Biogeosciences Discuss., 10, 927–965, 2013
www.biogeosciences-discuss.net/10/927/2013/
doi:10.5194/bgd-10-927-2013

Biogeosciences Discussions

Effects of soil temperature and moisture on methane uptakes 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
[*]now at: EMPA, Dübendorf, Switzerland

Received: 14 December 2012 – Accepted: 31 December 2012 – Published: 22 January 2013

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

Published by Copernicus Publications on behalf of the European Geosciences Union.

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 kg N ha^{-1} yr^{-1}; temperate forest: 0.67 kg N ha^{-1} yr^{-1}; steppe: 0.22 kg N ha^{-1} yr^{-1}), while rates of soil methane uptake were approximately equal for the temperate forest (3.45 kg C ha^{-1} yr^{-1}) and the steppe (3.39 kg C ha^{-1} yr^{-1}), but lower for the tropical forest site (2.38 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 sufficient high soil moisture contents. However, the explanatory power of relationships of soil moisture or soil temperature to nitrous oxide fluxes remained rather poor (≤ 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 better understanding 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 ppbv to 319 ppbv, and from 0.72 ppmv to 1.77 ppmv, contributing at present approximately 5 % and 12 % respectively to observed global warming (IPCC, 2007). Soils of natural and semi-natural terrestrial ecosystems, 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. Stehfest and Bouwman, 2006; Brumme and Borken, 1999; Dutaur and Verchot, 2007; Breuer et al., 2000; Pilegaard et al., 2006; Schaufler et al., 2010; Smith et al., 2000). 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., 2007; 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 which 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 (IPCC, 1997). Assuming that the observed variability of nitrous oxide and methane fluxes at our observation sites may be representative for their ecosystems type 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, (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 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). 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. Daily precipitation and air temperature at 2 m a.g.l. 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).

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 ForestDNDC-tropica model. This 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., 2007).

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 degrees, topsoil (at 0–5 cm soil depth) samples were taken at least twice a week for the determination of volumetric water content.

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 uptake and nitrous oxide 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 Material 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.

3 Results

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

All three ecosystem 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 (29 January 2008) and a maximum of 25.6 °C (19 July 2008) at a soil depth of 5 cm. Variability of 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 highest 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 shows 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 $\mu g N m^{-2} h^{-1}$;

steppe up to 50 $\mu g N m^{-2} h^{-1}$). 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 $\mu g N m^{-2} h^{-1}$ in the wet season) and were between 5 and 10 $\mu g N m^{-2} h^{-1}$ during the dry season from May 2002 to November 2002 (Fig. 3).

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 2002 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). Methane uptake rates varied at a range of 2.4–3.5 $kg CH_4–C ha^{-1} yr^{-1}$ in the following sequence temperate forest ≈ semi-arid steppe > tropical forest (Table 2).

A comparison of soil nitrous oxide and methane emission 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 sitesecosystems distinct peak emissions were observed during freezing and thawing period.

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 by 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 the temperate forest site maximum uptake rates are clearly associated with lowest soil moisture and highest soil temperature, methane uptake rates at the tropical forest site showed a bi-modal 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 analyzed 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).

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 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 byproduct of two key nitrogen cycling processes in soil: nitrification (the oxidation of ammonium to nitrate and nitrite) 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

($0.96\,kg\,N\,ha^{-1}\,yr^{-1}$), somewhat lower for the atmospheric N deposition affected temperate forest site Höglwald ($0.67\,kg\,N\,ha^{-1}\,yr^{-1}$), and lowest for the steppe site in Inner Mongolia (approximately $0.2\,kg\,N\,ha^{-1}\,yr^{-1}$). 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).

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, both 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 (≤ 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. Pilegaard et al., 2006; Morley and Baggs, 2010) 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 time datasets, spanning at least one year, have 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 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 (Table 5). Stronger correlations were also found when combined soil moisture and soil temperature models were tested, a result which is in agreement with observations for soil nitrous oxide fluxes from a mixed forest in Austria (Kitzler et al., 2006).

