Ecosystems (2010) 13: 1157–1170
DOI: 10.1007/s10021-010-9391-9

ECOSYSTEMS

Response of Terrestrial CH_4 Uptake to Interactive Changes in Precipitation and Temperature Along a Climatic Gradient

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Abstract

We determined the response of terrestrial methane (CH_4) uptake to 4 years of full-factorial manipulations of precipitation and temperature in four ecosystems along a 50 km warm and dry to cold and wet climatic gradient (desert grassland, pinyon-juniper woodland, ponderosa pine forest, and mixed conifer forest). Our goals were to determine whether ecosystem-specific, intraannual, and interactive responses to altered precipitation and warming are quantitatively important. Passive collectors and interceptors increased (+50% per event) and reduced (−30% per event) the quantity of precipitation delivered to experimental plant–soil mesocosms, and downward transfer along the elevation gradient warmed mesocosms by 1.8°C on average. Methane uptake in the colder and wetter ecosystems along the gradient decreased with increasing precipitation, especially during the wet season. The warmer and drier ecosystems, however, responded more strongly to warming, exhibiting less CH_4 uptake with increasing temperature. We found no interaction between altered precipitation and warming in any ecosystem. Soil CH_4 consumption in the laboratory was a strong predictor of ecosystem differences in field CH_4 consumption, but was a poor predictor of the effects of climatic change observed in the field. Based on our results, future climate scenarios that are wet and warm will cause the largest reduction in terrestrial CH_4 uptake across ecosystem types.

Key words: soil methane oxidation; methanotrophy; climate change; rainfall manipulation; experimental warming; elevation gradient.

Introduction

Projecting soil biological consumption of the potent greenhouse gas methane (CH_4) under future climate scenarios requires an improved understanding of how changes in water availability and temperature affect soil CH_4 consumption under present climatic conditions. Precipitation and temperature manipulations in the field can quantify these responses and have been shown to

Received 8 July 2009; accepted 23 June 2010;
published online 22 October 2010

Author Contributions: JRB performed research, analyzed data; PD conceived of and designed study, performed research, analyzed data; MCA designed study, performed research, analyzed data; BAH conceived of and designed study, performed research, analyzed data.

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significantly affect CH_4 uptake in some ecosystems (Peterjohn and others 1994; Billings and others 2000; Borken and others 2000, 2006; Sjögersten and Wookey 2002; Davidson and others 2004; Hart 2006; Blankinship and others 2010). However, because most studies focus on one component of climatic change (that is, either precipitation or temperature) in one ecosystem, we have little quantitative understanding of how the climate of an ecosystem influences the response of soil CH_4 consumption to altered precipitation and warming, and whether interactive effects between precipitation and temperature are small.

Atmospheric CH_4 consumption is highest at intermediate soil moisture (Bowden and others 1998; Gulledge and Schimel 1998), as methanotrophic bacteria shift from limitation by physiological water stress at low moisture to limitation by substrate diffusion at high moisture (Koschorreck and Conrad 1993; Striegl 1993). The response of CH_4 consumption to increased annual precipitation has only been tested in a sub-humid California annual grassland (Blankinship and others 2010), where a 50% increase in precipitation caused a 61% reduction in CH_4 uptake, and correlative measurements in a monsoonal climate in Japan showed lower CH_4 uptake in wetter soils along a 5-m-long moisture gradient (Itoh and others 2009). Reduced precipitation can significantly increase CH_4 uptake in tropical, temperate, and boreal forest ecosystems (Billings and others 2000; Borken and others 2000, 2006; Davidson and others 2004), probably due to reduced diffusional limitation. Billings and others (2000) provide evidence that the response of CH_4 consumption to precipitation depends on an ecosystem's climate. Lower amounts of precipitation caused an increase in CH_4 uptake at a relatively dry boreal forest site, but caused a decrease in CH_4 uptake at a relatively wet boreal forest site only 10 km apart. Thus, responses of CH_4 uptake to altered precipitation may vary along climatic gradients.

Soil warming increases CH_4 uptake (Peterjohn and others 1994; Sjögersten and Wookey 2002; Hart 2006) or has no effect (Torn and Harte 1996; Rustad and Fernandez 1998). Increased uptake is likely caused by a combination of direct effects of temperature on soil CH_4 transport and the enzyme activity of CH_4-oxidizing bacteria (King and Adamsen 1992), and an indirect response to soil drying associated with higher evapotranspiration (Torn and Harte 1996; Sjögersten and Wookey 2002). Across ecosystems, CH_4 consumption tends to respond more strongly to changes in soil moisture than to changes in soil temperature (Born and others 1990; King and Adamsen 1992; Nesbit and Breitenbeck 1992; Bowden and others 1998). However, the relative importance of future precipitation and temperature scenarios in controlling rates of CH_4 consumption has only been tested in a single ecosystem. In a California annual grassland, CH_4 uptake responded more strongly to elevated precipitation than to elevated temperature (Blankinship and others 2010).

There is growing evidence that effects of water availability and warming on terrestrial CH_4 consumption depend on natural intraannual variation in precipitation and temperature (Potter and others 1996). For example, lower amounts of rainfall caused a tropical forest to remain a net CH_4 sink during the wet season when high soil water contents otherwise limit CH_4 uptake (Davidson and others 2004). And warming in an alpine forest enhanced CH_4 uptake more early in the growing season by accelerating spring thaw and drying soils, whereas later in the growing season warming-induced drying was less important (Sjögersten and Wookey 2002). Ecosystems in climates with a distinct wet season and dry season are well suited to test intraannual variation in effects of altered precipitation and warming.

If models of terrestrial CH_4 consumption accurately incorporate ecosystem- and season-specific responses to individual components of climatic change, there is still the possibility that simultaneous changes in precipitation and temperature will interact to dampen or amplify these single-factor effects (Blankinship and others 2010), and lead to an inaccurate projection. For example, increased precipitation could relieve water stress on methanotrophy caused by warming-induced drying (Torn and Harte 1996). Or warming may exacerbate the negative effects of increasing precipitation on CH_4 consumption (Blankinship and others 2010). Therefore, it is important to test the interactive effects of warming and altered precipitation on terrestrial CH_4 uptake.

We measured CH_4 consumption in four ecosystems along a 50 km temperate, semiarid climatic gradient to determine whether ecosystem-specific, intraannual, and interactive responses to altered precipitation and warming are quantitatively important. The gradient in northern Arizona extends from warm and dry climates at lower elevations to cold and wet climates at higher elevations, and experiences strong seasonal variation in precipitation associated with the North American Monsoon. In situ CH_4 flux and laboratory soil CH_4 consumption were measured in four ecosystems exposed to 4 years of every combination of three levels of precipitation (ambient, +50%, and −30%

annual precipitation) and two levels of temperature (ambient and approx. 1.8°C increase in annual temperature). The fully factorial design and monsoonal climate allowed testing for differential ecosystem response of CH_4 consumption to altered precipitation and warming, seasonal variation in response, and interactions between altered precipitation and warming. We expected less CH_4 uptake with increasing precipitation in the wetter ecosystems (that is, diffusional limitation), and an opposite response in the drier ecosystems (that is, water stress). We expected warming to increase CH_4 consumption in the colder ecosystems (that is, direct effect on enzyme activity), and to have less of an effect in the warmer ecosystems (Potter and others 1996).

