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CARBON DIOXIDE AND METHANE FLUXES BY A FOREST SOIL UNDER LABORATORY-CONTROLLED MOISTURE AND TEMPERATURE CONDITIONS

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Summary—Carbon dioxide and methane are important greenhouse gases whose exchange rates between soils and the atmosphere are controlled strongly by soil temperature and moisture. We made a laboratory investigation to quantify the relative importance of soil moisture and temperature on fluxes of CO_2 and CH_4 between forest soils and the atmosphere. Forest floor and mineral soil material were collected from a mixed hardwood forest at the Harvard Forest Long-Term Ecological Research Site (MA) and were incubated in the laboratory under a range of moisture (air-dry to nearly saturated) and temperature conditions (5–25°C). Carbon dioxide emissions increased exponentially with increasing temperature in forest floor material, with emissions reduced at the lowest and highest soil moisture contents. The forest floor Q_{10} of 2.03 (from 15–25°C) suggests that CO_2 emissions were controlled primarily by soil biological activity. Forest floor CO_2 emissions were predicted with a multiple polynomial regression model ($r^2 = 0.88$) of temperature and moisture, but the fit predicting mineral soil respiration was weaker ($r^2 = 0.59$). Methane uptake was controlled strongly by soil moisture, with reduced fluxes under conditions of very low or very high soil moisture contents. A multiple polynomial model accurately described CH_4 uptake by mineral soil material ($r^2 = 0.81$), but only weakly ($r^2 = 0.45$) predicted uptake by forest floor material. The mineral soil Q_{10} of 1.11 for CH_4 uptake indicates that methane uptake is controlled primarily by physical processes. Our work suggests that inclusion of both moisture and temperature can improve predictions of soil CO_2 and CH_4 exchanges between soils and the atmosphere. Additionally, global change models need to consider interactions of temperature and moisture in evaluating effects of global climate change on trace gas fluxes.

INTRODUCTION

Carbon dioxide and methane are greenhouse gases whose atmospheric concentrations have been increasing over the last several centuries (Prather *et al.*, 1996; Schimel *et al.*, 1996). Methane is of increasing concern because it has a radiative potential 26 times more effective than CO_2 (Lilieveld and Crutzen, 1992), and because it influences the oxidative potential of the atmosphere (Thompson, 1992).

Soils are major global sources and sinks of CO_2 and CH_4 and thus play an important role in regulating atmospheric concentrations of these gases (Mooney *et al.*, 1987; Melillo *et al.*, 1989). Soil respiration by terrestrial ecosystems contributes 50–75×10^9 t C y^{-1} (Kicklighter *et al.*, 1994) to the atmosphere, which is an order of magnitude greater than the annual increase in atmospheric carbon (Watson *et al.*, 1990). Globally, consumption of atmospheric methane by both methanotrophic and nitrifying bacteria in aerobic soil (Bedard and Knowles, 1989) is 1.5–4.5×10^7 t C ha^{-1} y^{-1}, representing 1 to 8% of the oxidative potential of the atmosphere (Born *et al.*, 1990; Schutz *et al.*, 1990; Prather *et al.*, 1996). Of this total, temperate evergreen and deciduous forests consume up to 37% (Steudler *et al.*, 1989).

Understanding the dynamics of CO_2 and CH_4 exchanges between soils and the atmosphere is critical to construction of regional trace gas models and to prediction of trace gas fluxes under models of global climate change. Numerous field studies in temperate forests have shown a strong temporal pattern in CO_2 and CH_4 fluxes (e.g. Castro *et al.*, 1994; Peterjohn *et al.*, 1994; Castro *et al.*, 1995) that corresponds strongly with seasonal changes in soil moisture and temperature. Temperature is considered the primary predictor of CO_2 effluxes, but, not surprisingly, moisture also influences soil respiration rates (e.g. Wiant, 1967; Groffman *et al.*, 1992). Moisture usually exerts strong control over CH_4 uptake rates, although inclusion of both moisture and temperature in models can increase predictive capabilities. Lessard *et al.* (1994) suggested that the strong relationship between moisture and CH_4 uptake may mask relationships between tempera-

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ture and uptake, thus it has been difficult to determine the relative importance of these factors.