4.2 Controls of methane uptake

Depending on climate, soil, and ecosystem type, and land use/ management, all having impacts on soil aeration, oxygen, and methane availability, soils can either function as atmospheric sink or source of methane (Topp and Pattey, 1997). The total sink strength of terrestrial ecosystems is estimated to be approximately 15–45 $\mathrm{Tg\,yr^{-1}}$ 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 (Mosier et al., 1991; Steudler et al., 1989; Whalen and Reeburgh, 1990; Keller et al., 1983; Seiler et al., 1984). Topp and Pattey (1997) as well as Dutour and Verchot (2007) summarized representative methane fluxes for various ecological types including desert, temperate forest, tropical forest, and grass pasture. In their studies annual uptake rates typically ranged from 0 to approximately 20 $\mathrm{kg\,CH_4{-}C\,ha^{-1}\,yr^{-1}}$ (mean: temperate forest: 4.28 $\mathrm{CH_4{-}C\,ha^{-1}\,yr^{-1}}$; tropical forest: 2.50 $\mathrm{CH_4{-}C\,ha^{-1}\,yr^{-1}}$; grassland: 1.74 $\mathrm{CH_4{-}C\,ha^{-1}\,yr^{-1}}$) (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 forest ecosystems showed annual uptake of 3.45 $\mathrm{kg\,CH_4{-}C\,ha^{-1}\,yr^{-1}}$ (1997) and 2.79 $\mathrm{kg\,CH_4{-}C\,ha^{-1}\,yr^{-1}}$ (1995) for the temperate forest, 2.38 $\mathrm{kg\,CH_4{-}C\,ha^{-1}\,yr^{-1}}$ for the rain forest site, and 3.39 $\mathrm{kg\,CH_4{-}C\,ha^{-1}\,yr^{-1}}$ (1.24 $\mathrm{mg\,m^{-2}d^{-1}}$) for the semi-arid steppe site. Annual fluxes are thus within (temperate and tropical forest) or at the high end (steppe) of previous 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; Dunfield et al., 1995; Koschorreck and Conrad, 1993; van den Pol-van Dasselaar et al., 1998; Whalen and Reeburgh, 1996; Castro et al., 1994, 1995; 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 $\mathrm{NH_4^+}$ oxidation resulting in an inhibition of methane oxidation at elevated soil $\mathrm{NH_4}$ 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 (Butterbach-Bahl and Papen, 2002; Brumme and Borken, 1999), 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; Castro et al., 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. The optimum soil water content for methane uptake reflects the balance between gas transport rates and physiological water stress. A further increase of soil moisture content may also decrease atmospheric methane uptake, due to increased methane production, as a result of an increasing proportion of anaerobic sites (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 %. 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 (Sitaula et al., 1995), that an increase in soil moisture from 32 vol% to 42 vol% resulted in a significant reduction of methane uptake. Similar results were also obtained by a laboratory-based study with agricultural soils (Nesbit and Breitenbeck, 1992), with maximum methane uptake rates being observed at approximately 50–70 % of water-filled pore space.

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 °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 prolong periods limiting methanotrophic activity.

4.3 Across-ecosystem commonalities

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 for contrasting ecosystems in different climate zones has so far only rarely been undertaken. Multi-site 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 for identifying 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 sufficient 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 Conclusions

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-ecosystems 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.

Acknowledgements. The authors thank their colleagues for continuing support and Allison Kolar (IMK-IFU) for proof reading the manuscript.

The service charges for this open access publication have been covered by a Research Centre of the Helmholtz Association.

References

Bleakley, B. H. and Tiedje, J. M.: Nitrous-Oxide Production by Organisms Other Than Nitrifiers Or Denitrifiers, Appl. Environ. Microbiol., 44, 1342–1348, 1982.

Bouwman, A. F., Vanderhoek, K. W., and Olivier, J. G. J.: Uncertainties in the Global Source Distribution of Nitrous-Oxide, J. Geophys. Res., 100, 2785–2800, 1995.

Bowden, W. B.: Gaseous nitrogen emissions from undisturbed terrestrial ecosystems - an assessment of their impacts on local and global nitrogen budgets, Biogeochemistry, 2, 249–279, 1986.

Bowden, R. D., Newkirk, K. M., and Rullo, G. M.: Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions, Soil Biol. Biochem., 30, 1591–1597, 1998.

Breuer, L., Papen, H., and Butterbach-Bahl, K.: N_2O emission from tropical forest soils of Australia, J. Geophys. Res., 105, 26353–26367, 2000.

Brumme, R.: Mechanisms of carbon and nutrient release and retention in beech forest gaps. 3. environmental-regulation of soil respiration and nitrous-oxide emissions along a microclimatic gradient, Plant Soil, 168, 593–600, 1995.

Brumme, R. and Beese, F.: Effects of liming and nitrogen-fertilization on emissions of CO_2 and N_2O from a temporate forest, J. Geophys. Res., 97, 12851–12858, 1992.