Methods

Site Descriptions

Interactive changes in precipitation and temperature were simulated in ecosystems along a 50-km-long climatic gradient transect north of Flagstaff, Arizona, USA (35.3539 N 111.7306 W to 35.6927 N 111.4265 W). The C. Hart Merriam Elevation Gradient spans 1075 m in elevation (1540–2615 m) and four major temperate life zones: cool desert grassland (dominated by *Ericameria nauseosa*, *Gutierrezia sarothrae*, *Bouteloua eriopoda*), pinyon-juniper woodland (*Pinus edulis*, *Juniperus monosperma*, *Bouteloua gracilis*), ponderosa pine forest (*Pinus ponderosa*, *Festuca arizonica Vasey*), and mixed conifer forest (*Populus tremuloides*, *Muhlenbergia montana*, *Festuca arizonica Vasey*). The ecosystems vary in climate and soil characteristics (Table 1).

All sites along the climatic gradient are strongly influenced by the North American Monsoon and experience an annual synchronous shift in humidity and precipitation. The dry season generally lasts from May to mid-July (dry westerly winds) and the wet season generally lasts from mid-July to September (wet southeasterly winds). Though we did not measure snow cover (or CH_4 flux) at the sites during the winter, nearby long-term National Weather Service stations at similar elevations in northern Arizona (Wupatki National Monument, Walnut Canyon National Monument, Sunset Crater National Monument, Fort Valley Experimental Forest) show that mean annual snowfall varies from about 15 cm y^{-1} at low elevations to 230 cm y^{-1} at high elevations. At the bottom of the gradient, snowfall occurs between November and April, but there are no months with a mean snow depth greater than 2.5 cm. At the top

Table 1. Meteorological and Soil Properties of Sites Along a 50-km-Long Climatic Gradient in Northern Arizona, USA

Ecosystem	Elevation (m)	MAP[1] (mm y^{-1})	MAT[2] (°C)	Soil type	Soil texture	Soil bulk density (mg m^{-3})	Soil C (% by mass)	Soil N (% by mass)	Soil pH	Soil water-holding capacity (g H_2O g^{-1} soil)
Cool desert grassland	1760	230	8.5	Typic Haplustand	Clay	0.67	1.40	0.13	7.9	0.51
Pinyon-juniper woodland	2020	380	7.0	Calcic Haplustand	Loam	0.68	1.62	0.16	6.8	0.53
Ponderosa pine forest	2344	660	5.5	Mollic Eutroboralf	Sandy loam	0.86	1.35	0.11	6.8	0.44
Mixed conifer forest	2620	790	4.0	Pachic Udic Argiboroll	Loam	0.70	3.77	0.35	6.5	0.78

[1]*Based on modeled precipitation data from the Merriam Powell Center for Environmental Research.*
[2]*Based on monthly ANUSPLIN-interpolated climate surfaces from the Global Historical Climatology Network.*

of the gradient, snowfall occurs between September and July and the monthly mean snow depth is greater than 2.5 cm between December and March (with maximum monthly mean depth of 23 cm in February).

Treatment Design

In each of the four ecosystems, a 10 m × 15 m site was selected in grass dominated areas (meadows at the mixed conifer and ponderosa sites, grassy interspaces at the pinyon-juniper site, and open grasslands at the grassland site) and fenced to minimize physical disturbance from cattle grazing. Our experiment focused on the plant and soil communities in interspaces to minimize differences in vegetation type and because small-statured plants were easier to manipulate with high replication. Plant–soil monoliths served as experimental replicates and were collected between May 2002 and September 2002 by sinking a 30 cm diameter hardened steel corer approximately 30 cm into the soil. Monoliths were collected in undisturbed areas adjacent to the fenced site at each ecosystem and were selected to minimize differences in initial plant composition and represent dominant grass species within each ecosystem. Each plant–soil monolith (40 per site, 160 total) was placed intact into a PVC cylinder and the corer was retracted. The plant–soil monolith experimental unit is henceforth referred to as a 'mesocosm'. PVC cylinders were constructed of 1 cm walled PVC tube (30 cm diam. × 30 cm deep, surface area = 0.28 m^2) cemented and screwed to a 1 cm thick piece of flat PVC, with a basal hole (1 cm diam.) and approximately 2 cm of coarse sand at the bottom of the cylinder to facilitate drainage. Installation consisted of excavating an oversized hole for each mesocosm (35 cm wide × 40 cm deep) and placing them ten to a row at each site into grassland areas of the receiving ecosystem in a random order with respect to treatment. Soil moisture within mesocosms was monitored in 2004 using model EC-20 ECH_2O probes (Decagon Devices, Inc., Pullman, Washington, USA). Probes were installed in the center of the mesocosms and measured average volumetric soil water content throughout the top 20 cm of soil, and measurements were taken hourly at most sites during the Monsoon period in 2004. Soil temperature probes were installed, but, similar to the moisture probes, did not work consistently across sampling dates because of disturbance by rodents.

Projected magnitudes of warming during the next 50 years (Christensen and others 2007) were simulated by relocating 20 of the 40 plant–soil mesocosms from each site down in elevation to the next lower, warmer site. Grassland mesocosms were transferred to a Great Basin Desert site lower in elevation (1540 m) on the climatic gradient, a site which was only used for its warmer climate. Relocated mesocosms served as the 'increased temperature' treatment (1.8°C increase in mean annual temperature, on average), and mesocosms that remained at their native site served as the 'ambient temperature' treatment.

Because of the high variability in the magnitude and direction of projected precipitation changes for the Western US, which range from a 36% increase in winter precipitation to an 18% decrease in summer precipitation (Christensen and others 2007), we included both increased and decreased precipitation treatments to simulate the extremes of both wet and dry scenarios. For mesocosms that remained at their native site, precipitation was increased (+50% per event) using rain collection funnels (21.2 cm diam.) with PVC tubing (1.3 cm diam.) that intercepted and channeled rainwater and snowmelt into the center of the mesocosm (n = 7, Figure 1). Precipitation was reduced (−30% per event) by installing clear acrylic rain shelters consisting of two, 5 cm wide channels spaced 10 cm apart and mounted to four vertical posts placed outside of the mesocosm (n = 6). Rain shelters were installed approximately 30 cm above the center of the mesocosms and at a slight angle (approx. 20°) to allow intercepted water to flow away from the mesocosms. The rain shelters were oriented and placed high enough off the ground to minimize potential effects from shade and reduced airflow (Yahdjian and Sala 2002). For mesocosms that remained at their native site, the control had no precipitation manipulation (n = 7).