Using field studies to determine the relative importance of moisture and temperature in controlling flux rates is difficult because soil temperature and moisture usually covary seasonally in temperate ecosystems. Soil temperatures are usually highest by late summer, but strong evapotranspiration potentials usually reduce soil water even if precipitation stays relatively constant. Thus, it is not a straightforward exercise to determine if maximum rates of soil respiration or CH_4 uptake in late summer, for example, are due to high temperatures, lower soil moisture, or an interaction of both factors. Understanding the controls of moisture and temperature is important because there is increasing effort to construct regional trace gas models and accurate models cannot be produced if controlling factors are not well understood. To overcome limitations of field-based data in determining the importance of soil moisture and temperature, we did a full-factorial laboratory study to evaluate the relative contribution of each factor, as well as interactions, on CO_2 emissions and CH_4 uptake by a well-drained temperate forest soil.

MATERIALS AND METHODS

Site description

Soil material was collected at the Harvard Forest Long-Term Ecological Research Site in north-central Massachusetts, U.S.A., from an approximately 50-y-old mixed hardwood stand established following abandonment from pastures in the early 1900's (Magill *et al.*, 1997). Total biomass in the stand was 111 t ha^{-1}, and was dominated by black oak (*Quercus velutina* Lam.), which comprises 76% of the total basal area. Remaining vegetation includes black birch (*Betula lenta* L.), paper birch (*Betula papyrifera* March.) and red maple (*Acer rubrum* L.). Soils at the site are of the Canton series (*Typic Dystrochrepts*) which formed in glacial till. At our site, the Canton soil has a sandy loam texture and a soil pH of 3.8 (1:1 soil:water); the forest floor is 6.5 cm thick and has a pH of 3.3.

Soil preparation and analysis

Forest floor and mineral soil (0–10 cm) were collected from four locations at the site, separated, sieved (forest floor: 5.6 mm; mineral soil: 2 mm) to remove rocks and roots, and homogenized so that soil moisture contents could be manipulated accurately. Total water-holding capacity (WHC) of the soil was determined by placing soil into 7 cm dia by 6 cm tall polyethylene tubes and saturating them with water. After the tubes were drained for 4 h, WHC was determined gravimetrically by drying soil at 105°C to constant weight. For forest floor material, WHC (g water g $soil^{-1}$) was 3.22 ± 0.04 (SE, $n = 15$) for forest floor and 0.86 ± 0.02 (SE, $n = 17$) for mineral soil. Bulk density (g soil cm^{-3}) of soil material, determined after soil was placed into the polyethylene tubes, was 0.25 ± 0.004 (SE, $n = 90$) for forest floor and 0.79 ± 0.01 (SE, $n = 90$) for mineral soil.

For each incubation, separate assays were made for forest floor and mineral soil material. Soil material (forest floor: 40 g oven-dry weight (ODW); mineral soil: 130 g ODW) was packed into triplicate polyethylene tubes (7 cm dia by 6 cm deep) open at both ends, and was held in the tube with a nylon stocking. Water was added or removed (via air-drying) to approximate the desired percentages of total WHC. Soil moisture contents were adjusted to approximately 20%, 40%, 60%, 80% and 100% of WHC immediately prior to each soil conditioning. Soil materials were then conditioned for 48 h at 5°, 9°, 12.5°, 16.5°, 20° or 25°C. Upon completion of each assay, the actual gravimetric soil moisture (g water g^{-1} soil) content (at 105°C) was measured.

Flux measurements

Trace gas measurements were made by placing soil tubes into 0.91-L air-tight glass jars equipped with sample ports and a variable headspace reservoir that maintained constant pressure within the glass jar by decreasing the headspace by an amount equal to the air volume removed during sampling. After soils were incubated at the desired moisture, they were placed into jars and sealed for 3 h. Headspace gas samples were collected after 0, 1, 2 and 3 h.

Concentrations of CO_2 and CH_4 were measured using gas-chromatography. Carbon dioxide was analyzed with a Shimadzu GC-8A electron capture gc (Porapak Q column maintained at 45°C, injector and detector temperatures at 250°C (Bowden *et al.*, 1993)), and CH_4 concentrations were measured using a Shimadzu GC-8A flame ionization gc (Hayesep Q column, 91 cm long, 3 mm dia, stainless steel, 80/100 mesh, maintained at 100°C, with injector and detector at 130°C (Steudler *et al.*, 1989)). Fluxes were calculated using the linear portion of the gas concentration change over the 3-h time step.

