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Effects of soil temperature and moisture on methane uptake and nitrous oxide emissions across three different ecosystem types

G. J. Luo[1], **R. Kiese**[1], **B. Wolf**[1,*], **and K. Butterbach-Bahl**[1]

[1]Institute for Meteorology and Climate Research, Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany
[*]current address: EMPA, Dübendorf, Switzerland

Correspondence to: K. Butterbach-Bahl (klaus.butterbach-bahl@kit.edu)

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Abstract. In this paper, we investigate similarities of effects of soil environmental drivers on year-round daily soil fluxes of nitrous oxide and methane for three distinct semi-natural or natural ecosystems: temperate spruce forest, Germany; tropical rain forest, Queensland, Australia; and ungrazed semi-arid steppe, Inner Mongolia, China. Annual cumulative fluxes of nitrous oxide and methane varied markedly among ecosystems, with nitrous oxide fluxes being highest for the tropical forest site (tropical forest: $0.96\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$; temperate forest: $0.67\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$; steppe: $0.22\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$), while rates of soil methane uptake were approximately equal for the temperate forest ($-3.45\,\mathrm{kg\,C\,ha^{-1}\,yr^{-1}}$) and the steppe ($-3.39\,\mathrm{kg\,C\,ha^{-1}\,yr^{-1}}$), but lower for the tropical forest site ($-2.38\,\mathrm{kg\,C\,ha^{-1}\,yr^{-1}}$).

In order to allow for cross-site comparison of effects of changes in soil moisture and soil temperature on fluxes of methane and nitrous oxide, we used a normalization approach. Data analysis with normalized data revealed that, across sites, optimum rates of methane uptake are found at environmental conditions representing approximately average site environmental conditions. This might have rather important implications for understanding effects of climate change on soil methane uptake potential, since any shift in environmental conditions is likely to result in a reduction of soil methane uptake ability. For nitrous oxide, our analysis revealed expected patterns: highest nitrous oxide emissions under moist and warm conditions and large nitrous oxide fluxes if soils are exposed to freeze–thawing effects at sufficiently high soil moisture contents. However, the explanatory power of relationships of soil moisture or soil temperature to nitrous oxide fluxes remained rather poor ($R^2 \leq 0.36$). When combined effects of changes in soil moisture and soil temperature were considered, the explanatory power of our empirical relationships with regard to temporal variations in nitrous oxide fluxes were at maximum about 50 %. This indicates that other controlling factors such as N and C availability or microbial community dynamics might exert a significant control on the temporal dynamic of nitrous oxide fluxes. Though underlying microbial processes such as nitrification and denitrification are sensitive to changes in the environmental regulating factors, important regulating factors like moisture and temperature seem to have both synergistic and antagonistic effects on the status of other regulating factors. Thus we cannot expect a simple relationship between them and the pattern in the rate of emissions, associated with denitrification or nitrification in the soils.

In conclusion, we hypothesize that our approach of data generalization may prove beneficial for the development of environmental response models, which can be used across sites, and which are needed to help achieve a better understanding of climate change feedbacks on biospheric sinks or sources of nitrous oxide and methane.

1 Introduction

Nitrous oxide and methane are two of the most important radiative trace gases in the atmosphere. Since the industrial revolution, the concentration of these greenhouse gases have increased from 270 to 319 ppbv, and from 0.72 to 1.77 ppmv, contributing at present approximately 5 and 12 %, respectively, to observed global warming (Solomon et al., 2007). Soils of natural and semi-natural terrestrial ecosys-

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tems, such as grasslands and forests, are major global sources and sinks/sources of nitrous oxide and methane and thus play an important role in regulating atmospheric concentration of these gases. However, soil–atmosphere exchange of methane and nitrous oxide varies considerably across different terrestrial ecosystem types such as steppe, temperate, and tropical forests (e.g. Breuer et al., 2000; Brumme and Borken, 1999; Dutaur and Verchot, 2007; Pilegaard et al., 2006; Schaufler et al., 2010; Smith et al., 2000; Stehfest and Bouwman, 2006). Differences in plant and soil microbial communities, soil chemistry and physics, management, soil acidification, and atmospheric nitrogen deposition are drivers for site variation in methane and nitrous oxide fluxes. Furthermore, seasonal variability of fluxes is likely to be controlled by soil temperature and moisture and their effects on substrate availability, soil aeration, gas diffusivity, and thus on microbial processes such as mineralization, nitrification, denitrification, methane oxidation, and methanogenesis.

Methane and nitrous oxide are both produced (or consumed) as a result of microbial processes in the soil (Conrad, 1996). In soils, methane can be formed under anaerobic conditions by methanogens. Under aerobic conditions, both methane that has been produced in anaerobic parts of the soil and atmospheric methane diffusing into the topsoil can be oxidized by methanotrophs (Le Mer and Roger, 2001). Nitrous oxide is naturally produced in soils by microbial processes of nitrification and denitrification (Bleakley and Tiedje, 1982; Bowden, 1986).

Soil temperature and water content directly affect production and consumption of these greenhouse gases through their effects on metabolic activity of microorganisms and plants, soil aeration, substrate availability, and redistribution. Effective gas diffusivity, which increases with increased air-filled porosity, controls the exchange of gases between the atmosphere and soil and affects soil aeration. This process indirectly controls the capacity of the soil to produce or consume nitrous oxide and methane. In soils from different ecosystems, moisture and temperature have been identified as key controls on nitrous oxide and methane trace gas production and consumption by many field investigations. Studies in temperate forest (Butterbach-Bahl and Papen, 2002; Castro et al., 1994, 1995; Peterjohn et al., 1994; Wu et al., 2010a) and temperate grassland (Chen et al., 2010; van den Pol-van Dasselaar et al., 1998; Wu et al., 2010b) have revealed strong temporal patterns in nitrous oxide and methane fluxes corresponding closely with seasonal changes in moisture and temperature. Reports on C and N trace gas exchange between tropical rain forest soils and the atmosphere are still limited. However, results from previous experiments at different tropical rain forest sites (Breuer et al., 2000; Butterbach-Bahl et al., 2004; Kiese et al., 2003; Seiler et al., 1984; Teh et al., 2008; Teh and Silver, 2006; Werner et al., 2007a; Yan et al., 2008; Yashiro et al., 2008) indicate that the seasonality of fluxes of methane and nitrous oxide are mainly driven by changes in these two environmental parameters as well. However, to our knowledge there is no study available that comprehensively compares responses of C- and N-trace gas fluxes to changes in temperature and soil moisture across different ecosystem types. The study by Groffman et al. (2000) only evaluates nitrous oxide fluxes across ecosystems at the annual scale, thereby finding that coherent patterns in annual nitrous oxide fluxes at the ecosystem scale in forest, cropland, and rangeland ecosystems exist, but these patterns vary by regions and only emerge with continuous (in a resolution of at least daily) flux measurements over multiple years.

All three investigated ecosystems in this study (temperate forest, semi-arid steppe, and tropical forest) are among the dominating ecosystem types on earth. For instance, emissions of nitrous oxide from tropical rain forest soils are thought to contribute approximately 20 % to the global atmospheric budget of this primary climate-relevant trace gas (Solomon et al., 2007). Assuming that the observed variability of nitrous oxide and methane fluxes at our observation sites may be representative for their ecosystem types and the respective climatic regime, a cross-site comparison of fluxes may help to identify overarching patterns of soil moisture and temperature effects on soil greenhouse gas (GHG) emissions. Specific objectives addressed in this study were (1) to evaluate seasonal variations and event based patterns of methane and nitrous oxide fluxes in three different ecosystem types, (2) to relate temporal changes of GHG fluxes to changes in temperature and moisture for the given ecosystem, and (3) to investigate overarching patterns in GHG fluxes as a response to changes in soil moisture and temperature across the three ecosystem types.