To compensate for lower annual precipitation with the warming treatment, the ambient precipitation treatment for transferred mesocosms used rain collection funnels to simulate native precipitation based on historical precipitation data (14, 26, 24, and 16 cm diam. funnels used for transferred mixed conifer, ponderosa pine, pinyon-juniper, and grassland mesocosms, respectively). Altered precipitation treatment targets on transferred mesocosms were relative to the native site, and not to the transferred site. Of the 20 transferred mesocosms at each site, seven mesocosms were treated with ambient precipitation, seven were treated with increased precipitation (+50% per event relative to native precipitation using 24, 33, 32, and 26 cm diam. rain collection funnels for transferred mixed conifer, ponderosa pine, pinyon-juniper,

Figure 1. A photograph of the ponderosa pine site showing interactive precipitation and temperature treatments. The 20 native ponderosa pine mesocosms (that is, ambient temperature) are in rows of ten on the far right of the photograph and in the third row from the right. The 20 transferred mixed conifer mesocosms (that is, increased temperature) are in the second and fourth rows from the right. For the native ponderosa pine mesocosms, precipitation was either reduced by 30% per event using a rain shelter (first mesocosm in foreground in far right row), not manipulated (second mesocosm in far right row), or increased by 50% prevent using a funnel (third mesocosm in far right row). For the transferred mixed conifer mesocosms, precipitation was either reduced by 30% relative to the wetter, higher-elevation site from which it was transferred (first mesocosm in foreground in second row from the right), increased by 50% (second mesocosm in second row from the right; notice that the funnel is larger than the funnel used for ponderosa pine mesocosms), or increased (using smaller funnels) to approximate native mixed conifer ambient precipitation and isolate the effect of temperature (third mesocosm in second row from the right). The *circular black covers* with rocks on them mark pits (approx. 75 cm deep) used to access leachate collectors that are connected to the bottom of each mesocosm.

and grassland mesocosms, respectively), and six were treated with reduced precipitation (−30% per event relative to native site using appropriately sized rain shelters). Although precipitation treatments were calculated to approximate mean annual precipitation, the transferred mesocosms likely experienced a lower frequency of precipitation events. Interactive precipitation and temperature treatments in all four ecosystems resulted in a three-way full-factorial design, with three levels of precipitation, two levels of temperature, and four types of ecosystems. Treatments began in October 2002.

At the end of the 2003 dry season (July 7), we simulated the first rainfall event of the wet monsoon season to determine whether the response of CH_4 consumption to seasonal precipitation depended on climate treatments and ecosystem type. Deionized water was added with a watering can to all of the mesocosms. The amount of water added approximated a rainfall event in the upper 90% of first precipitation events in the wet season based on the 30-year average of first precipitation events over 10 mm at the ponderosa site (National Climatic Data Center). This amount (19 mm) was adjusted for other ecosystems (grassland = 7 mm, pinyon-juniper = 11 mm, mixed conifer = 23 mm) to account for variation in mean annual precipitation across the gradient. Field CH_4 flux was measured before water addition (hour 0), and 2, 4, 8, and 24 h after water addition.

Treatment Attainment

Mean monthly climate data from all five sites during the first 4 years of treatments between December 2002 and November 2006 confirmed that the warming treatment (that is, downward transfer of mesocosms along the elevation gradient) was successful (Figure 2A). The magnitude and variability of the warming treatment were smaller at lower elevations (annual mean ± S.D. was 2.7 ± 1.2°C for mixed conifer mesocosms, 2.3 ± 0.6°C for ponderosa mesocosms, 1.8 ± 0.4°C for pinyon-juniper mesocosms, and 0.5 ± 0.2°C for grassland mesocosms). The air temperature gradient across the elevation gradient was strongest during the summer (10.0°C difference between Great Basin and mixed conifer sites in July) and weakest during the late fall and early winter (3.2°C difference between Great Basin and mixed conifer sites in December).

Mean monthly precipitation between December 2002 and November 2006 typically increased with increasing elevation (Figure 2B). The precipitation treatments successfully increased and decreased volumetric soil water content (Figure 3), aboveground net primary productivity (Wu and others unpublished), and soil CO_2 efflux (Brown and others unpublished). The precipitation gradient was weakest in June (that is, at the end of the dry season) and strongest in August (that is, the middle of the rainy season). The mixed conifer and ponderosa sites were relatively wet in 2003 (942 and 630 mm precipitation y^{-1}, respectively), and quite dry in 2006 (383 and 265 mm y^{-1}, respectively). The pinyon-juniper (301 ± 15 mm y^{-1}), grassland (186 ± 22 mm y^{-1}), and Great Basin (142 ± 14 mm y^{-1}) sites showed little interannual variation in precipitation during the 4 years of treatments.

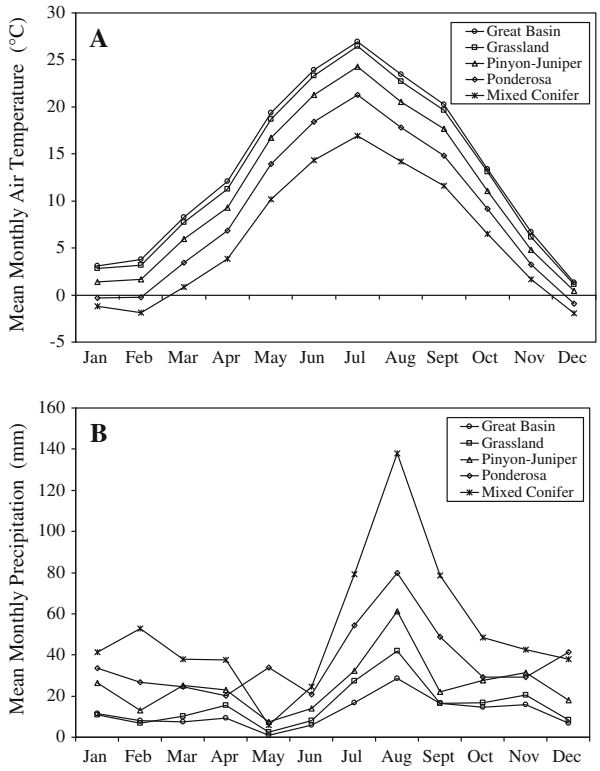

Figure 2. **A** Mean monthly air temperature and **B** precipitation between December 2002 and November 2006 measured at weather stations installed at five sites along an elevation gradient in northern Arizona, USA. *Note*: The Great Basin site is at the lowest elevation (1540 m) and the mixed conifer site is at the highest elevation (2620 m).

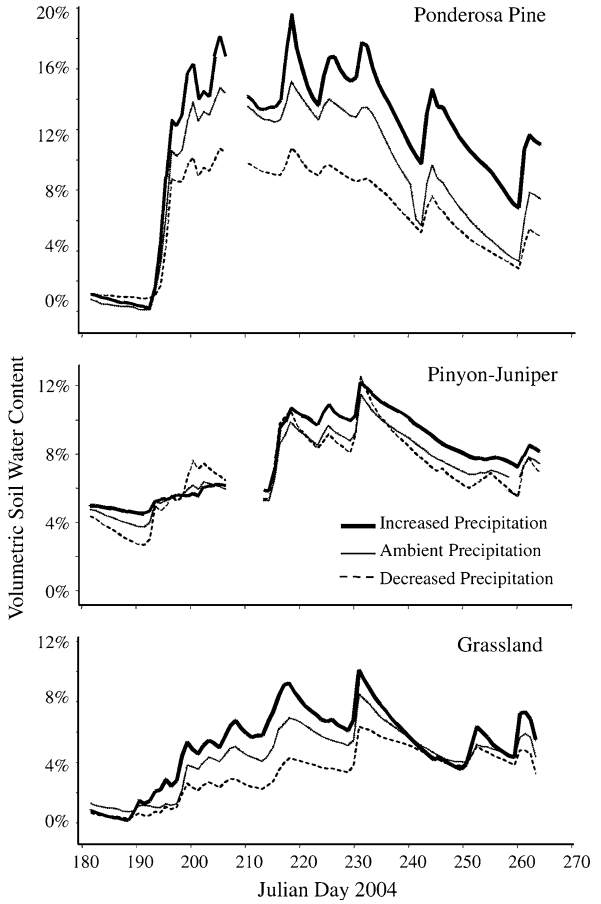

Figure 3. Volumetric soil water content (0–20 cm deep) in the ponderosa, pinyon-juniper, and grassland mesocosms exposed to increased (+50% per event, *bold line*), decreased (−30% per event, *dashed line*), and ambient (*solid line*) amounts of precipitation during the Monsoon period in 2004 (late June through late September).