Brumme, R. and Borken, W.: Site variation in methane oxidation as affected by atmospheric deposition and type of temperate forest ecosystem, Global Biogeochem. Cy., 13, 493–501, 1999.

Butterbach-Bahl, K. and Papen, H.: Four years continuous record of CH_4-exchange between the atmosphere and untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany, Plant Soil, 240, 77–90, 2002.

Butterbach-Bahl, K., Gasche, R., Willibald, G., and Papen, H.: Exchange of N-gases at the Hoglwald Forest – a summary, Plant Soil, 240, 117–123, 2002.

Butterbach-Bahl, K., Kock, M., Willibald, G., Hewett, B., Buhagiar, S., Papen, H., and Kiese, R.: Temporal variations of fluxes of NO, NO_2, N_2O, CO_2 and CH_4 in a tropical rain forest ecosystem, Global Biogeochem. Cy., 18, GB3012, doi:10.1029/2004GB002243, 2004.

Castro, M. S., Melillo, J. M., Steudler, P. A., and Chapman, J. W.: Soil-moisture as a predictor of methane uptake by temperate forest soils, can. J. Forest Res., 24, 1805–1810, 1994.

Castro, M. S., Steudler, P. A., Melillo, J. M., Aber, J. D., and Bowden, R. D.: Factors Controlling Atmospheric Methane Consumption by Temperate Forest Soils, Global Biogeochem. Cy., 9, 1–10, 1995.

Chen, W. W., Wolf, B., Yao, Z. S., Bruggemann, N., Butterbach-Bahl, K., Liu, C. Y., Han, S. H., Han, X. G., and Zheng, X. H.: Annual methane uptake by typical semiarid steppe in Inner Mongolia, J. Geophys. Res., 115, D15108, doi:10.1029/2009JD013783, 2010.

Chen, W. W., Wolf, B., Zheng, X. H., Yao, Z. S., Butterbach-Bahl, K., Bruggemann, N., Liu, C. Y., Han, S. H., and Han, X. G.: Annual methane uptake by temperate semiarid steppes as regulated by stocking rates, aboveground plant biomass and topsoil air permeability, Global Change Biol., 17, 2803–2816, 2011.

Conrad, R.: Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO), Microbiological Reviews, 60, 609–640, 1996.

Dinsmore, K. J., Skiba, U. M., Billett, M. F., Rees, R. M., and Drewer, J.: Spatial and temporal variability in CH_4 and N_2O fluxes from a Scottish ombrotrophic peatland: implications for modelling and up-scaling, Soil Biol. Biochem., 41, 1315–1323, 2009.

Dunfield, P. F., Topp, E., Archambault, C., and Knowles, R.: Effect of nitrogen fertilizers and moisture-content on CH_4 and N_2O fluxes in a humisol – measurements in the field and intact soil cores, Biogeochemistry, 29, 199–222, 1995.

Dutaur, L. and Verchot, L. V.: A global inventory of the soil CH_4 sink, Global Biogeochem. Cy., 21, GB4013, doi:10.1029/2006GB002734, 2007.

Fujikawa, T. and Miyazaki, T.: Effects of bulk density and soil type on the gas diffusion coefficient in repacked and undisturbed soils, Soil Sci., 170, 892–901, 2005.

Galbally, I. E., Kirstine, W. V., Meyer, C. P., and Wang, Y. P.: Soil-atmosphere trace gas exchange in semiarid and arid zones, J. Environ. Qual., 37, 599–607, 2008.

Groffman, P. M., Brumme, R., Butterbach-Bahl, K., Dobbie, K. E., Mosier, A. R., Ojima, D., Papen, H., Parton, W. J., Smith, K. A., and Wagner-Riddle, C.: Evaluating annual nitrous oxide fluxes at the ecosystem scale, Global Biogeochem. Cy., 14, 1061–1070, 2000.

Henckel, T., Jackel, U., Schnell, S., and Conrad, R.: Molecular analyses of novel methanotrophic communities in forest soil that oxidize atmospheric methane, Appl. Environ. Microb., 66, 1801–1808, 2000.

Kammann, C., Muller, C., Grunhage, L., and Jager, H. J.: Elevated CO_2 stimulates N_2O emissions in permanent grassland, Soil Biol. Biochem., 40, 2194–2205, 2008.

Keller, M., Goreau, T. J., Wofsy, S. C., Kaplan, W. A., and Mcelroy, M. B.: Production of Nitrous-Oxide and Consumption of Methane by Forest Soils, Geophys. Res. Lett., 10, 1156–1159, 1983.