2 Materials and methods

2.1 Study sites

In this study, a cross-site comparison of soil nitrous oxide and methane fluxes, soil temperature, and soil moisture was conducted for three different ecosystems: spruce forest, temperate climate; ungrazed steppe, semi-arid climate; and tropical rain forest, wet tropical climate (with pronounced dry and wet seasons). The main characteristics of the sites are given in Table 1.

Data for temperate forest was obtained from continuous measurements at the Höglwald Forest, a well-studied spruce plantation site in southern Germany, which receives high rates of atmospheric N deposition (20–30 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$) (Luo et al., 2012). Continuous measurements of soil methane and nitrous oxide fluxes were started in November 1993 and were continued since then. For cross-site analysis, we used observational data of the years 1995 and 1997, since these years are typical years with regard to flux magnitudes, seasonal flux patterns, and environmental conditions (Luo et al., 2012). We did not use average values across all observation years, since averaging would have dampened the observed

Table 1. Main characteristics of the different measuring sites.

	Höglwald, Germany[a]	Bellenden Ker, Austalia[b]	UG99, Inner Mongolia, China[c]
Location	11°11′ E 48°30′ N	145°54′ E 17°16′ S	116°40′ E 43°33′ N
Climate (Köppen–Geiger climate classification)[d]	Temperate oceanic climate [Dfb]	Tropical rainforest climate [Af]	Temperate semi-arid climate[Dwb]
Height above sea level (m)	540	80	1268
Annual precipitation (mm)	997 (1995) 627 (1997)	2678 (Nov 2001–Oct 2002)[f]	356 (15 Aug 2007–14 Aug 2008)
Annual temperature (°C)	7.9 (1995) 9.4 (1997)	23.8 (Nov 2001–Oct 2002)[f]	2.1 (15 Aug 2007–14 Aug 2008)
Vegetation type	*Picea abies*	Complex mesophyll vine forest	*Leymus chinensis*
Slope (°)	–	9.0–12.0	2.2–2.7
Soil parent material	Pleistocene loess over tertiary sand deposits	Granite	Loess
Soil parameters (0–10 cm mineral soil)			
Soil type	Typic Hapludalf	Ustochrept	Calcic Chernozem
pH ± SE	3.59	4.1 ± 0.03 [f]	6.8 ± 0.27 [f]
Bulk density (g cm^{-3}) ± SE	1.033 ± 0.05	1.09 ± 0.03	1.09 ± 0.12
C : N ratio	19	12.1	9.7 ± 0.7[e]
Organic C content (%)	1.91	3.11	2.55 ± 0.63
Soil texture (%)[d]			
Sand	50-64	57	48.3
Silt	30–38	21	25.8
Clay	5–11	22	25.9

[a] Kreutzer (1995); Rothe et al. (2002); Butterbach-Bahl et al. (2002); Luo et al. (2012).
[b] Kiese und Butterbach-Bahl (2002).
[c] Compiled from data from Chen et al. (2010) and Liu et al. (2007).
[d] Peel et al. (2007).
[e] 0–4 cm soil depth.
[f] Kiese et al. (2003).
"–" not determined.
[Dfb] Warm summer (dry winter) climate.
[Af] Tropical rainforest climate.
[Dwb] Warm summer climate (with dry season).

response of microbial processes involved in soil–atmosphere CH$_4$ and N$_2$O exchange to changes in soil temperature and moisture. High soil-thawing nitrous oxide fluxes occur occasionally at the Höglwald site (approximately every third year, Luo et al., 2012). In order to consider such irregular events in our cross-site data analysis, we randomly chose 365 observation days from the years 1995 and 1997 to form a new, more representative dataset for this site. For the specific site analysis (e.g. Table 2), all data obtained in both years were considered, whereas for cross site comparison a synthetic dataset was derived by randomly selecting 50 % of data for the year 1995 and 50 % of data from the year 1997. Daily precipitation and air temperature at 2 m above ground level for 1995 and 1997 were obtained from the German Weather Service station Augsburg-Mühlhausen, which is about 20 km northwest from the Höglwald Forest site. Soil temperature at 5 cm soil depth was measured every minute by PT100 probes (IMKO GmbH, Germany) in close vicinity to the chambers (Values at 10 cm are not available across the entire observation period.). Hourly soil moisture measurements were carried out with horizontally installed TDR probes (IMKO GmbH, Germany, or UMS, Germany) at 10 cm soil depth. Due to instrumental failure and removal of the soil moisture sensors, in situ soil moisture measurements were not available for 1997. To fill this gap, a machine-learning technique, known as support vector machine (SVM), was employed (for details see Luo et al., 2012).

Table 2. Flux rates of nitrous oxide and methane from soils of each land use type as observed for all temperature and moisture conditions. Annual cumulative values are summed after linear interpolation. All parameters are significantly ($p < 0.05$) different between sites.

Land use types	Höglwald (1997)	Höglwald (1995)	Rain forest	Steppe
Mean soil temperature (°C)	6.9 ± 0.2	7.2 ± 0.3	22.33 ± 0.2	4.95 ± 0.6
Mean volumetric water content (vol %)	29.1 ± 0.2	33.0 ± 0.2	22.09 ± 0.5	13.51 ± 0.5
Annual methane uptake (kg CH_4-C ha^{-1} yr^{-1})	−3.45	−2.79	−2.38	−3.39
Annual nitrous oxide emission (kg N_2O-N ha^{-1} yr^{-1})	0.67	0.82	0.96	0.22

Nitrous oxide and methane fluxes of the tropical rain forest site were obtained at a site in the coastal lowlands of the "Wet Tropics", Queensland, Australia, approximately 70 km south of Cairns. Plant biodiversity is relatively high with over 130 plant species including 63 different kinds of trees occurring in a defined plot of 20 m by 50 m, and thus comparable to many of the lowland rain forests in South East Asia (Kiese et al., 2003). For further information about site properties, see Kiese and Butterbach-Bahl (2002) and Table 1. In this study, we used a full year dataset on nitrous oxide emissions and methane uptake as recorded for the period from 1 November 2001, to 31 October 2002. Details of the measuring system and modes of calibration have already been described by Kiese and Butterbach-Bahl (2002), and Kiese et al. (2003). Measurements of climate parameters were recorded by an on-site climate station. In this study, daily air temperature and rainfall data were used to simulate soil moisture (vol %) and soil temperature time series for 10 cm soil depth – which were only sporadically recorded - by the ForestD-NDC (DeNitrification-DeComposition)-tropica model. Simulated soil moisture and soil temperature values agreed with observed data by ±3 % WFPS (water-filled pore space) or ±1 °C, respectively. The model itself has been successfully evaluated for this site for its predicting capability with regard to nitrous oxide fluxes and soil environmental conditions in earlier studies (Kiese et al., 2005; Werner et al., 2007b).

Nitrous oxide and methane flux data for temperate semi-arid steppe were obtained at a site in the Xilin River catchment near the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Ecosystem Research Network. Additional details of the site are provided by Liu et al. (2007), Chen et al. (2010, 2011) and in Table 1. The full year dataset on methane and nitrous oxide fluxes was obtained in the period of time between 15 August 2007 and 15 August 2008. Details on flux measurements can be found in Wolf et al. (2010) and Chen et al. (2010). Soil temperature (at 5 cm soil depth) as well as volumetric water content of the topsoil (at 0–6 cm soil depth) were continuously recorded in 1 min intervals using PT100 thermocouples (Th2-h; UMS GmbH, Munich, Germany) or ECH2O FD probes (Decagon Devices, Pullman, WA, USA), respectively. During the wintertime, when soil temperatures dropped below zero degree, topsoil (at 0–5 cm soil depth) samples were taken at least twice a week for the determination of volumetric water content.