The quantity of water delivered to the transferred mesocosms (which was based on historical averages) was comparable to the quantity of water delivered to untransferred mesocosms during the 4 years of this study (that is, close to 1:1 ratio). Major axis regression was used to compare monthly precipitation delivered to the control treatments (ambient temperature and increased temperature mesocosms only) between December 2002 and November 2006, with untransferred water delivery (mm month^{-1}) on the *x*-axis and transferred water delivery on the *y*-axis. Across all ecosystems, the slope of the regression was 0.89 ($r = 0.75$). Stronger correlation between transferred and untransferred water delivery occurred in the grassland and pinyon-juniper mesocosms ($r = 0.91$ and 0.93, respectively), and relatively weaker correlation occurred in the ponderosa and mixed conifer mesocosms ($r = 0.56$ and 0.77, respectively). The slope of the grassland regression was close to 1 (that is, 0.98), whereas transplantation tended to increase water delivery in the pinyon-juniper and ponderosa mesocosms (slope = 1.20 and 1.24, respectively) and decrease water delivery in the mixed conifer mesocosms (slope = 0.77).

Field CH_4 Flux

Field CH_4 fluxes were measured using a modified static chamber technique (Hutchinson and Mosier 1981) on 19 sampling dates between July 2003 and November 2006 ($n = 4$), during the first 4 years of treatments. The sampling program was intended to evaluate the dynamics of the monsoon season, both intraannually in 2004 and interannually. Mesocosms were sampled between 10:00 AM and 2:00 PM on 7 Jul 2003 (before water addition), 12 Apr 2004, 17 May 2004, 15 Jun 2004, 13 Jul 2004, 20 Jul 2004, 27 Jul 2004, 3 Aug 2004, 10 Aug 2004, 16 Aug 2004, 14 Sept 2004, 15 Aug 2005, 29 Aug

2005, 23 Oct 2005, 18 May 2006, 26 Aug 2006, 10 Oct 2006, 6 Nov 2006, and 9 May 2007. The sample size reflected our need to balance replication with complete treatment coverage and to conduct measurements during the same limited time of day for each measurement.

Chambers were constructed of a 1 cm walled PVC tube (30 cm diam. × 15 cm tall) cemented to a 1 cm thick piece of flat PVC and were equipped with a sampling port and vent tube. White PVC was used to minimize warming in the chambers by solar radiation during the 40 min sampling period. The sample port was located on the top center of the chamber and consisted of a stainless steel quick-connect bulkhead valve. A double-walled rubber sleeve was attached to the base of the chamber to create an airtight seal with the mesocosm PVC cylinder in the field. A vinyl vent tube (1.3 cm diam. × 15 cm long) passed through the top of the chamber and was attached to the inside wall of the chamber. The length and diameter of the vent tube were calculated to minimize chamber air mixing with outside air due to sample collection and perturbations from wind (that is, the Venturi effect). Methane fluxes were not measured on days with forecasted wind speeds greater than 32 km h^{-1}.

Chamber headspace air samples and field standards were collected in pre-evacuated 100-ml Silonite™ coated stainless steel sample canisters (Entech Instruments, Inc., Simi Valley, California) equipped with quick-disconnect valves. During each CH_4 flux measurement, a chamber top was sealed onto each mesocosm, and gas samples from the chamber atmosphere were collected within 1 min after sealing the chamber, and then again 20 and 40 min later. Headspace samples were collected by attaching one end of a pre-evacuated canister to the chamber bulkhead fitting, which immediately forced 100 ml of chamber air into the canister. To over-pressurize the field sample for the gas chromatograph's auto-sampler in the laboratory, an additional 60 ml of chamber air was drawn into a syringe connected to the opposite end of the sample canister. The canister was then disconnected from the chamber and the additional 60 ml was injected into the canister. Methane flux was measured at all sites within a 48 h period for each sampling event.

Gas samples were analyzed for CH_4 concentration within 48 h of field collection using an Agilent Technologies Model 6890A gas chromatograph system (Agilent Technologies, Inc., Palo Alto, California) with a 31-port auto-sampler and GC ChemStation Rev. A.09.01 software. Methane concentrations were measured using helium as the carrier gas and a flame ionization detector (250°C). The flame ionization detector was equipped with a 2-ml sample loop and in-line Haye Sep Q 60/80 (50°C) and Porapak Q 60/80 (32°C) columns as part of an integrated backflush system. Field CH_4 flux was calculated using least squares regression of concentrations over time and expressed as mg CH_4-C m^{-2} h^{-1}, after accounting for air pressure, volume, and surface area. We chose to express field rates per hour because of the likely (but untested) side effects of diurnal temperature change in these ecosystems. During the more intensive sampling program in 2004, the mean R^2 value for linear regressions was 0.88 ± 0.14 S.D. Different ecosystems had similar R^2 values, but weaker correlations were observed in all ecosystems late in the dry season (mean R^2 value for late June and early July = 0.66 ± 0.19 S.D.).

Laboratory CH_4 Consumption

Soil cores (3 cm diam. × 20 cm deep) were collected from every mesocosm between 31 October and 2 November 2003 and between 7 September and 12 September 2005, approximately 1 and 3 years after climate treatments began. The frequency of soil collection was limited by mesocosm surface area and intended to assess accumulated effects of climate treatments at the end of the wet season. Soils were homogenized by hand and large roots and rocks were removed using a 2-mm sieve. After overnight storage in sealed plastic bags at room temperature, followed by air-drying of all samples for 48 h to lower soil water content below 35% of water-holding capacity (WHC), soils (15 g) were placed in 250-ml screw-top glass serum bottles. Deionized water was added using a spray bottle approximately 2 h before the incubations began, to standardize soil moisture at an assumed optimum of 35% WHC (Gulledge and Schimel 1998). Soil WHC was determined by saturating 15 g of air-dried sieved soil (n = 8), and calculating a mass of water absorbed after samples were allowed to drain over Grade 2 filter paper for 2 h (Table 1).

Incubations began within 72 h of soil collection. After standardizing soil moisture, incubation bottles were sealed with screw caps lined with airtight Teflon®–silicone septa. To reduce substrate limitation, CH_4 concentrations inside the bottles were elevated to approximately 10× ambient concentrations (18 ppmv) by adding 1 ml of CH_4 in air at a concentration of 4800 ppmv. A CH_4 concentration of 18 ppmv is high enough to reduce substrate limitation to high-affinity CH_4-oxidizing bacteria,

which have half-saturation constants (K_m) between 10 and 80 ppm in temperate meadow and forest soils (Bender and Conrad 1993; Czepiel and others 1995; Benstead and King 1997; Gulledge and others 2004), but low enough to have little effect on low-affinity CH_4-oxidizing bacteria (Bender and Conrad 1992). Optimal moisture and elevated CH_4 concentrations enhanced rates of CH_4 oxidation relative to CH_4 production, thereby increasing the possibility of observing a treatment-induced change in methanotrophic activity. As an assay of methanotrophic enzyme activity and population size, we expected a positive correlation between laboratory CH_4 consumption and field CH_4 consumption.