RESULTS

Carbon dioxide fluxes were much greater from forest floor material than from mineral soil material (Fig. 1). Efflux rates from forest floor material increased with temperature, but were lowest under both dry and the wet conditions. In contrast, effluxes from mineral soil material were less responsive to temperature and only slightly responsive to moisture.

Methane uptake rates were related strongly to soil moisture and somewhat to temperature. Uptake rates increased from low values under dry con-

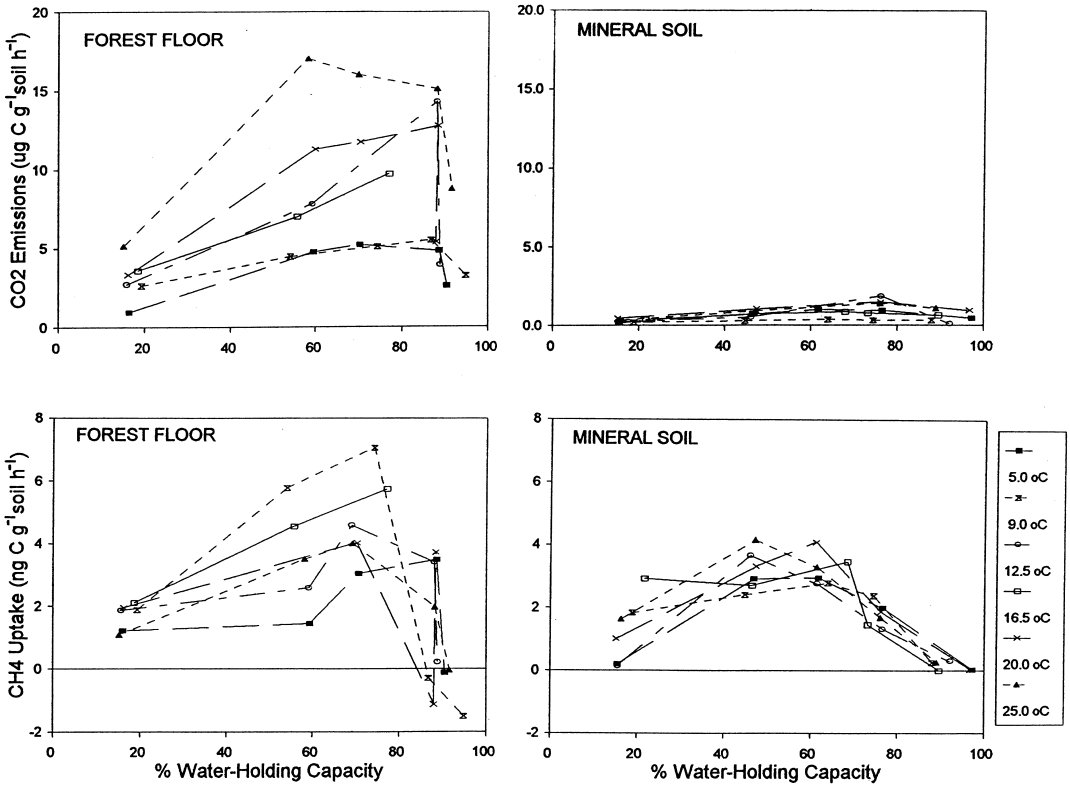

Fig. 1. Fluxes of CO_2 and CH_4 by laboratory-incubated temperate forest soil

ditions to maximum rates at approximately 70% of WHC for forest floor material and 50% for mineral soil. Uptake rates then declined to near zero as soil water content approached 100% of capacity. Uptake rates were generally highest under the highest temperature conditions, but the influence of temperature was not nearly so strong as that of moisture. Mineral soil and forest floor material generally showed the same rates of uptake.

The relationship of the ln-normally-transformed CO_2 effluxes and un-transformed CH_4 uptake to moisture and temperature variation was modelled using multiple polynomial regressions (Fig. 2). The model developed for CO_2 emissions from forest floor material contained significant contributions from both temperature and moisture (Table 1). For CH_4 uptake by mineral soil, only moisture contributed significantly to the model prediction and there were no interaction terms; for the forest floor, there was a significant moisture × temperature interaction term.