Flux data as well as measurements of soil moisture/ soil temperature at all sites were obtained in subdaily resolution either in approx. 2-hourly (fluxes) or in even shorter time intervals (temperature/moisture). In this study we only use daily average values.

2.2 Statistics

The software packages SPSS 8.0 (SPSS Inc., Chicago, USA) and SigmaPlot 10.0 (Systat Software Inc., Chicago, USA) were used for statistical data analysis. Annual methane and nitrous oxide fluxes represent the amount of cumulative uptake and emission using a linear interpolation approach. As each site is subject to different climate and site characteristics (see Introduction and Materials and methods), different averages and ranges of fluxes, soil temperature, and moisture were observed. Therefore, flux (nitrous oxide and methane) as well as environmental data (soil temperature and moisture) for each study site were normalized to values ranging between 0 and 1 in Origin 7.0 (Origin Lab Corporation, USA) before exploring relationships between trace gas fluxes and both soil moisture and temperature to allow a comparison across these different sites. Note that before normalization of methane uptake rate values were multiplied by (−1).

3 Results

3.1 Temporal variability of climate, methane uptake, and nitrous oxide emission

All three sites have shown a pronounced seasonal variability in soil temperature and moisture (Figs. 1–3). The seasonal variability in soil temperature conditions was highest for the steppe site in Inner Mongolia (Figs. 2, 4) with a minimum of −11.3 °C (January 29, 2008) and a maximum of 25.6 °C (July 19, 2008) at a soil depth of 5 cm. Variability of

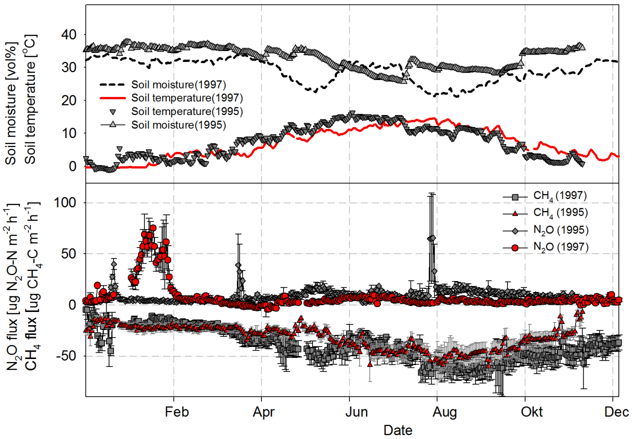

Fig. 1. Seasonal variability of daily average soil volumetric water content (at 10 cm depth) and soil temperature (at 5 cm depth) as well as of soil nitrous oxide and methane fluxes at the Höglwald Forest site in the years 1995 and 1997.

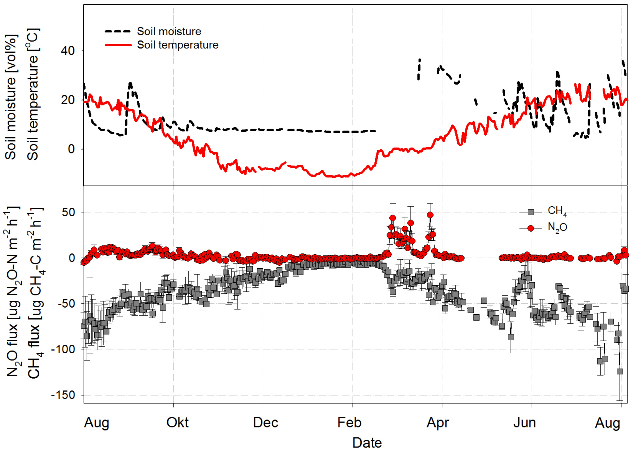

Fig. 2. Seasonal variability of daily average soil volumetric water content (at 0–6 cm depth) and soil temperature (at 5 cm depth) as well as of soil nitrous oxide and methane fluxes at the semi-arid steppe site in Inner Mongolia for the period 15 August 2007 to 15 August 2008.

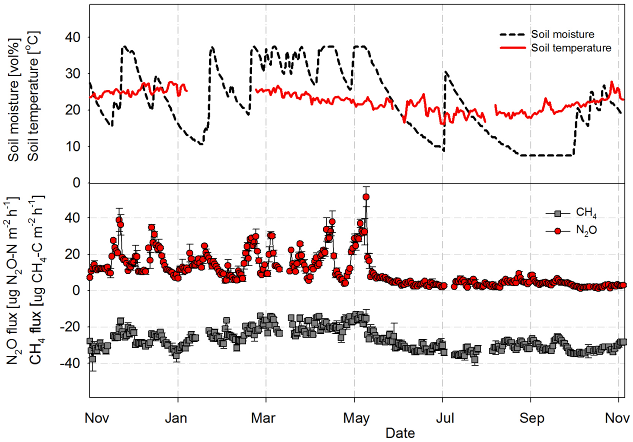

Fig. 3. Seasonal variability of daily average soil volumetric water content (at 10 cm depth) and soil temperature (at 10 cm depth) as well as of soil nitrous oxide and methane fluxes at the tropical forest site Bellenden Ker, Queensland, Australia, for the period 2 November 2001 to 31 October 2002.

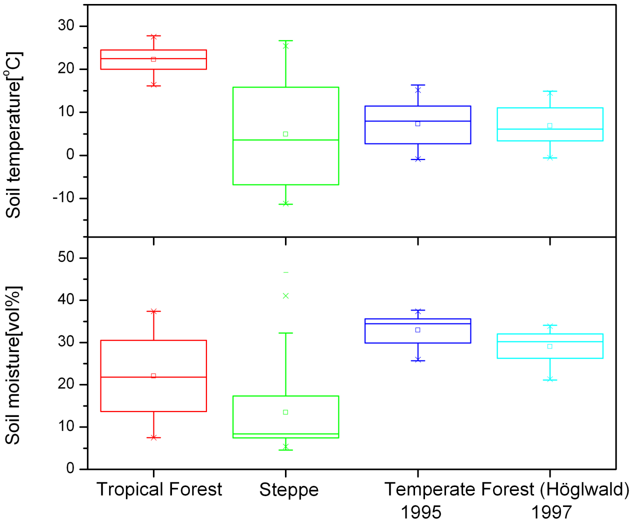

Fig. 4. Box plot of average daily soil volumetric water content and soil temperature for the three investigated ecosystem types: tropical forest, semi-arid steppe, and temperate forest (Höglwald forest: data both in years 1995 and 1997). The boxes are determined by 25th and 75th percentiles. The whiskers are determined by the 5th and 95th percentiles. Additional values can be represented in box chart, including the minimum and maximum (dashes), median (line in the box), mean (square), 1st percentile and 99th percentiles (crosses)

soil temperature (11 °C at a soil depth of 10 cm) was lowest for the tropical rainforest site at Bellenden Ker (Figs. 3, 4) with minimum values of 16 °C. However, variability of soil moisture was significantly higher at the tropical forest site (soil volumetric water content: 7.5 % to 37.4 % at 10 cm soil depth), but lowest for the temperate spruce forest site at Höglwald Forest (soil volumetric water content: 21.1 % to 31.1 % at 10 cm soil depth in the year 1997) (Figs. 1–4).