The laboratory incubations were conducted for 48 h in the dark at 25°C. Methane fluxes were calculated from three 15-ml headspace samples taken 30–60 min, 24 h, and 48 h after sealing bottles and adding CH_4. Gas samples were immediately injected into sealed pre-evacuated 12-ml glass vials with capped 20-mm butyl rubber stoppers that are known to be airtight for at least 10 weeks (data not shown), and were over-pressurized (+3 ml) so that any leaks would be evident when vials were analyzed (that is, under-pressurized sampling syringe). All vials were analyzed on the same gas chromatograph system used to measure field CH_4 flux within 4 weeks after the incubations ended. Laboratory soil CH_4 flux was calculated from the difference in concentration over 48 h and expressed as ng CH_4-C g^{-1} soil h^{-1}.

Statistical Analyses

To test for interactions between ecosystem type and climate treatments, the rates of field CH_4 consumption (19 sampling dates between July 2003 and November 2006) and laboratory CH_4 consumption (October 2003 and September 2005) were analyzed using three-way repeated-measures ANOVA ($\alpha = 0.05$, JMP IN 5.1.2, SAS Institute, Cary NC). Data transformation was not required for either response variable. The main factors, in full-factorial design, were temperature (ambient and elevated), precipitation (ambient, reduced, and elevated), and ecosystem type (grassland, pinyon-juniper, ponderosa pine, and mixed conifer). Because the temperature manipulations were not uniform across ecosystems, the temperature treatment was analyzed as the expected warming rather than the magnitude of warming.

Post-hoc Tukey's HSD tests were used to determine the nature of significant interactions between warming, altered precipitation, ecosystem type, and sampling date. Relative treatment effect sizes were calculated as: % effect = 100% * [treatment mean − ambient mean]/ambient mean. Least squares regression analysis was used to test relationships between field and laboratory CH_4 fluxes (when both were measured at the same time in September 2005), gravimetric soil water content (when both were measured at the same time in September 2005), and air temperature (across all sampling dates, ambient temperature treatments only, mean of five thermometer readings during field CH_4 flux sampling at 1 m height).

Results

Treatment Effects

Across all four ecosystems and 19 sampling dates between July 2003 and November 2006 (approximately 1–4 years after treatments began), the increased precipitation treatments caused a 4.5% decrease in field CH_4 consumption and the decreased precipitation treatments caused a 5.5% increase in field CH_4 consumption. These general effects of altered precipitation depended on ecosystem type (Table 2): increased precipitation had no effect in the grassland or pinyon-juniper mesocosms, but caused a 24% reduction in CH_4 uptake in the ponderosa mesocosms and a 12% reduction in the mixed conifer mesocosms (Figure 4). Reduced precipitation had no effect in the grassland or pinyon-juniper mesocosms, but increased CH_4 uptake by 11% in the ponderosa and mixed conifer mesocosms.

The effect of warming varied by ecosystem type: warming had no effect on ponderosa or mixed conifer field CH_4 fluxes, but caused a 14% reduction in field CH_4 uptake in the grassland mesocosms and a 20% reduction in the pinyon-juniper mesocosms (Figure 5; Table 2). We found no significant interactive effects of altered precipitation and warming on field or laboratory CH_4 fluxes (Table 2).

Altered precipitation had no effect on laboratory CH_4 consumption in any ecosystem. Warming had no effect on laboratory CH_4 consumption in the grassland or pinyon-juniper soils, but significantly reduced laboratory CH_4 consumption in the ponderosa and mixed conifer soils, irrespective of sampling date (Figure 6).

Seasonal Variation

There were no ecosystem differences in field CH_4 flux during the dry season (that is, six sampling dates between May and mid-July), and rates were quite similar, with mean rates (±95% C.I.) of

Table 2. Full-Factorial Effects of Climate Treatments, Ecosystem Type, and Sampling Date on Field CH_4 Flux (19 Sampling Dates Between July 2003 and November 2006) and Laboratory Soil CH_4 Consumption (Two Sampling Dates in October 2003 and September 2005)

Effect	Field CH_4 Flux			Laboratory CH_4 Flux		
	df	*F*-statistic	*P* value	df	*F*-statistic	*P* value
Precip	2	9.27	0.0009*	2	1.22	0.27
Temp	1	6.03	0.02*	1	9.02	0.004*
Ecosystem	3	65.62	<0.0001*	3	108.43	<0.0001*
Date	18	116.98	<0.0001*	1	108.26	<0.0001*
Precip × Temp	2	0.11	0.90	2	0.89	0.41
Precip × Ecosys	6	3.14	0.02*	6	2.06	0.07
Precip × Date	36	2.12	0.04*	2	1.03	0.32
Temp × Ecosys	3	5.38	0.005*	3	13.04	<0.0001*
Temp × Date	18	2.53	0.07	1	0.03	0.86
Ecosys × Date	54	5.30	<0.0001*	3	0.55	0.56
Precip × Temp × Ecosys	6	0.88	0.52	6	1.38	0.24
Precip × Temp × Date	36	1.13	0.40	2	1.32	0.27
Precip × Ecosys × Date	108	1.74	0.008*	6	1.21	0.31
Temp × Ecosys × Date	54	1.43	0.15	3	0.98	0.38
Precip × Temp × Ecosys × Date	108	1.18	0.24	6	1.88	0.10

A three-way repeated-measures ANOVA was performed for each response variable, with precipitation (ambient, +50%, and −30%), temperature (ambient and +1.8°C on average), and ecosystem type (cool desert grassland, pinyon-juniper woodland, ponderosa pine forest, and mixed conifer forest) as the main factors.
**Significant at α level of 0.05; data transformation was not required.*

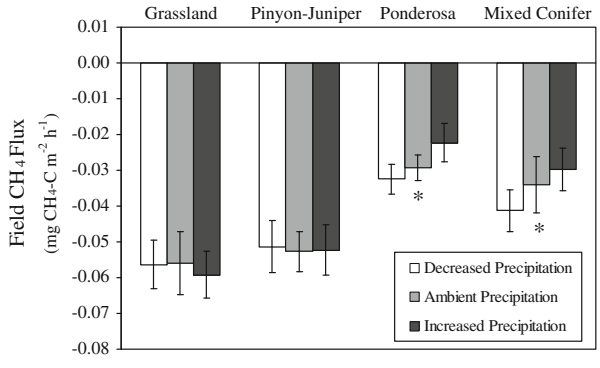

Figure 4. Effect of altered precipitation on field CH_4 flux (mean ± 95% confidence interval) in four ecosystems on a warm/dry to cold/wet climatic gradient during 19 sampling dates between July 2003 and November 2006 (negative fluxes indicate net CH_4 uptake). There was a significant two-way interaction between precipitation and ecosystem type ($P = 0.02$ in the three-way repeated-measures ANOVA). Increasing precipitation reduced CH_4 uptake (*significant at an alpha level of 0.05 in Tukey's HSD test) in the ponderosa ($P = 0.005$) and mixed conifer mesocosms ($P = 0.05$), but not in the grassland ($P = 0.80$) or pinyon-juniper mesocosms ($P = 0.96$). No effects of precipitation treatments were significantly different from the ambient control.