DISCUSSION

Carbon dioxide

The relationships we found between temperature and CO_2 effluxes are comparable to numerous field studies that have documented strong relationships between temperature and CO_2 flux rates in temperate soils (e.g. Crill, 1991; Fernandez *et al.*, 1993; Yavitt *et al.*, 1995), including work at the Harvard Forest (Bowden *et al.*, 1993; Peterjohn *et al.*, 1994). The Q_{10} values (from 15°C to 25°C, at 50% of soil moisture capacity) of 2.03 for the forest floor and 2.39 for the mineral soil are within the range of 1.4 to 3.8 reported for a variety of temperate forest soils (Schlesinger, 1977; Dorr and Munnich, 1987; Crill, 1991; Kicklighter *et al.*, 1994).

Although many field studies fail to find relationships between soil moisture and CO_2 emissions, our results agree with other laboratory studies that found reduced soil respiration rates under very dry or very wet conditions (Linn and Doran, 1984; Doran *et al.*, 1990). A notable result of our incubations was that the influence of moisture was stronger at high temperatures than it was at lower temperatures (Fig. 2). This is relevant in that moisture effects on soil respiration may become more pronounced at higher soil temperatures.

Inclusion of both moisture and temperature in our multiple polynomial models resulted in much better predictions of CO_2 emissions than predictions obtained using temperature alone. For the forest floor, the relationship of temperature vs ln[CO_2] flux resulted in an r^2 of 0.47, approximately half the r^2 of 0.89 (Table 2) obtained using the full multiple polynomial equation. The enhanced predictive capability that we observed agrees with other field studies in temperate forest soils (e.g. Vogt *et al.*, 1980;