The pronounced variability in soil environmental conditions was mirrored by an evident variability in soil nitrous oxide and methane fluxes. Figures 1–3 show that at the temperate forest site as well as at the semi-arid steppe site, highest nitrous oxide fluxes were observed during the spring-thaw period (temperate forest up to 80 µg N m^{-2} h^{-1}; steppe up to 50 µg N m^{-2} h^{-1}). However, during the vegetation period, hardly any variability of nitrous oxide fluxes was observed (Figs. 1, 2). In contrast, nitrous oxide fluxes at the tropical forest site were obviously linked to changes in soil moisture (up to 50 µg N m^{-2} h^{-1} in the wet season) and were between 5 and 10 µ N m^{-2} h^{-1} during the dry season from May 2002 to November 2002 (Fig. 3).

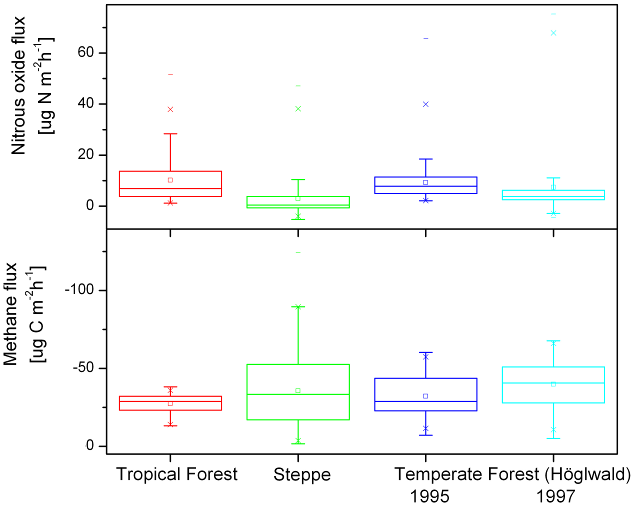

Fig. 5. Box plot of daily average soil nitrous oxide and methane fluxes in tropical forest, semi-arid steppe, and temperate forest (Höglwald: data from both years 1995 and 1997). The boxes are determined by 25th and 75th percentiles. The whiskers are determined by the 5th and 95th percentiles. Additional values can be represented in box chart, including the minimum and maximum (dashes), median (line in the box), mean (square), 1st percentile and 99th percentiles (crosses).

Methane uptake at the semi-arid steppe and temperate forest sites in general followed the course of soil temperature with maximum uptake rates in summer (steppe: $-125\,\mu g\,C\,m^{-2}\,h^{-1}$; temperate forest: $-70\,\mu g\,C\,m^{-2}\,h^{-1}$). This seasonality was modified by changes in soil moisture, with periods of high soil moisture values leading to lower methane uptake rates. For the tropical forest site, an effect of soil temperature on methane uptake is not directly visible. Rather, uptake rates are mainly linked to changes in soil moisture with the highest rates of methane uptake ($-40\,\mu g\,C\,m^{-2}\,h^{-1}$) during the dry period from May to November 2002.

Besides differences in the seasonality and dynamics of methane and nitrous oxide fluxes to changes in soil environmental conditions, there were also distinct differences in the overall magnitude of observed fluxes across the three study sites. Annual cumulative nitrous oxide fluxes for the different ecosystems varied at a range of 0.2–1.0 kg N_2O-N $ha^{-1}\,yr^{-1}$ and were decreasing in the following sequence: tropical rainforest > temperate forest ≫ semi-arid steppe (Table 2). Soil methane uptake rates varied at a range of −2.4 to −3.5 kg CH_4-C $ha^{-1}\,yr^{-1}$ in the following sequence: temperate forest ≈ semi-arid steppe > tropical forest (Table 2).

A comparison of soil nitrous oxide and methane flux characteristics for the three investigated ecosystems is presented in Fig. 5. For the semi-arid steppe, the largest variations in methane oxidation rates were observed, whereas the annual variability of methane uptake was lowest for the tropical rainforest site. In contrast to the variability of methane uptake, the nitrous oxide flux variability was highest for the tropical rainforest site. However, in the semi-arid steppe and temperate forest ecosystems distinct peak emissions were observed during freezing and thawing periods.

3.2 Effects of soil temperature and moisture on methane and nitrous oxide fluxes

Combined effects of soil moisture and temperature on methane and nitrous oxide fluxes are depicted in Figs. 6–8. The contour graphs for nitrous oxide (Fig. 6) show that maximum nitrous oxide fluxes at the temperate forest and semi-arid steppe sites were observed during freeze–thaw periods when the soil was cold but wet. When the freeze–thaw periods were excluded (Fig. 7), highest nitrous oxide fluxes occurred during warm and wet periods in the temperate forest, and during warm and dry periods (following a few days after rainfall events (data not shown)) at the steppe site. Due to a weak correlation of nitrous oxide fluxes with soil temperature, highest emissions in the tropical rainforest were generally observed at high soil moisture, independent of the soil temperature (Fig. 7).

In both the tropical rain forest and temperate forest sites, changes in soil temperature and moisture were controlling methane uptake rates (Fig. 8). While at the temperate forest site maximum uptake rates were clearly associated with lowest soil moisture and highest soil temperature, methane uptake rates at the tropical forest site showed a bimodal distribution (Fig. 8). The first optimum was in line with observations for the temperate forest, i.e. high soil temperature and low soil moisture. However, a second optimum with even higher methane uptake rates was found for conditions with comparable lower soil temperatures and slightly elevated soil moisture (normalized values of soil temperature and moisture of approximately 0.4). For the semi-arid steppe site, contour lines are running approximately parallel to the y-axis, which represents the soil moisture vector. This shows that a significant effect of soil moisture changes on methane uptake rates is not visible, at least for the range of soil moisture conditions underlying this analysis.

Regression analyses using normalized data has shown for all sites that combined changes in soil temperature and soil moisture exert a stronger control on methane uptake (R^2 values: 0.67–0.77; Table 3) as on nitrous oxide emission (R^2 values: 0.19–0.41; Table 4). However, if soil moisture and temperature effects on nitrous oxide fluxes are analysed for freeze–thaw periods (only 1997 dataset for the temperate forest site and the steppe dataset), the predicting power of a simple soil moisture–soil temperature relationship for nitrous oxide fluxes increases remarkably (R^2: 0.71–0.77) (Table 5).

Table 3. Temperature and moisture control on methane fluxes.

Predictors	Ecosystems	Functions	a	b	c	$x0$	$y0$	n	R^2
soil temperature (T)	steppe	*Gaussian:* $f = a \times \exp(-,5 \times ((T - x0)/b)^2) \times (-1)$	0.50***	0.56***		1.05***		259	0.71***
	rain forest		–	–		–		–	–
	temperate forest		0.66***	0.51***		0.83***		300	0.49***
soil moisture (M)	steppe	*Gaussian:* $f = a \times \exp(-0.5 \times ((M - x0)/b)^2) \times (-1)$	0.45***	0.24***		0.36***		259	0.22***
	rain forest		0.77***	0.47***		0.25***		277	0.67***
	temperate forest		0.88***	0.54***		–0.0036		300	0.70***
soil temperature (T), soil moisture (M)	steppe	*Gaussian:* $f = a \times \exp(-,5 \times (((T - x0)/b)^2 + ((M - y0)/c)^2)) \times (-1)$	0.54***	0.52***	1.17	0.99***	−0.23	259	0.73***
	rain forest		2.73	11.19	0.45***	−17.27	0.27***	277	0.67***
	temperate forest		0.92***	0.55***	0.65***	0.67***	−0.067	300	0.77***

*** $p < 0.0001$.
– no significant regression results.

Table 4. Temperature and moisture control on nitrous oxide fluxes. Note that for these analyses, freeze and thaw periods were excluded (steppe and temperate forest site 1997).