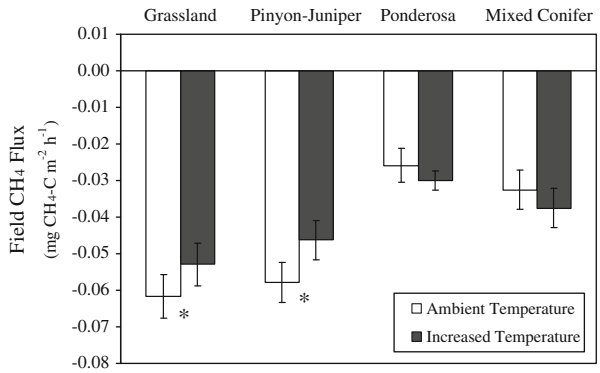

Figure 5. Effects of warming on field CH_4 flux across all 19 sampling dates. There was a significant two-way interaction between warming and ecosystem type ($P = 0.005$ in three-way repeated-measures ANOVA). Significant effects of the warming treatment (*significant at an alpha level of 0.05 in Tukey's HSD test) were detected in the grassland ($P = 0.04$, 14% reduction in uptake) and pinyon-juniper mesocosms ($P = 0.003$, 20% reduction in uptake), but not in the ponderosa ($P = 0.12$) or mixed conifer mesocosms ($P = 0.24$).

-0.028 ± 0.008, -0.035 ± 0.008, -0.024 ± 0.005, and -0.030 ± 0.010 mg CH_4-C m^{-2} h^{-1} in the grassland, pinyon-juniper, ponderosa, and mixed conifer mesocosms, respectively. There was higher CH_4 consumption during the wet season (13 sampling dates between mid-July and April) in the grassland, pinyon-juniper, and ponderosa mesocosms, but the mixed conifer mesocosms showed no difference between seasons (Figure 7). Ecosystems differed in CH_4 flux during the wet season, with CH_4 consumption decreasing in the

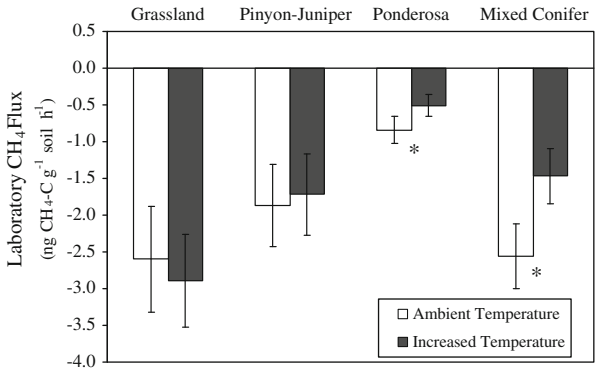

Figure 6. Effects of warming on laboratory CH_4 flux that were independent of sampling date. There was a significant two-way interaction between warming and ecosystem type ($P < 0.0001$ in three-way repeated-measures ANOVA). Significant effects of the warming treatment (*significant at an alpha level of 0.05 in Tukey's HSD test) were detected in the ponderosa ($P = 0.05$, 39% reduction in CH_4 uptake) and mixed conifer mesocosms ($P = 0.0002$, 43% reduction in CH_4 uptake), but not in the grassland ($P = 0.55$) or pinyon-juniper mesocosms ($P = 0.68$).

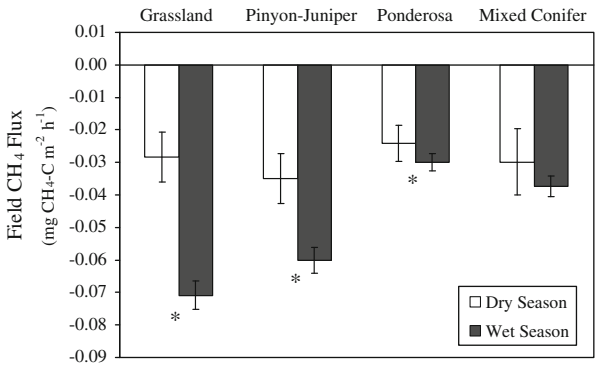

Figure 7. The response of field CH_4 flux to seasonal variation in precipitation associated with the North American Monsoon between July 2003 and November 2006. There was a significant two-way interaction between ecosystem type and sampling date ($P < 0.0001$ in three-way repeated-measures ANOVA). The dry season measurements included six sampling dates between May and mid-July, and the wet season included 13 sampling dates between mid-July and April. Seasonal differences (*significant at an alpha level of 0.05 in Tukey's HSD test) were detected in the grassland ($P < 0.0001$, 150% increase in CH_4 uptake during wet season), pinyon-juniper ($P < 0.0001$, 72% increase), and ponderosa mesocosms ($P = 0.03$, 24% increase), but not in the mixed conifer mesocosms ($P = 0.08$).

order: grassland > pinyon-juniper > mixed conifer > ponderosa (-0.071 ± 0.005, -0.060 ± 0.004, -0.038 ± 0.003, and -0.030 ± 0.003 mg CH_4-C m^{-2} h^{-1}).

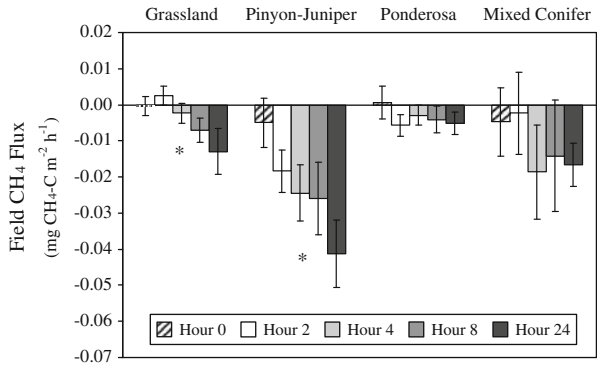

Figure 8. Effects of experimental water addition (simulating the first rain event of the wet season) on field CH_4 flux in July 2003. There was a significant two-way interaction between water addition and ecosystem type ($P < 0.0001$ in three-way repeated-measures ANOVA). *Negative values* indicate net CH_4 uptake and *positive values* indicate net CH_4 emission before water addition ('hour 0'), and 2, 4, 8, and 24 h after water addition. Effects of water addition on CH_4 flux (*significant at an alpha level of 0.05 in Tukey's HSD test) were detected in the grassland ($P < 0.0001$) and pinyon-juniper mesocosms ($P < 0.0001$), but not in the ponderosa ($P = 0.06$) or mixed conifer mesocosms ($P = 0.27$).