Kiese, R. and Butterbach-Bahl, K.: N_2O and CO_2 emissions from three different tropical forest sites in the wet tropics of Queensland, Australia, Soil Biol. Biochem., 34, 975–987, 2002.

Kiese, R., Hewett, B., Graham, A., and Butterbach-Bahl, K.: Seasonal variability of N_2O emissions and CH_4 uptake by tropical rainforest soils of Queensland, Australia, Global Biogeochem. Cy., 17, 1043, doi:10.1029/2002GB002014, 2003.

Kiese, R., Li, C., Hilbert, W., Papen, H., Butterbach-Bahl, K.: Regional application of PnET-N-DNDC for estimating the N_2O source strength of tropical rainforests in the wet tropics of Australia, Global Change Biol., 11, 128–144, 2005.

Kitzler, B., Zechmeister-Boltenstern, S., Holtermann, C., Skiba, U., and Butterbach-Bahl, K.: Controls over N_2O, NO_x and CO_2 fluxes in a calcareous mountain forest soil, Biogeosciences, 3, 383–395, doi:10.5194/bg-3-383-2006, 2006.

Koschorreck, M. and Conrad, R.: Oxidation of atmospheric methane in soil – measurements in the field, in soil cores and in soil samples, Global Biogeochem. Cy., 7, 109–121, 1993.

Kreutzer, K.: Effects of forest liming on soil processes, Plant Soil, 168, 447–470, 1995.

Le Mer, J. and Roger, P.: Production, oxidation, emission and consumption of methane by soils: a review, Eur. J. Soil Biol., 37, 25–50, 2001.

Liu, C. Y., Holst, J., Bruggemann, N., Butterbach-Bahl, K., Yao, Z. S., Yue, J., Han, S. H., Han, X., Krummelbein, J., Horn, R., and Zheng, X. H.: Winter-grazing reduces methane uptake by soils of a typical semi-arid steppe in Inner Mongolia, China, Atmos. Environ., 41, 5948–5958, 2007.

Luo, G. J., Brüggemann, N., Wolf, B., Gasche, R., Grote, R., and Butterbach-Bahl, K.: Decadal variability of soil CO_2, NO, N_2O, and CH_4 fluxes at the Höglwald Forest, Germany, Biogeosciences, 9, 1741–1763, doi:10.5194/bg-9-1741-2012, 2012.

Morley, N. and Baggs, E. M.: Carbon and oxygen controls on N_2O and N2 production during nitrate reduction, Soil Biol. Biochem., 42, 1864–1871, 2010.

Mosier, A., Schimel, D., Valentine, D., Bronson, K., and Parton, W.: Methane and nitrous-oxide fluxes in native, fertilized and cultivated grasslands, Nature, 350, 330–332, 1991.

Mosier, A. R., Parton, W. J., Valentine, D. W., Ojima, D. S., Schimel, D. S., and Delgado, J. A.: CH_4 and N_2O fluxes in the Colorado shorgrass steppe. 1. impact of landscape and nitrogen addition, Global Biogeochem. Cy., 10, 387–399, 1996.

Nesbit, S. P. and Breitenbeck, G. A.: A laboratory study of factors influencing methane uptake by soils, Agr. Ecosyst. Environ., 41, 39–54, 1992.

Peterjohn, W. T., Melillo, J. M., Steudler, P. A., Newkirk, K. M., Bowles, F. P., and Aber, J. D.: Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures, Ecol. Appl., 4, 617–625, 1994.

Pilegaard, K., Skiba, U., Ambus, P., Beier, C., Brüggemann, N., Butterbach-Bahl, K., Dick, J., Dorsey, J., Duyzer, J., Gallagher, M., Gasche, R., Horvath, L., Kitzler, B., Leip, A., Pihlatie, M. K., Rosenkranz, P., Seufert, G., Vesala, T., Westrate, H., and Zechmeister-Boltenstern, S.: Factors controlling regional differences in forest soil emission of nitrogen oxides (NO and N_2O), Biogeosciences, 3, 651–661, doi:10.5194/bg-3-651-2006, 2006.

Peel, M. C., Finlayson, B. L., and McMahon, T. A.: Updated world map of the Köppen-Geiger climate classification, Hydrol. Earth Syst. Sci., 11, 1633–1644, doi:10.5194/hess-11-1633-2007, 2007.

Regan, K., Kammann, C., Hartung, K., Lenhart, K., Müller, C., Philippot, L., Kandeler, E., and Marhan, S.: Can differences in microbial abundances help explain enhanced N_2O emissions in a permanent grassland under elevated atmospheric CO_2?, Global Change Biol., 17, 3176–3186, 2011.

