middle of the meadow rarely emitted CH_4. In contrast to a Rocky Mountain subalpine meadow (Mosier et al., 1993) and a lower-elevation Sierra Nevada wetland (Oates et al., 2008), the subalpine meadow that we studied emitted little CH_4, perhaps because of a lower water table (Smith et al., 2003) or the coarse-textured, well-drained soils in the High Sierra (USDA NRCS, 2007; Bales et al., 2011). It is also likely that we missed pulses of CH_4 emission in the middle of the meadow during thawing and post-snowmelt flooding (Mosier et al., 1993). The edge of the meadow showed more CH_4 uptake, supporting the negative relationship be-

tween soil moisture and CH_4 consumption in montane meadows (Mosier et al., 1993; Torn and Harte, 1996; Lin et al., 2009; Jiang et al., 2010). Drier soils transport more atmospheric oxygen and CH_4, thus inhibiting methanogenesis and reducing diffusional limitation on methanotrophy (Conrad, 1996; Hanson and Hanson, 1996). Therefore, CH_4 fluxes varied more predictably than CO_2 and N_2O fluxes, showing little temporal variation and a high degree of spatial organization according to soil moisture.

As the first measurements of field N_2O fluxes in a high-elevation Sierra Nevada meadow, it surprised us that net N_2O consumption was so prevalent. We expected wet soils to emit more N_2O because of less oxygen and greater denitrification (Smith et al., 2003). Instead, it appears that nitrification was the main source of N_2O (Firestone and Davidson, 1989; Stark et al., 2002), at least when surface soil was warm enough (i.e., July) and dry enough (i.e., edge of meadow). Drier conditions increase oxygen diffusion into the soil from the atmosphere and may prevent denitrifying microbes from reducing N_2O to dinitrogen gas (N_2), thus increasing N_2O emission (Burgin and Groffman, 2012). Wetter conditions, on the other hand, can favor the reduction of N_2O to N_2, causing less N_2O production (Avrahami and Bohannan, 2009) or net N_2O consumption, especially when soil NO_3^- concentration is sufficiently low (<1 mg N kg^{-1}; Rosenkranz et al., 2005; Chapuis-Lardy et al., 2007; Wu et al., 2013). Observed rates of N_2O uptake were greater than those found in other meadows (Mosier et al., 1993; Filippa et al., 2009; Jiang et al., 2010), and rates of N_2O emission were an order of magnitude lower than other meadows (Filippa et al., 2009; Lin et al., 2009; Hu et al., 2010), but similar to a low-elevation Sierra Nevada wetland (Oates et al., 2008). Mosier et al. (1993) found the highest rates of N_2O emission in a Rocky Mountain meadow 3 to 7 weeks after snowmelt, which is the time period when we first visited our site. However, the N_2O pulse could have happened earlier; during spring thaw, for example (Christensen and Tiedje, 1990). There is evidence from a variety of Sierra Nevada ecosystems—including a wet meadow—that the largest N_2O pulse from denitrification occurs during winter instead of summer (Walker et al., 1992). The Sierra Nevada meadow we studied supports this pattern because it was not a strong N_2O source during the growing season, and it could perhaps switch from sink to source with future climate-induced soil drying.

Methane and N_2O contributed most to the net GHG flux on the dry side of the hydrological gradient, not the wet side as predicted. Net GHG emission was foremost determined by CO_2, but CH_4 and N_2O were more important to account for in drier soils and later in the growing season after plant senescence. In terms of CO_2-equivalents, CH_4 consumption in drier soils reduced GHG emission by up to 2%. This contribution of CH_4 uptake to the net GHG flux was greater than found in a Tibetan Plateau meadow (~0.2%), despite similar ranges of soil moisture and temperature (Jiang et al., 2010). Soil N_2O production at our site accounted for up to 4% of GHG emission in relatively warm (July) and dry soils (edge of meadow). In colder (September) and wetter soils (middle of meadow), however, N_2O consumption reduced net GHG emission by up to 11%. Although the spatially averaged N_2O flux for July showed consumption, the negative correlation between CO_2 emission and N_2O emission ($P = 0.0016$; $R^2_{adj} = 0.18$; $N = 48$) probably explains why N_2O showed an overall positive—albeit small—contribution to radiative forcing. Because lower CO_2 emission indicates bare ground, perhaps less N uptake by plants resulted in more N available for N_2O emission. Unfortunately, we did not measure soil N concentrations earlier in the growing season. Nevertheless, the warming effect of N_2O emission at the edge of the meadow slightly outweighed the cooling effect at the middle of the meadow. These results demonstrate the potential for hydrological changes in high-elevation meadows to impact both the magnitude and direction of the effects of non-CO_2 GHGs on net radiative forcing.

Because of the low sampling frequency (twice during the snow-free season), we had no intention of upscaling to an annual GHG budget, or upscaling beyond this single meadow. We no doubt missed important GHG emissions during freeze-thaw and flooding events in the winter and spring before we could access the site (Teepe et al., 2001; Goldberg et al., 2008; Liptzin et al., 2009). Another limitation of our study is that soil chemistry was measured only on one date; thus we cannot determine the relative importance of hydrology vs. chemistry in explaining GHG fluxes across dates. Our intention—rather—was to use space as a surrogate for time to indicate what happens when the soil dries during the summer and what could happen when the climate dries in the future.

In conclusion, we found no evidence that the wet middle of a montane meadow was a hotspot of GHG emission during the snow-free season compared to the drier edges. Soil CO_2 and net GHG emission varied little across the hydrological gradient. However, soil drying enhanced CH_4 uptake and N_2O emission, at least in the short-term, which highlights the importance of quantifying the balance of non-CO_2 gases for GHG budgets in heterogeneous montane landscapes. Other factors could also interact with hydrological changes in high-elevation meadows to impact GHG fluxes. For example, recreational packstock use and livestock grazing, which are common in Sierra Nevada meadows, can compact soil (i.e., less gas diffusivity and water-filled pore space), increase coverage of bare ground, and alter C and N inputs to soil (Kosco and Bartolome, 1981; McClaran, 1989; Cole et al., 2004), perhaps creating a more heterogeneous pattern of GHG emission with more hotspots. Furthermore, shifts in meadow plant community composition associated with climate change, exotic species, and conifer encroachment could impact C and N inputs, microclimate (Dyer and Moffett, 1999; Haugo and Halpern, 2007; Debinski et al., 2010; Zald et al., 2012), and thus GHG fluxes. Amidst all these changes, hydrological gradients in montane meadows can serve as the context for spatial upscaling and an improved understanding of the underlying mechanisms of GHG emissions.

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