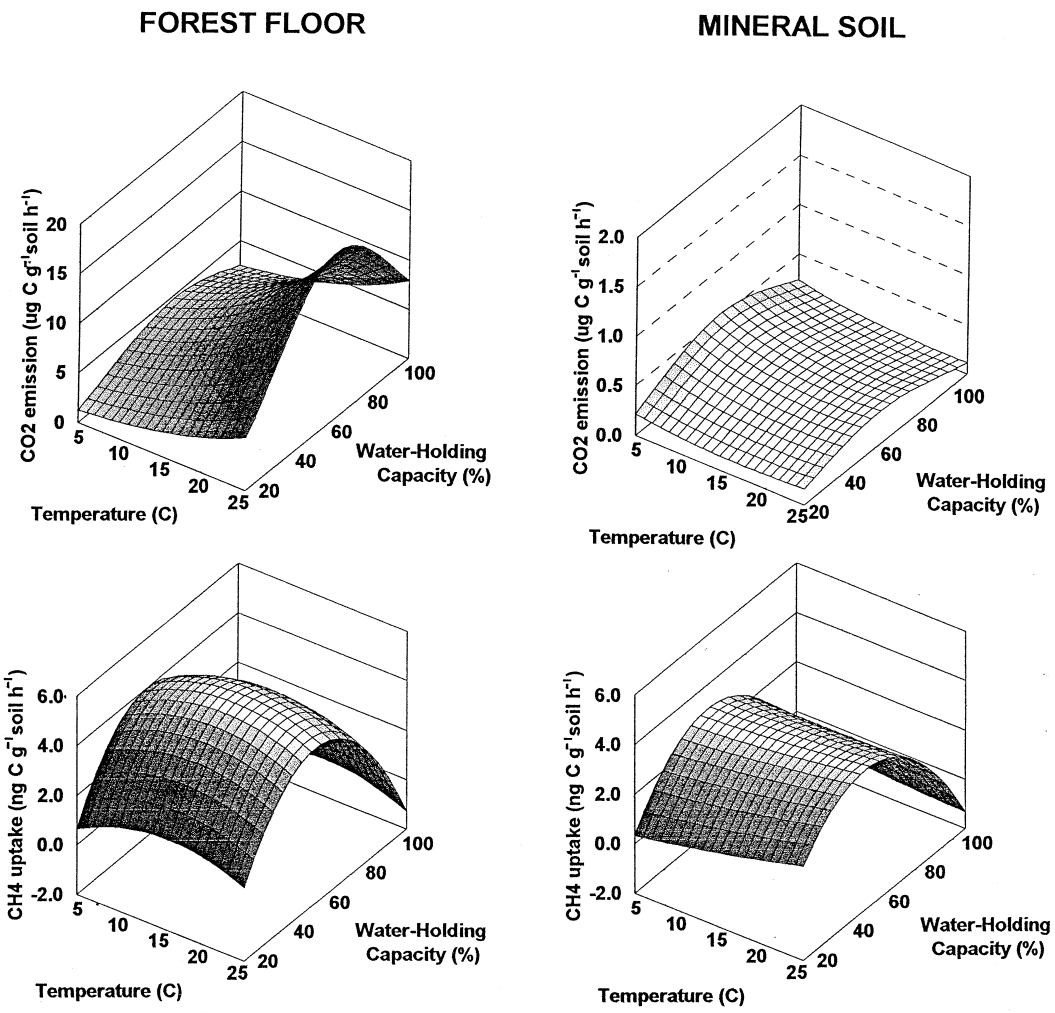

Fig. 2. Multiple polynomial regression models of temperature and moisture used to predict CO_2 and CH_4 fluxes

Dorr and Munnich, 1987; Weber, 1990; Fernandez *et al.*, 1993; Hanson *et al.*, 1993) and even across global forest datasets (Raich and Schlesinger, 1992). Our model indicates an unexplained weakly-negative relationship between temperature and CO_2 effluxes for mineral soil between 5° and 10°C. We do not know the reason for this counterintuitive result, but we believe it is a stems from the relatively high variability, even under laboratory conditions, at the very low flux rates in mineral soil.

Methane

Methane uptake was very strongly correlated with moisture content in mineral soil, as found in other field and laboratory studies (e.g. Whalen *et al.*, 1990; Striegl *et al.*, 1992; Adamsen and King, 1993; Koschorreck and Conrad, 1993; Castro *et al.*, 1995; Yavitt *et al.*, 1995).

In a laboratory-based study on agricultural soils, Nesbit and Breitenbeck (1992) found a response to moisture comparable to ours, with maximum methane uptake observed at approximately 50–70% of water-filled porespace (WFPS). We calculated porespace volumes for our soils, and found similarly that maximum methane uptake occurred at approximately 60% of WFPS for both forest floor and mineral soil. We did not, however, express our data on a WFPS basis due to our inability to accurately estimate WFPS. At high moisture contents, using our volumetric water content and bulk density, as well as measured particle density (forest floor: 1.19; mineral soil 2.06), WFPS values exceeded 100% (up to 115%). We believe that the presence of considerable organic matter in our soil complicates the ability to calculate WFPS because as organic matter is moistened, it both absorbs moisture and expands into nearby porespaces. Thus, we cannot as accurately determine porespace volume as can be done for soils lower in organic

Table 1. Polynomial equations used to predict ln[CO_2] and CH_4 (CO_2: μg C g^{-1} soil h^{-1}; CH_4: ng C g^{-1} soil h^{-1}) fluxes for laboratory-incubated forest soil material

Gas	Soil material	Coefficients for gas flux = $A + BT + CW + DT^2 + EW^2 + F(T \times W)$					
		A	*B*	*C*	*D*	*E*	*F*
ln[CO_2]	forest floor ($r^2 = 0.89$), $p < 0.0001$	−0.9851	0.0610*	0.0686*	0.00046	−0.00052*	−0.00017
	mineral soil ($r^2 = 0.62$), $p < 0.002$	−1.8655	−0.0954*	0.0575*	0.0028	−0.00048*	0.00023
CH_4	forest floor ($r^2 = 0.47$), $p < 0.02$	−3.8087	0.2807	0.2537	−0.00875	−0.00242	−0.00008*
	mineral soil ($r^2 = 0.84$), $p < 0.0001$	−2.5179	0.0678	0.1982*	0.00082	−0.00179*	−0.00117

T = temperature (°C); W = % water-holding capacity. Mineral soil = 0–10 cm depth. % Soil organic matter content (loss-on-ignition at 550°C for 24 h) is 63.7 ± 0.9 (SE, $n = 20$) for forest floor and 12.5 ± 0.4 (SE, $n = 20$) for mineral soil. % N = 1.83 ± 0.06 (SE, $n = 10$) for forest floor, 0.31 ± 0.02 (SE, $n = 10$) for mineral soil.
*significant model component ($p < 0.05$).

matter and where particle densities are much closer to 2.65.