Roslev, P., Iversen, N., and Henriksen, K.: Oxidation and assimilation of atmospheric methane by soil methane oxidizers, Appl. Environ. Microb., 63, 874–880, 1997.

Rothe, A., Huber, C., Kreutzer, K., and Weis, W.: Deposition and soil leaching in stands of Norway spruce and European Beech: results from the Hoglwald research in comparison with other European case studies, Plant Soil, 240, 33–45, 2002.

Schaufler, G., Kitzler, B., Schindlbacher, A., Skiba, U., Sutton, M. A., and Zechmeister-Boltenstern, S.: Greenhouse gas emissions from European soils under different land use: effects of soil moisture and temperature, Eur. J. Soil Sci., 61, 683–696, 2010.

Schindlbacher, A., Zechmeister-Boltenstern, S., and Butterbach-Bahl, K.: Effects of soil moisture and temperature on NO, NO_2, and N_2O emissions from European forest soils, J. Geophys. Res., 109, D17302, doi:10.1029/2004JD004590, 2004.

Seiler, W., Conrad, R., and Scharffe, D.: Field studies of methane emission from termite nests into the atmosphere and measurements of methane uptake by tropical soils, J. Atmos. Chem., 1, 171–186, 1984.

Sitaula, B. K., Bakken, L. R., and Abrahamsen, G.: CH_4 uptake by temperate forest soil – effect of N input and soil acidification, Soil Biol. Biochem., 27, 871–880, 1995.

Smith, K. A., Dobbie, K. E., Ball, B. C., Bakken, L. R., Sitaula, B. K., Hansen, S., Brumme, R., Borken, W., Christensen, S., Prieme, A., Fowler, D., Macdonald, J. A., Skiba, U., Klemedtsson, L., Kasimir-Klemedtsson, A., Degorska, A., and Orlanski, P.: Oxidation of atmospheric methane in Northern European soils, comparison with other ecosystems, and uncertainties in the global terrestrial sink, Global Change Biol., 6, 791–803, 2000.

Smith, K. A., Ball, T., Conen, F., Dobbie, K. E., Massheder, J., and Rey, A.: Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes, Eur. J. Soil Sci., 54, 779–791, 2003.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., B., Tignor, M., and Miller, H. L.: The physical science basis, in: Climate Change 2007, Cambridge Univ. Press, United Kindom and New York, 129–235, 2007.

Stehfest, E. and Bouwman, L.: N_2O and NO emission from agricultural fields and soils under natural vegetation: summarizing available measurement data and modeling of global annual emissions, Nutr. Cycl. Agroecosys., 74, 207–228, 2006.

Steinkamp, R., Butterbach-Bahl, K., and Papen, H.: Methane oxidation by soils of an N limited and N fertilized spruce forest in the Black Forest, Germany, Soil Biol. Biochem., 33, 145–153, 2001.

Steudler, P. A., Bowden, R. D., Melillo, J. M., and Aber, J. D.: Influence of nitrogen-fertilization on methane uptake in temperate forest soils, Nature, 341, 314–316, 1989.

Teh, Y. A. and Silver, W. L.: Effects of soil structure destruction on methane production and carbon partitioning between methanogenic pathways in tropical rain forest soils, J. Geophys. Res., 111, G01003, doi:10.1029/2005JG000020, 2006.

Teh, Y. A., Dubinsky, E. A., Silver, W. L., and Carlson, C. M.: Suppression of methanogenesis by dissimilatory Fe(III)-reducing bacteria in tropical rain forest soils: implications for ecosystem methane flux, Global Change Biol., 14, 413–422, 2008.

Topp, E. and Pattey, E.: Soils as sources and sinks for atmospheric methane, Can. J. Soil Sci., 77, 167–178, 1997.

van den Pol-van Dasselaar, van Beusichem, M. L., and Oenema, O.: Effects of soil moisture content and temperature on methane uptake by grasslands on sandy soils, Plant Soil, 204, 213–222, 1998.

Verchot, L. V., Davidson, E. A., Cattanio, J. H., Ackerman, I. L., Erickson, H. E., and Keller, M.: Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia, Global Biogeochem. Cy., 13, 31–46, 1999.

Whalen, S. C. and Reeburgh, W. S.: Consumption of Atmospheric Methane by Tundra Soils, Nature, 346, 160–162, 1990.

Whalen, S. C. and Reeburgh, W. S.: Moisture and temperature sensitivity of CH_4 oxidation in boreal soils, Soil Biol. Biochem., 28, 1271–1281, 1996.