After water addition at the end of the 2003 dry season, all ecosystems switched from zero net CH_4 consumption to significant net CH_4 consumption within 2–8 h (Figure 8). Precipitation treatments had no effect on the field CH_4 flux of any ecosystem after water addition, but warming significantly enhanced pinyon-juniper CH_4 uptake (from -0.014 ± 0.004 to -0.033 ± 0.006 mg CH_4-C m^{-2} h^{-1}) and reduced mixed conifer CH_4 uptake (from -0.025 ± 0.007 to 0.001 ± 0.008 mg CH_4-C m^{-2} h^{-1}) during the 24 h after water addition.

The reduction in ponderosa and mixed conifer field CH_4 consumption with increasing precipitation depended on sampling date. Increasing precipitation was more likely to reduce CH_4 uptake in these ecosystems during the wet season (Figure 9). Conversely, increasing precipitation was more likely to enhance CH_4 uptake or have no effect in these ecosystems during the dry season. Because of the strong influence of seasonal precipitation (that is, season explained more variation than year), the *x*-axis in Figure 9 is not in sequence and amalgamates dates from contrasting years.

Predictors of Field CH_4 Flux

Within an ecosystem type, laboratory CH_4 consumption was not correlated with field CH_4 consumption ($P = 0.12$, 0.26, 0.99, and 0.94 for

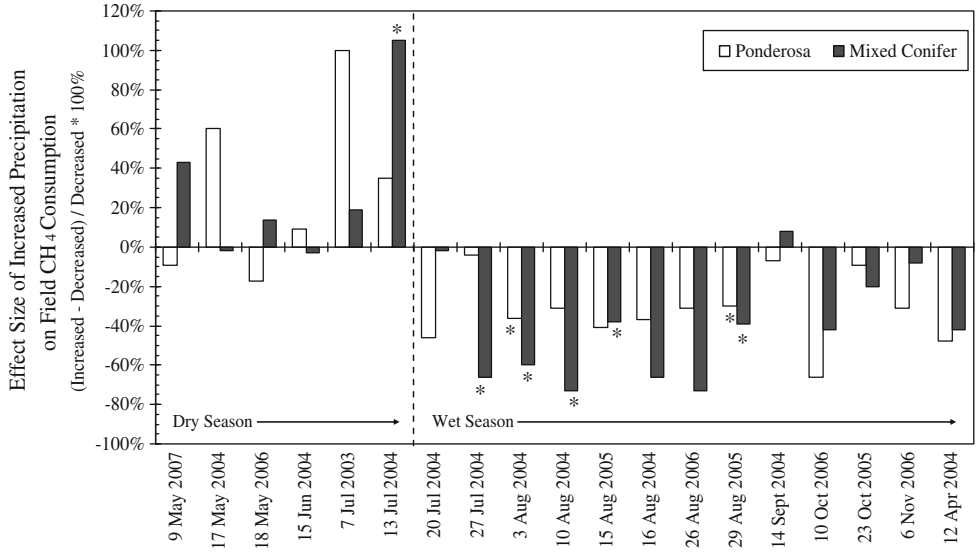

Figure 9. Temporal variation in effects of increasing precipitation on field CH_4 uptake in the ponderosa and mixed conifer mesocosms. There was a significant interaction between precipitation, ecosystem type, and time ($P = 0.008$ in three-way repeated-measures ANOVA; *significant difference between increased and decreased precipitation treatments at an alpha level of 0.05 in Tukey's HSD test). The *x*-axis is not in sequence and amalgamates dates from contrasting years. All treatment means used to calculate effect sizes were negative (that is, net CH_4 uptake).

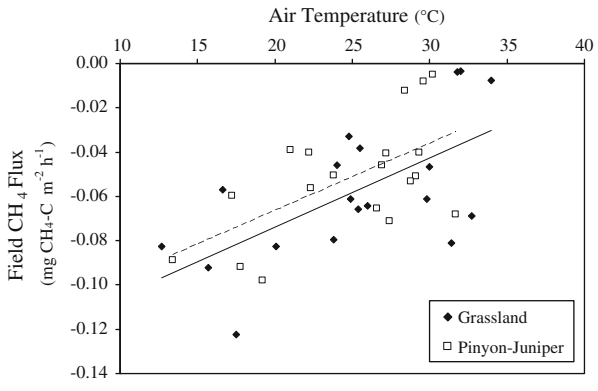

Figure 10. Least squares regression of air temperature with field CH_4 flux (ambient temperature treatment only) for the grassland (*solid line*, $y = 0.08x - 3.28$, $F = 11.28$, $P = 0.004$, $R^2 = 0.40$) and pinyon-juniper mesocosms (*dashed line*, $y = 0.07x - 3.04$, $F = 9.49$, $P = 0.007$, $R^2 = 0.36$) across all sampling dates between July 2003 and November 2006.

grassland, pinyon-juniper, ponderosa, and mixed conifer, respectively). Across ecosystems, laboratory CH_4 consumption was positively correlated with field CH_4 consumption ($P = 0.02$, $F = 5.71$, $R^2 = 0.07$, slope = 1.5), with the highest rates in grassland soils (-2.7 ± 0.5 ng CH_4-C g^{-1} soil h^{-1}), lower rates in mixed conifer (-2.0 ± 0.3 ng CH_4-C g^{-1} soil h^{-1}) and pinyon-juniper soils (-1.8 ± 0.4 ng CH_4-C g^{-1} soil h^{-1}), and the lowest rates in the ponderosa soils (-0.6 ± 0.1 ng CH_4-C g^{-1} soil h^{-1}).

Soil water content correlated positively with field CH_4 flux across ecosystems (that is, less CH_4 uptake in wetter soils; $P = 0.04$, $F = 4.15$, $R^2 = 0.05$, slope = -0.16), but there was no correlation within individual ecosystems ($P = 0.70$, 0.19, 0.49, and 0.20 for grassland, pinyon-juniper, ponderosa, and mixed conifer, respectively). Air temperature significantly explained variability in grassland and pinyon-juniper field CH_4 fluxes across sampling dates, with less CH_4 uptake in both ecosystems on warmer sampling dates (Figure 10). There was no correlation between air temperature and field CH_4 flux in the ponderosa ($P = 0.08$, $F = 3.53$, $R^2 = 0.17$, slope = +0.02) or mixed conifer mesocosms ($P = 0.18$, $F = 1.98$, $R^2 = 0.10$, slope = +0.03).

Discussion

All four ecosystems along the elevation gradient were strong CH_4 sinks, and our results suggest that changes in climate will substantially alter future terrestrial CH_4 uptake in the Colorado Plateau ecoregion. There was strong interaction between ecosystem type and climatic change treatments: wetter ecosystems responded more strongly to altered precipitation and drier ecosystems responded more strongly to increased temperature. Weighted seasonal CH_4 consumption in the mixed conifer

and ponderosa pine forest soils (3.8 and 3.0 kg CH_4 ha^{-1} y^{-1}, respectively) was in between other cool and warm temperate forests (mean of 5.1 and 1.7 kg CH_4 ha^{-1} y^{-1}, respectively; Dutaur and Verchot 2007). Methane consumption in the cool desert grassland and pinyon-juniper woodland (7.2 and 6.8 kg CH_4 ha^{-1} y^{-1}, respectively) was much higher than in other grassland and chaparral ecosystems (mean of 2.6 and 2.2 kg CH_4 ha^{-1} y^{-1}, respectively; Dutaur and Verchot 2007).