Predictors	Ecosystems	Functions	a	b	c	$x0$	$y0$	n	R^2
soil temperature (T)	steppe	$f = a \times \exp(-,5 \times ((T - x0)/b)^2)$	0.48***	0.42***		0.58***		241	0.28***
	rain forest		0.27***	0.29***		0.76***		290	0.21***
	temperate forest		0.54***	0.97*		1*		262	0.13***
soil temperature (T)	steppe	$\ln(f) = aT + x0$	0.17***			0.57***		241	0.15***
	rain forest		−0.57***			0.77***		290	0.33***
	temperate forest		0.13***			0.70*		262	0.10***
soil moisture (M)	steppe	$\ln(f) = b \times M + y0$		–			–	241	–
	rain forest			−0.36***			0.65***	290	0.28***
	temperate forest			–			–	262	–
soil temperature (T), soil moisture (M)	steppe	$\ln(f) = a \times T + b \times M + y0$	0.23***	−0.18**			0.59***	241	0.19***
	rain forest		−0.41***	−0.22***			0.80***	290	0.41***
	temperate forest		0.25***	0.20***			0.52***	262	0.21***

–: no significant regression results.
***: $p < 0.0001$, **: $p < 0.001$, *: $p < 0.05$.

3.3 Ecosystem cross-comparison of fluxes and drivers

For cross-comparison of ecosystems we used the normalized data as shown in Figs. 9–11. Using all data, including nitrous oxide fluxes during freeze–thaw periods, the cross-ecosystem analysis reveals that two optima for high nitrous oxide emissions exist: (a) for warm and moist conditions and (b) for wet and cold conditions (Fig. 9). Excluding freeze–thaw nitrous oxide emissions from the cross-ecosystem analysis reveals that maximum nitrous oxide fluxes are unequivocally associated with warm and wet soil conditions (Fig. 10).

The contour plot for methane uptake fluxes with normalized data from all three ecosystems (Fig. 11) shows that the highest methane uptake rates can be expected for average annual soil environmental conditions. The highest uptake rates were predicted for soil temperature conditions representing 50–70 % (0.5–0.7 in Fig. 11) of the observed temperature range at a given site or 30–50 % (0.3–0.5 in Fig. 11) with regard to soil moisture.

4 Discussion

4.1 Controls of nitrous oxide emission

Nitrous oxide is mainly a product of two key nitrogen cycling processes in soil: nitrification (the oxidation of ammonium to nitrite and nitrate) and denitrification (the reduction of nitrate and nitrite to nitric oxide, nitrous oxide, and dinitrogen). The magnitude of fluxes largely depends on soil environmental conditions, with temperature and soil moisture, besides substrate availability, being major determinants. For the years being evaluated here, annual nitrous oxide fluxes were highest for the rainforest site (0.96 kg N $\mathrm{ha^{-1}\,yr^{-1}}$), somewhat lower for the atmospheric N deposition affected temperate forest site Höglwald (0.67 kg N $\mathrm{ha^{-1}\,yr^{-1}}$), and lowest for the steppe site in Inner Mongolia (0.22 kg N $\mathrm{ha^{-1}\,yr^{-1}}$). The mentioned annual emission rates are within the range of reported nitrous oxide fluxes for the specific ecosystem types (see e.g. for tropical forests: Breuer et al., 2000; temperate forests: Bouwman et al., 1995; Brumme and Beese, 1992; and steppe ecosystems: Galbally et al., 2008).

Table 5. Regression results between nitrous oxide fluxes and both soil temperature and soil moisture for freeze and thaw periods as observed in the dataset of the steppe site and the temperate forest site (only in the dataset of the year 1997).

Predictors	Ecosystems	Functions	a	b	c	$x0$	$y0$	n	R^2
soil temperature (T)	steppe	$f = a \times \exp(-,5 \times ((T - x0)/b)^2)$	0.71***	0.15***		0.25***		27	0.54***
	temperate forest		0.87***	0.19***		0.33***		81	0.50***
soil moisture (M)	steppe	$f = a \times \exp(-,5 \times ((M - x0)/b)^2)$	0.93***	0.36***		0.88***		27	0.7***
	temperate forest		0.92*	0.35*		−0.07		81	0.32***
soil temperature (T), soil moisture (M)	steppe	$f = a \times \exp(-,5 \times (((T - x0)/b)^2 + ((M - y0)/c)^2))$	1.05**	0.20**	0.54*	0.27***	1.01 *	27	0.77***
	temperate forest		1.18***	0.21***	0.31***	0.27***	0.23***	81	0.71***

– no significant regression results.
*** $p < 0.0001$, ** $p < 0.001$, * $p < 0.05$.

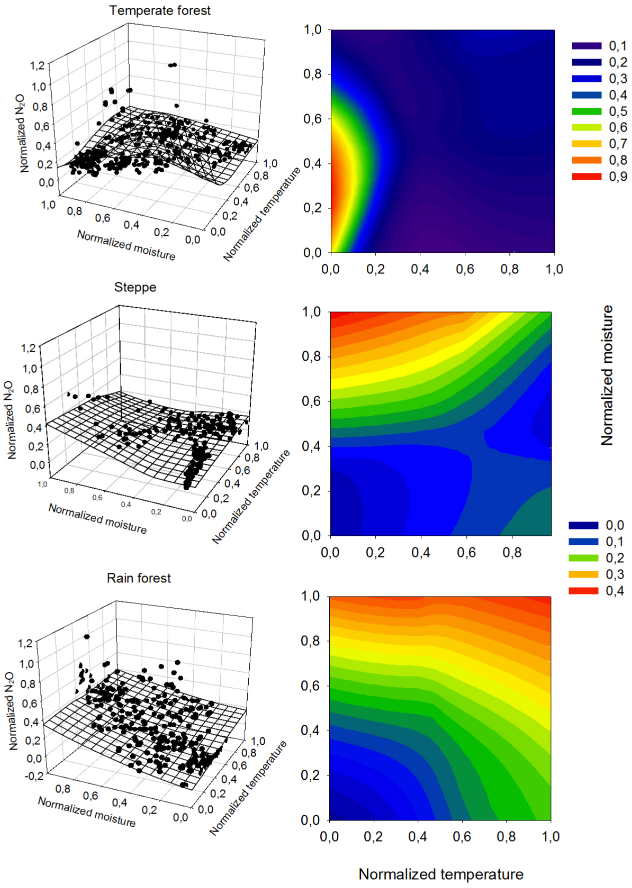

Fig. 6. Temperature and moisture effects on soil nitrous oxide fluxes for the three different ecosystems (temperate forest, semi-arid steppe, and tropical rain forest). Freeze and thaw periods were included. For this analysis nitrous oxide fluxes, soil temperature, and moisture data were normalized at site scale to a range of 0–1 (0: lowest observed value; 1: highest observed value). Nitrous oxide data for Höglwald Forest were randomly selected from observations in the years 1995 and 1997. Prior to the calculation of contour lines, data were smoothed with the loess algorithm or negative exponential algorithm (sampling proportion 0.6–1.0).