Werner, C., Kiese, R., and Butterbach-Bahl, K.: N_2O, CH_4 and CO_2 flux measurements from tropical rainforest soils in western Kenya, J. Geophys. Res., 112, D03308, 1–15, doi:10.1029/2006JD007388, 2007.

Werner, C., Butterbach-Bahl, K., Haas, E., Hickler, T., and Kiese, R.: A global inventory of N_2O emissions from tropical rainforest soils using a detailed biogeochemical model, Global Biogeochem. Cy., 21, GB3010, doi:10.1029/2006GB002909, 2007.

Wolf, B., Zheng, X. H., Brueggemann, N., Chen, W. W., Dannenmann, M., Han, X. G., Sutton, M. A., Wu, H. H., Yao, Z. S., and Butterbach-Bahl, K.: Grazing-induced reduction of natural nitrous oxide release from continental steppe, Nature, 464, 881–884, 2010.

Wu, X., Bruggemann, N., Gasche, R., Shen, Z. Y., Wolf, B., and Butterbach-Bahl, K.: Environmental controls over soil-atmosphere exchange of N_2O, NO, and CO_2 in a temperate Norway spruce forest, Global Biogeochem. Cy., 24, GB2012, doi:10.1029/2009GB003616, 2010a.

Wu, X., Yao, Z., Bruggemann, N., Shen, Z. Y., Wolf, B., Dannenmann, M., Zheng, X., and Butterbach-Bahl, K.: Effects of soil moisture and temperature on CO_2 and CH_4 soil atmosphere exchange of various land use/cover types in a semi-arid grassland in Inner Mongolia, China, Soil Biol. Biochem., 42, 773–787, 2010b.

Yan, Y. P., Sha, L. Q., Cao, M., Zheng, Z., Tang, J. W., Wang, Y. H., Zhang, Y. P., Wang, R., Liu, G. R., Wang, Y. S., and Sun, Y.: Fluxes of CH_4 and N_2O from soil under a tropical seasonal rain forest in Xishuangbanna, Southwest China, J. Environ. Sci.-China, 20, 207–215, 2008.

Yashiro, Y., Kadir, W. R., Okuda, T., and Koizumi, H.: The effects of logging on soil greenhouse gas (CO_2,CH_4, N_2O) flux in a tropical rain forest, Peninsular Malaysia, Agr. Forest Meteorol., 148, 799–806, 2008.

Yavitt, J. B., Fahey, T. J., and Simmons, J. A.: Methane and carbon-dioxide dynamics in a northern hardwood ecosystem, Soil Sci. Soc. Am. J., 59, 796–804, 1995.

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° 40.2′ E 43° 33.1′ N
Climate (Köppen-Geiger climate classification)[d]	Temperate-oceanic climate (Dfb)	Tropical rainforest climate (Af)	Temperate semi-arid climate (Dwb)
Height a.s.l. (m)	540	80	1268
Mean annual precipitation (mm)	932 (mean 2004–2010)	4395[g]	330[h]
Mean annual temperature (°C)	8.6 (mean 2004–2010)	24.3[g]	0.7[h]
Soil type	Typic Hapludalf	Ustochrept	Calcic Chernozem
Soil parent material	Pleistocene loess over tertiary sand deposits	Granite	Loess
Vegetation type	Picea abies	Complex mesophyll vine forest	Leymus chinensis
Slope (°)	–	9.0–12.0	2.2–2.7
pH ± SE	3.6–4.0[e]	4.1 ± 0.03[e]	6.8 ± 0.27[f]
Bulk density ($g\,cm^{-3}$) ± SE 0–5 cm	1.033 ± 0.05[e]	1.09 ± 0.03[e]	1.09 ± 0.12
C-to-N ratio	18–19[e]	12.1[e]	9.7 ± 0.7[f]
Organic C content (%)	1.63–2.87[e]	3.11[e]	2.55 ± 0.63[f]
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)
[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] 0–10 cm soil depth.
[f] 0–4 cm soil depth.
[g] Data from Bureau of Meteorology, Brisbane.
[h] from Climate station at Inner Mongolia Grassland Ecosystem Research Station (IMGERS). mean: 1982–2007. –not determined.

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.

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

Table 3. Temperature and moisture control on methane fluxes.