The cold and wet ecosystems along the elevation gradient exhibited less CH_4 uptake with increasing precipitation quantity. This effect was likely caused by diffusional limitation under higher soil moisture (Koschorreck and Conrad 1993; Castro and others 1995), considering that effects in the field disappeared in the laboratory when diffusional limitation was lower and standardized among treatments. The reduced precipitation treatment enhanced CH_4 uptake by 11–22%, which is smaller in magnitude than responses found with complete throughfall exclusion (41–300% increase; Borken and others 2000; Davidson and others 2004) but in the same direction as found in other reduced precipitation experiments (Billings and others 2000; Borken and others 2006). We found that increased precipitation can induce an opposite effect as drought in forest ecosystems, causing a 12–24% decrease in CH_4 uptake. The direction of response to elevated and reduced precipitation in the mixed conifer and ponderosa pine forests validates earlier projections for temperate forests (Potter and others 1996). The magnitude of response was also close to expectations. Potter and others (1996) predicted 4–7% less CH_4 consumption due to a 20% increase in precipitation, and 4–7% more CH_4 consumption due to a 20% decrease in precipitation. Because our precipitation manipulations were greater than 20% (that is, +50% and −30%), the observed effect sizes of 11–24% are proportional to the treatment magnitude. Therefore, model projections that incorporate soil moisture generally capture the response of CH_4 consumption to altered water availability observed in field manipulations (Curry 2009).

The drier ecosystems, however, were unaffected by the precipitation treatments, both in the field and in the laboratory. We expected methanotrophs in the drier ecosystems to experience water stress and respond positively to increasing precipitation (Striegl and others 1992; King 1997; Curry 2007). This expectation was partly supported by a twofold increase in CH_4 uptake between the dry and wet seasons, and the switch from zero CH_4 uptake to net CH_4 uptake immediately following water addition at the end of the dry season. Methanotrophy was indeed generally water stressed in the drier ecosystems (Potter and others 1996), and the annual CH_4 sink of these ecosystems is very likely to be limited by the length of the dry season. Water stress was relieved during the wet season, but methanotrophic CH_4 uptake was unaffected by the quantity of precipitation received during the wet season in these semiarid ecosystems. This result supports the hypothesis that certain soil methanotrophic communities are adapted to drier conditions and can respond differently than communities in wetter ecosystems to altered precipitation (Billings and others 2000). Alternatively, the changes in soil moisture content in the grassland and pinyon-juniper woodland may have been too small to limit diffusion.

The response of CH_4 consumption to experimental soil warming also changed in the middle of the climatic gradient. We expected the colder ecosystems to respond more strongly to warming, but, at least in the field, the warmer ecosystems responded more strongly. The negative effect of warming on CH_4 consumption in the grassland and pinyon-juniper woodland was confirmed by a negative correlation between air temperature and field CH_4 consumption in these ecosystems during the months sampled. The reduction in CH_4 uptake associated with warming was probably explained by short-term heat stress in the field, because the effects disappeared under standardized laboratory temperature. There is no evidence that soil drying and water stress explained the effects of warming (Torn and Harte 1996; Sjögersten and Wookey 2002), because supplemental precipitation would have likely relieved any water stress during the wet season, and the warming treatment (that is, transplantation with supplemental precipitation) either had no effect on water delivery (grassland) or increased water delivery (pinyon-juniper woodland). Negative effects of warming on CH_4 consumption are in contrast to positive effects found in other ecosystems (Peterjohn and others 1994; Sjögersten and Wookey 2002; Hart 2006) and suggest that models need to incorporate climate-specific responses to warming, with higher CH_4 uptake or no change in CH_4 uptake in colder climatic zones (Torn and Harte 1996; Rustad and Fernandez 1998; Hart 2006) and lower CH_4 uptake in warmer climatic zones.

The laboratory assay of soil CH_4 consumption successfully captured ecosystem differences in field CH_4 consumption, but did a poor job of

capturing differences in field CH_4 consumption caused by climate treatments. Therefore, the negative effects of precipitation and warming on field CH_4 consumption were likely caused by short-term physical limitations on methanotrophy rather than a longer-term reduction in methanotroph population size or specific enzyme activity. Warming significantly reduced the laboratory CH_4 consumption of colder ecosystems, yet this effect was not reflected in field fluxes. In the warmer ecosystems, warming treatments caused a reduction in CH_4 consumption in the field but not in the laboratory, perhaps because the 25°C incubation temperature was too warm to reveal the highest rates of CH_4 consumption (Figure 10) and potential differences in methanotrophic activity. These results confirm that laboratory CH_4 oxidation data should be interpreted carefully with respect to field conditions because diffusion resistance may override any differences in population size or enzyme activity (Bender and Conrad 1993).

The effects of altered precipitation on field CH_4 uptake in the wetter ecosystems depended on seasonal precipitation, but the effect of warming in the drier ecosystems was independent of seasonal precipitation. It is unknown whether the seasonality of precipitation effects is also higher than the seasonality of warming effects in other parts of the world. In the ponderosa pine and mixed conifer forest soils considered in this study, precipitation was more likely to reduce CH_4 consumption during the wet season (that is, diffusional limitation) and increase CH_4 consumption or have no effect during the dry season (that is, water stress). If this heterogeneous seasonal response is ignored, and rather the wet season response to precipitation is modeled throughout the year, then annual CH_4 uptake could be underestimated by as much as 10% in both forest ecosystems.

We found no evidence for interactive effects of precipitation and temperature on CH_4 consumption in any ecosystem. Rather, CH_4 uptake along the climatic gradient responded to either altered precipitation or warming. It is surprising that soil drying associated with warming did not alleviate diffusional limitation in the wetter ecosystems, and that higher water availability did not alleviate heat stress in the warmer ecosystems. It is possible that the magnitudes of our precipitation and warming alterations were not large enough to reveal interactions. It is also possible that methanotrophic communities in colder and wetter ecosystems are well acclimatized to temperature change, but less adept at dealing with precipitation change, whereas methanotrophic communities in warmer and drier ecosystems are well-acclimatized to precipitation change, but less adept at dealing with temperature change.

The present study is a first attempt to quantify the response of CH_4 flux to interaction between ecosystem type and multiple components of climatic change. Although our manipulations of temperature and precipitation were not uniform across ecosystems during the 4 years of this study, the manipulations simulated an approximate 300 m upward shift in climate on a mountain, which is an expected consequence of climatic change during the next 50–100 years. We found that interactions between ecosystem type and climatic change are more important than interactions between different components of climatic change for predicting the ecosystem service of CH_4 consumption. The temperature-dependency of CH_4 consumption in warm climatic zones and the precipitation-dependency in wet climatic zones are key areas for future experimental and modeling research. By incorporating ecosystem-specific responses to expected warming and precipitation change, this study suggests that the Colorado Plateau ecoregion will become a smaller CH_4 sink in a warmer (and wetter) world, not a larger sink (Curry 2009).

ACKNOWLEDGMENTS

Thanks to Jeff Coyle, Sam Granum, Patrick Reyes, and Mario Montes-Helu for their help with field sampling, Karen Adair, Sam Chapman, and Adam Langley for their help with soil collection and processing, and Stephen Hart, Maribeth Watwood, and two anonymous reviewers for their insightful comments on earlier drafts. This research was supported by the National Science Foundation, DEB-0092642.

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