The low Q_{10} value (1.11) we observed for CH_4 uptake by the mineral soil is comparable to weak relationships between CH_4 uptake and temperature observed by Born *et al.* (1990), Nesbit and Breitenbeck (1992) and Koschorreck and Conrad (1993).

A second order polynomial regression of CH_4 uptake (by mineral soil) to moisture produced a model with $r^2 = 0.80$. Addition of temperature to the model increased predictability by 5% ($r^2 = 0.84$). This agrees with field work at the Harvard Forest (Bowden *et al.*, 1993), where a multiple linear regression of CH_4 fluxes to temperature and moisture showed that these two factors together strongly predicted CH_4 uptake ($r^2 = 0.80$).

Methane uptake is limited by both biotic and abiotic factors. Work at the Harvard Forest (Castro *et al.*, 1995) and elsewhere (Crill, 1991; Adamsen and King, 1993) found that methane uptake in spring is strongly correlated to soil temperature, but soil moisture is much more closely related to uptake during the growing season. Early in spring, methanotrophs may be metabolically limited by low soil temperatures, but as soils become simultaneously warmer and drier, metabolic limitations are overcome, and uptake activity is then controlled by the ability of CH_4 to diffuse to the active methanotrophic sites in mineral soil (Born *et al.*, 1990; Striegl, 1993; Washington *et al.*, 1994). Reduced consumption under dry conditions was probably due to moisture stress on methanotrophs; soils at 20% WHC were noticeably air-dry. High moisture conditions probably create a physical barrier to gaseous diffusion.

Table 2. Relative change in soil forest floor CO_2 efflux and mineral soil CH_4 uptake for typical summer soil conditions in response to a 20% increase in soil temperature (13 to 15.6°C for forest floor; 10 to 12°C for mineral soil) and a 20% decrease in soil moisture (from 60 to 48% of water-holding capacity)

Condition change	% Change in forest floor CO_2 efflux	% Change in mineral soil CH_4 uptake
Warmer	+21.9	+2.0
Drier	−11.2	+3.6
Warmer and drier	+8.9	+7.0

Implications

We used our models to compare trace gas fluxes during typical summer temperature and moisture conditions to fluxes under conditions of increased soil temperature and decreased soil moisture. We estimated changes in CO_2 effluxes by forest floor material and CH_4 uptake by mineral soil in response to a 20% increase in soil temperature and a 20% decrease in soil moisture, using, as typical conditions, a soil moisture content of 60% water-holding capacity, and a temperature of 12°C for mineral soil and 15°C for forest floor. Under warming conditions alone, both CO_2 emissions and CH_4 uptake increased (Table 2). Under drier conditions, CO_2 emissions decreased, but CH_4 uptake increased. For both CO_2 and CH_4, alteration simultaneously of both variables produced relative changes that were markedly different than the additive response of individual variable changes would have predicted; CO_2 emissions were 17% less than would have been predicted and CH_4 uptake was 25% greater than would have been predicted.

We applied the relative flux changes to typical field flux rates during summer, using a CO_2 efflux of 12.5 mmol CO_2 m^{-2} h^{-1} (Peterjohn *et al.*, 1994), and a CH_4 uptake of 0.010 mmol CH_4 m^{-2} h^{-1} (Castro *et al.*, 1995), and assumed that all CO_2 was emitted by the forest floor and all CH_4 was consumed by mineral soil. We also used a global warming CO_2 equivalent (GWE) of 26 for CH_4 (Lilieveld and Crutzen, 1992). Under typical conditions, combining CO_2 emissions and CH_4 uptake provides a GWE efflux of 12.24 mmol CO_2 m^{-2} h^{-1}. Under warmer and drier conditions, the summer soil GWE flux increases by 1.09 mmol CO_2 m^{-2} h^{-1}. This represents an increase of 8.9% over the current GWE emissions during typical summer soil conditions. Clearly other factors must be considered in producing final estimates as illustrated by Jenkinson *et al.* (1991) and Lloyd and Taylor (1994), but our results indicate that single-factor equations used to predict exchanges in fluxes of greenhouse gases between soils and the atmosphere may be insufficient to predict changes in trace gas fluxes, and that inclusion of both moisture and temperature in models of trace gas fluxes can increase the accuracy of trace

gas budgets and can enhance assessments of trace gas fluxes under models of climate change.

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