Soil nitrous oxide fluxes have been observed to increase exponentially with soil temperature (Brumme, 1995; Dinsmore et al., 2009; Schindlbacher et al., 2004; Smith et al., 2003), which can be explained by a combination of an expansion in anaerobic zones triggered by the acceleration of soil respiration, the increasing denitrification rate per unit of anaerobic volume (Smith et al., 2003), and the temperature sensitivity of the underlying enzymatic processes. Accordingly, moisture effects on soil nitrous oxide fluxes are a result of the limitations of O_2 diffusion into the soil and expansion of soil anaerobiosis, which in turn promotes reductive microbial processes such as denitrification. At our temperate forest site, temperature and moisture effects were both important with regard to inducing temporal changes in nitrous oxide fluxes. For the steppe site, temperature was the dominant driver, and for the tropical forest site soil moisture was the dominant driver of the daily variability in nitrous oxide fluxes (Fig. 7, Table 4). However, the explanatory power of relationships of soil moisture or soil temperature to nitrous oxide fluxes remained rather poor ($R^2 \leq 0.33$). Even for the tropical forest site in our study, combined changes in soil moisture and soil temperature could only explain less than 50 % of the observed temporal variations in nitrous oxide fluxes, indicating that other controlling factors such as N and C availability (e.g. Morley and Baggs, 2010; Pilegaard et al., 2006) or microbial community dynamics (e.g. Regan et al., 2011) exert a significant control on the temporal dynamic of nitrous oxide fluxes as well. This lack of predictive power of simple relationships between environmental drivers and nitrous oxide fluxes for long-period datasets, spanning at least one year, has been observed for other natural and semi-natural systems as well, e.g. for temperate humid grassland systems in Germany (Kammann et al., 2008), prairie systems in North America (Mosier et al., 1996) or a mixed forest in a mountainous region in Austria (Kitzler et al., 2006). This represents that important regulating factors such as moisture and temperature might have both synergistic and antagonistic effects on the status of other regulating factors. Thus we cannot expect a simple relationship between them and the pattern in the rate of emissions associated with denitrification or nitrification in the soils. For shorter observation periods, in our case nitrous oxide fluxes during freeze–thaw periods, stronger, non-linear correlations – specifically between nitrous oxide fluxes and soil moisture – can be found

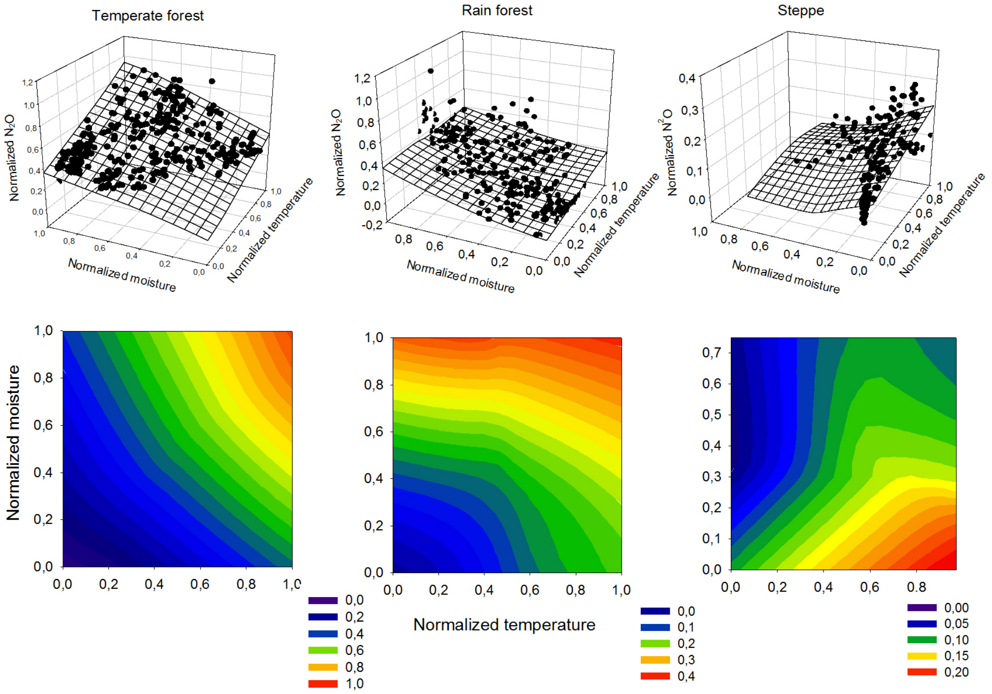

Fig. 7. Temperature and moisture effects on soil nitrous oxide fluxes for the three different ecosystems (temperate forest, semi-arid steppe, and tropical rain forest). For this analysis nitrous oxide fluxes, soil temperature, and moisture data were normalized at site scale to a range of 0–1 (0: lowest observed value; 1: highest observed value). Nitrous oxide data for the Höglwald Forest were randomly selected from observations in the years 1995 and 1997, though for this analysis nitrous oxide fluxes during the freeze–thaw period was excluded. Prior to the calculation of contour lines, data were smoothed with the loess algorithm (sampling proportion = 1).

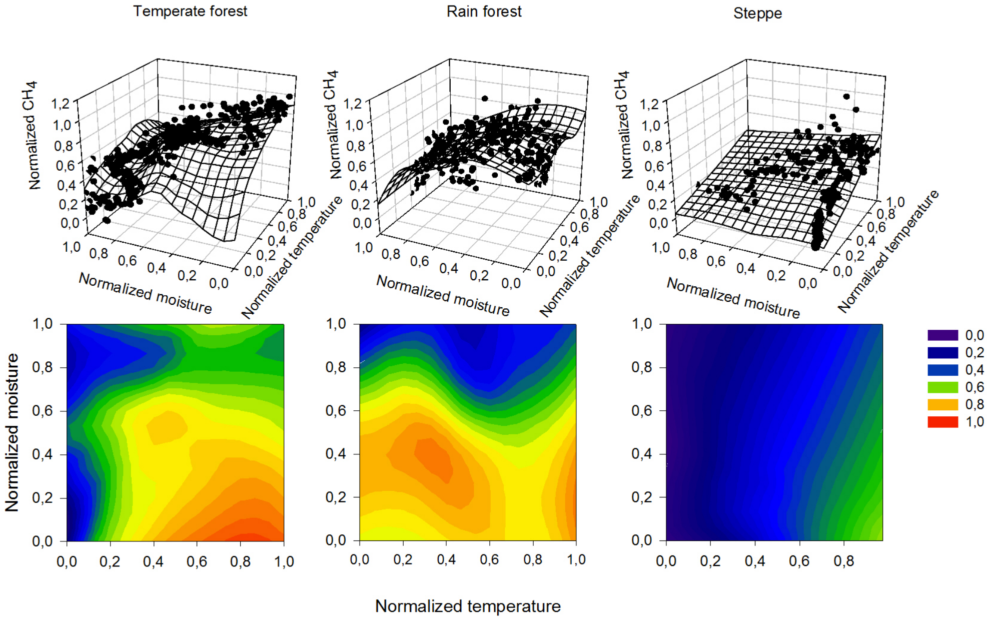

Fig. 8. Temperature and moisture effects on soil methane uptake rates for the three different ecosystems (temperate forest, semi-arid steppe, and tropical rain forest). For this analysis methane flux, soil temperature, and moisture data were normalized at site scale to a range of 0–1 (0: lowest observed value; 1: highest observed value). Prior to the calculation of contour lines, data were smoothed with the loess algorithm or negative exponential algorithm (sampling proportion 0.3–0.6).