Predictors	Ecosystems	Functions	a	b	c	x_0	y_0	n	R square
soil temperature (T)	steppe	Gaussian:	0.50[a]	0.56[a]		1.05[a]		259	0.71[a]
	rain forest	$f = a \cdot \exp(-0.5 \cdot ((T - x_0)/b)^2)$	–	–		–		–	–
	temperate forest		0.66[a]	0.51[a]		0.83[a]		300	0.49[a]
soil moisture (M)	steppe	Gaussian:	0.45[a]	0.24[a]		0.36[a]		259	0.22[a]
	rain forest	$f = a \cdot \exp(-0.5 \cdot ((M - x_0)/b)^2)$	0.77[a]	0.47[a]		0.25[a]		277	0.67[a]
	temperate forest		0.88[a]	0.54[a]		−0.0036		300	0.70[a]
soil temperature (T),	steppe	Gaussian:	0.54[a]	0.52[a]	1.17	0.99[a]	-0.23	259	0.73[a]
soil moisture (M)	rain forest	$f = a \cdot \exp(-0.5 \cdot (((T - x_0)/b)^2 + ((M - y_0)/c)^2))$	2.73	11.19	0.45[a]	−17.27	0.27[a]	277	0.67[a]
	temperate forest		0.92[a]	0.55[a]	0.65[a]	0.67[a]	−0.067	300	0.77[a]

[a]: $p < 0.0001$
–: no significant regression results.

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

Predictors	Ecosystems	Functions	a	b	c	x_0	y_0	n	R square
soil temperature (T)	steppe	$f = a \cdot \exp(-0.5 \cdot ((M - x_0)/b)^2)$	0.48[a]	0.42[a]		0.58[a]		241	0.28[a]
	rain forest		0.27[a]	0.29[a]		0.76[a]		290	0.21[a]
	temperate forest		0.54[a]	0.97[c]		1[c]		262	0.13[a]
soil temperature (T)	steppe	$\ln(f) = a \cdot T + x_0$	0.17[a]			0.57[a]		241	0.15[a]
	rain forest		-0.57[a]			0.77[a]		290	0.33[a]
	temperate forest		0.13[a]			0.70[c]		262	0.10[a]
soil moisture (M)	steppe	$\ln(f) = b \cdot M + y_0$		–			–	241	–
	rain forest			−0.36[a]			0.65[a]	290	0.28[a]
	temperate forest			–			–	262	–
soil temperature (T),	steppe		0.23[a]	−0.18[b]			0.59[a]	241	0.19[a]
soil moisture(M)	rain forest	$\ln(f) = a \cdot T + b \cdot M + y_0$	−0.41[a]	−0.22[a]			0.80[a]	290	0.41[a]
	temperate forest		0.25[a]	0.20[a]			0.52[a]	262	0.21[a]

–: no significant regression results.
[a]: $p < 0.0001$,
[b]: $p < 0.001$,
[c]: $p < 0.05$.

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	x_0	y_0	n	R square
soil temperaturen (T)	steppe	$f = a \cdot \exp(-0.5 \cdot ((T - x_0)/b)^2)$	0.71[a]	0.15[a]		0.25[a]		27	0.54[a]
	temperate forest		0.87[a]	0.19[a]		0.33[a]		81	0.50[a]
soil moisture (M)	steppe	$f = a \cdot \exp(-0.5 \cdot ((M - x_0)/b)^2)$	0.93[a]	0.36[a]		0.88[a]		27	0.7[a]
	temperate forest		0.92[c]	0.35[c]		-0.07		81	0.32[a]
soil temperature (T),	steppe	$f = a \cdot \exp(-0.5 \cdot (((T - x_0)/b)^2 + ((M - y_0)/c)^2))$	1.05[b]	0.20[b]	0.54[c]	0.27[a]	1.01[c]	27	0.77[a]
soil moisture (M)	temperate forest		1.18[a]	0.21[a]	0.31[a]	0.27[a]	0.23[a]	81	0.71[a]

–: no significant regression results.
[a]: $p < 0.0001$,
[b]: $p < 0.001$,
[c]: $p < 0.05$.