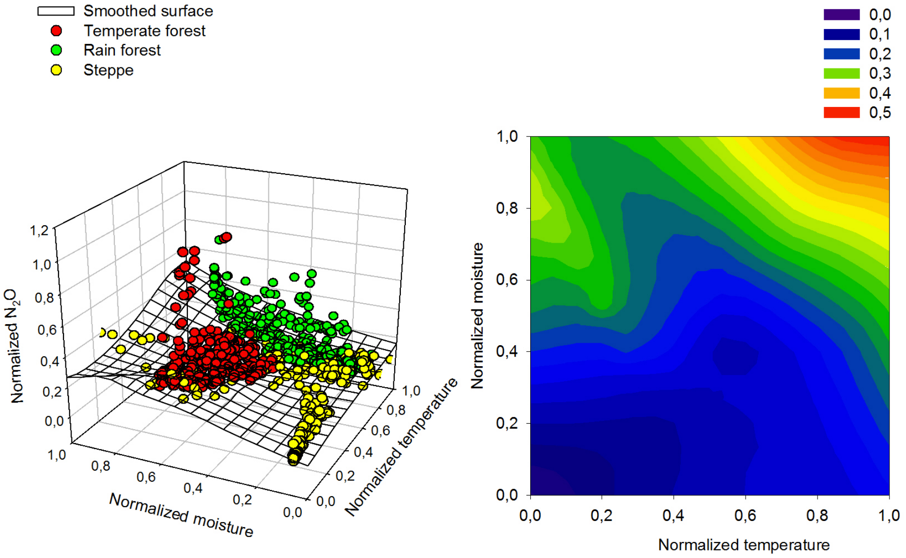

Fig. 9. Temperature and moisture effects on nitrous oxide fluxes (all data) across all three ecosystems (temperate forest, semi-arid steppe, and tropical forest). For this analysis soil moisture and soil temperature as well as nitrous oxide fluxes were first normalized across ecosystems to a range of 0–1 (0: lowest observed value in all ecosystems; 1: highest observed value in all ecosystems). Prior to the calculation of contour lines, data were smoothed with the loess algorithm (sampling proportion = 0.6). Data for temperate forest were randomly selected from observations in the years 1995 and 1997.

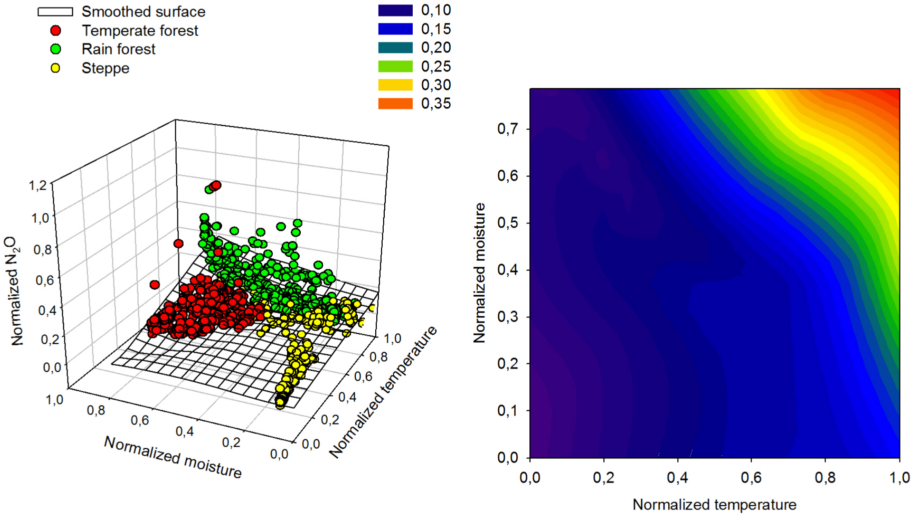

Fig. 10. Temperature and moisture effects on nitrous oxide fluxes (data for freeze–thaw periods at the temperate forest and steppe sites excluded) across all three ecosystems (temperate forest, semi-arid steppe, tropical forest). For this analysis soil moisture and soil temperature as well as nitrous oxide fluxes were normalized across ecosystems (see Fig. 9). Prior to the calculation of contour lines, data were smoothed with the loess algorithm (sampling proportion = 0.5). Data for temperate forest were randomly selected from observations in the years 1995 and 1997.

(Table 5). Stronger correlations were also found when models with combined soil moisture and soil temperature were tested, a result that is in agreement with observations of soil nitrous oxide fluxes from a mixed forest in Austria (Kitzler et al., 2006).

4.2 Controls of methane uptake

Depending on climate, soil, ecosystem type, land use/management, all having impacts on soil aeration, oxygen, and methane availability, soils can either function as an atmospheric sink or source of methane (Topp and Pattey, 1997). The total sink strength of terrestrial ecosystems is

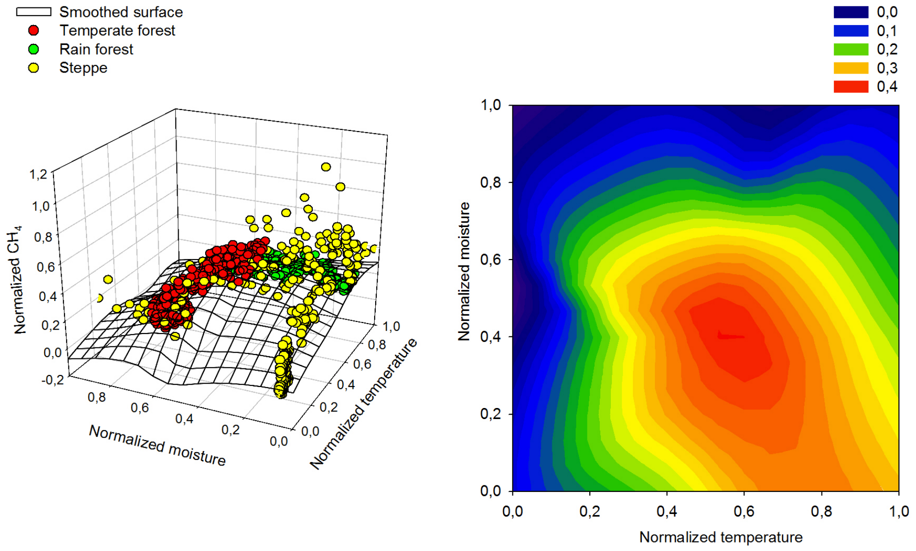

Fig. 11. Temperature and moisture effects on methane uptake fluxes across all three ecosystems (temperate forest, semi-arid steppe, and tropical forest). For this analysis, soil moisture and soil temperature as well as methane uptake flux data were normalized across ecosystems (see Fig. 9). Prior to the calculation of contour lines, data were smoothed with the loess algorithm (sampling proportion = 0.5). Data for temperate forest were randomly selected for the observation years 1995 and 1997.

estimated to be approximately 15–45 Tg yr^{-1}, which roughly equals the increase of atmospheric methane concentrations during the 1990s (Dutaur and Verchot, 2007). Observations that upland temperate and tropical forest as well as steppe soils serve as significant sinks for atmospheric methane have been confirmed in a large number of studies (Keller et al., 1983; Mosier et al., 1991; Seiler et al., 1984; Steudler et al., 1989; Whalen and Reeburgh, 1990). Topp and Pattey (1997) as well as Dutour and Verchot (2007) summarized representative methane fluxes for various ecosystem types including desert, temperate forest, tropical forest, and grass pasture. In their studies, annual uptake rates typically ranged from 0 to approximately -20 kg CH$_4$-C ha^{-1} yr^{-1} (mean: temperate forest: -4.28 kg CH$_4$-C ha^{-1} yr^{-1}; tropical forest: -2.50 kg CH$_4$-C ha^{-1} yr^{-1}; grassland: -1.74 kg CH$_4$-C ha^{-1} yr^{-1}) (Dutaur and Verchot, 2007). However, it still needs to be noted that most of these estimates are based on low measuring frequencies, often not covering a total year, which introduces high uncertainty to the estimation of annual uptake rates of methane. Values from our year-round observation in different ecosystems showed annual uptake of -3.45 kg CH$_4$-C ha^{-1} yr^{-1} (1997) and -2.79 kg CH$_4$-C ha^{-1} yr^{-1} (1995) for the temperate forest, -2.38 kg CH$_4$-C ha^{-1} yr^{-1} for the rain forest site, and -3.39 kg CH$_4$-C ha^{-1} yr^{-1} for the semi-arid steppe site. Annual fluxes are thus within (temperate and tropical forests) or at the high end (steppe) of previously published data for these ecosystem types.

Environmental controls of atmospheric methane uptake by soils have been assessed in many studies. For non-arable upland soils, (e.g. grassland or forest soils; Bowden et al., 1998; Castro et al., 1994, 1995; Dunfield et al., 1995; Koschorreck and Conrad, 1993; van den Pol-van Dasselaar et al., 1998; Whalen and Reeburgh, 1996; Yavitt et al., 1995), temperature, soil gas permeability, and N availability were identified to be the primary controlling factors. Though atmospheric N deposition may also affect the methane uptake potential of a given site, specifically at the Höglwald Forest (Butterbach-Bahl and Papen, 2002), due to the ability of methanotrophic bacteria for NH$_4^+$ oxidation resulting in an inhibition of methane oxidation at elevated soil NH$_4$ levels (Castro et al., 1995), this parameter is of little interest in the frame of this study with focus on a cross comparison of temporal controls of methane uptake for the three contrasting ecosystem types in this study.

Gas diffusion to the sites of actual methanotrophic activity, often found at 5–15 cm soil depth (Henckel et al., 2000; Roslev et al., 1997), has been identified for forest as well as for grassland ecosystems as the major rate-limiting step of methane uptake (Le Mer and Roger, 2001; Smith et al., 2003). Gas diffusion is controlled by site properties such as soil bulk density (Fujikawa and Miyazaki, 2005), soil structural features such as effective pore length and gas permeability (Liu et al., 2007), and the thickness and structure of the organic layer covering the mineral topsoil where methanotrophic activity is highest (Brumme and Borken, 1999). While the mentioned factors can be used to explain site differences in methane uptake activity between different forest types (Brumme and Borken, 1999; Butterbach-Bahl and Papen, 2002), seasonal variations in uptake activity have often been observed to be closely linked to soil moisture and the effect of soil moisture on soil gas permeability (e.g. incubation experiment: Bowden et al., 1998; Dunfield et al., 1995; Koschorreck and Conrad, 1993; van den Pol-van Dasselaar et al., 1998; Whalen and Reeburgh, 1996; e.g. field measurements: Castro et al., 1994, 1995; Yavitt et al., 1995).

Both at low and high soil moisture contents, methane uptake capacity may be suppressed, either by physiological water stress of methanotrophs or by restriction of diffusive methane and O_2 transport (Del Grosso et al., 2000). The optimum soil water content for methane uptake is thought to reflect the balance between gas transport rates and physiological water stress. A further increase of soil moisture content may also increase soil methane production due to an increasing proportion of anaerobic sites (Butterbach-Bahl and Papen, 2002; Yavitt et al., 1995). At all of our sites, a close link of methane uptake to soil moisture fluctuations could be demonstrated. This was strongest for temperate forest (Table 3) and less pronounced at the steppe site. Since topsoil bulk densities are not significantly different across sites (Table 1), this can be explained best by the rather low amount of precipitation at the investigated steppe site (approximately 330 mm – the site with the lowest topsoil soil moisture), which seldom was sufficient to result in soil moisture levels critical for limiting gas diffusion (Table 2). At our temperate forest as well as at the rain forest site, oxidation of methane was hampered when soil moisture was higher than 60 % of the moisture range (Fig. 8), which converted to WFPS values equals 44 and 43 %, respectively. This threshold value is comparable to a study by Sitaula et al. (1995) who found in their study on methane uptake by soils at a 100 yr-old Scots pine forest in Norway that an increase in soil moisture from 32 to 42 vol % resulted in a significant reduction of methane uptake. However, for Scottish woodland soils (Dobbie and Smith, 1996; Smith et al., 2000) with a sandy texture and a high porosity, oxidation rates were still high even at 80 % WFPS, indicating that site specific soil properties and soil gas diffusion potentials control soil moisture thresholds for optimal CH_4 uptake.

Rates of soil methane uptake increase with increasing soil temperature due to the temperature sensitivity of the underlying enzymatic process. This has been demonstrated in various field and laboratory studies (e.g. Bowden et al., 1998; Butterbach-Bahl and Papen, 2002; Steinkamp et al., 2001). Although temperature effects may be most pronounced for soil temperature $< 15\,^{\circ}C$, at higher temperatures gas diffusion limitations and drought effects may override temperature responses (e.g. Steinkamp et al., 2001). This explains why in our study only a weak effect of temperature on methane uptake could be found for the tropical forest, while the temperature effect is most pronounced at the steppe site (Table 3). For the latter site, the pronounced seasonality of methane uptake is thus a combination of temperature dependency (during autumn, winter and spring) and diffusion limitations due to occasional rainfall events and drought effects during prolonged periods limiting methanotrophic activity.

4.3 Across-ecosystem commonalities

In our across-ecosystem analyses as well as in our analyses on site scale we used daily average values of N_2O and CH_4 fluxes and soil moisture and temperature for the different sites to identify relationships between environmental drivers and soil N_2O and CH_4 fluxes. It should be noted that a further aggregation at weekly or monthly timescales will likely result in a weakening of displayed relationships as was e.g. shown for the Höglwald dataset by Luo et al. (2012).

Though there is a wealth of information available examining temporal and spatial variation of nitrous oxide and methane fluxes, a comparison of environmental response functions to contrast ecosystems in different climate zones has so far only rarely been undertaken. Multisite analyses of soil methane uptake for natural and managed systems have been presented (e.g. Smith et al., 2000), for forest soil nitrous oxide emissions by Pilegaard et al. (2006) and Schindlbacher et al. (2004), and for various ecosystem types by Schaufler et al. (2010). While the latter two publications are based on laboratory incubation studies allowing a more direct comparison of sites and flux magnitudes, the other mentioned studies are comparing field measurements at various sites. However, our study is to our knowledge the first study where a data generalization approach has been used to identify commonalities of effects of environmental drivers on methane and nitrous oxide fluxes. The generalization approach demonstrates that coherent patterns of methane uptake, soil moisture, and soil temperature exist across different ecosystems. We have strong evidence that optimum rates of methane uptake are found in environmental conditions representing approximately average site environmental conditions across these ecosystems. Thus, changes in soil environmental conditions (temperature/moisture) will likely reduce soil methane uptake potentials. This has rather important implications for understanding effects of climate change on soil methane uptake activity, since any shift in environmental conditions is likely to result in a reduction of methane uptake activity. For nitrous oxide, our analysis revealed expected patterns: highest nitrous oxide emissions under moist and warm conditions, and large nitrous oxide fluxes if soils are exposed to freeze–thawing effects at sufficiently high soil moisture contents.

Our approach of data generalization may prove beneficial for the development of environmental response models needed to better understand climate change feedbacks on biospheric sinks and sources of nitrous oxide and methane. However, the entire approach and its predictive power will depend on the availability of high quality flux datasets, which are currently available only for a few selected systems.

5 Conclusion

Despite the huge number of flux measurements and modeling efforts at the process levels and field scales, it has proven difficult to establish strong predictive relationships between nitrous oxide and methane fluxes and environmental parameters such as temperature and moisture. The normalization approach of flux data and environmental parameters presented here allows for better identifying cross-ecosystem commonalities of drivers of trace gas fluxes from soils in natural and semi-natural environments. However, such an approach depends on high data quality and the accessibility of data to the wider research community. Our approach may contribute to the improvement of parameterization of models simulating biosphere–atmosphere exchange processes and evaluations of feedbacks of climate change on soil fluxes of nitrous oxide and methane.

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