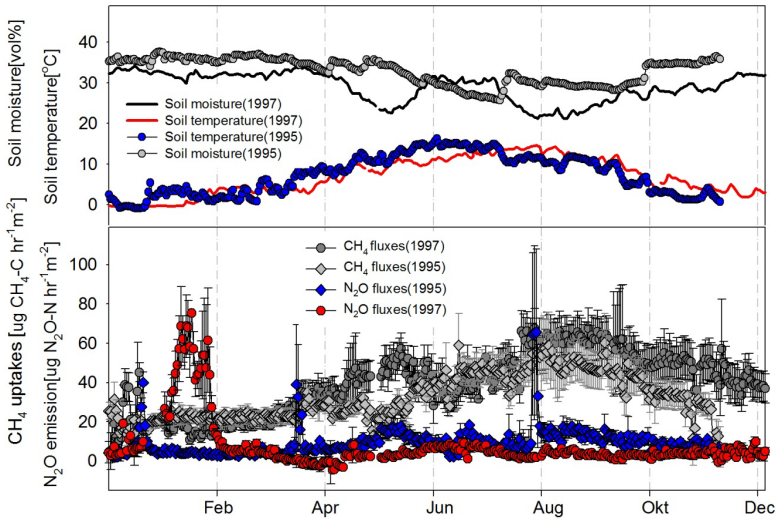

Fig. 1. Seasonal variability of soil volumetric water content (at 10 cm depth) and soil temperature (at 5 cm depth) as well as of soil nitrous oxide and methane fluxes at the Höglwald Forest site in the year 1995 and 1997.

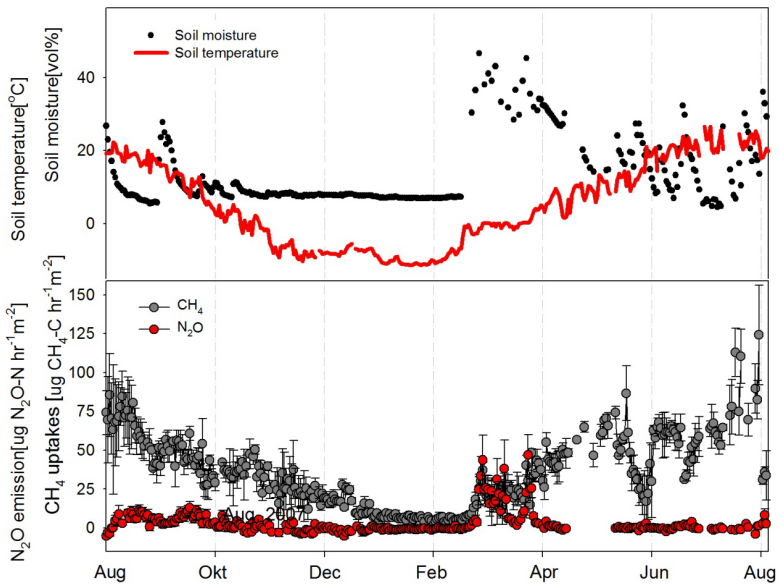

Fig. 2. Seasonal variability of soil volumetric water content (at 0–6 cm depth) and soil temperature (at 5 cm depth) as well as of soil nitrous oxide and methane fluxes at the semi-arid steppe site in Inner Mongolia for the period 15 August 2007 to 15 August 2008

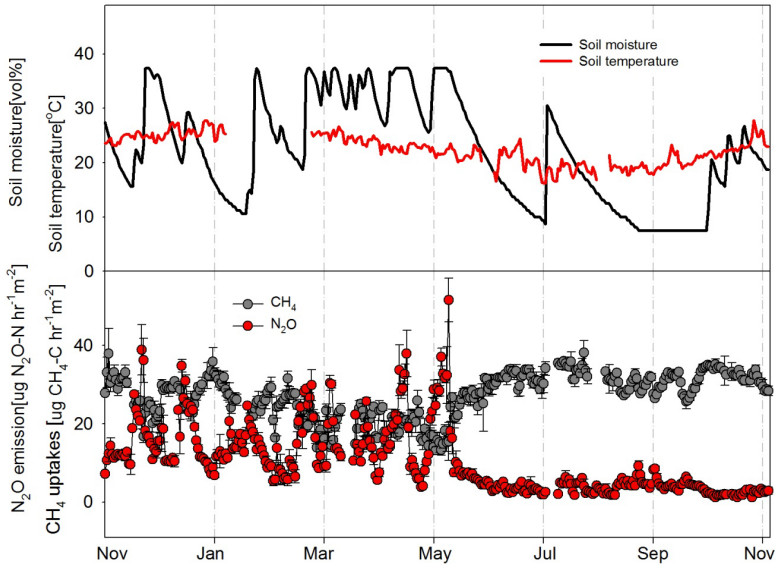

Fig. 3. Seasonal variability of soil volumetric water content (at 10 cm depth) and soil temperature (at 10 cm depth) as well as of soil nitrous oxide and methane fluxes at the tropical forest site Bellenden Ker, Queensland, Australia, for the period 2 November 2001–31 October 2002.

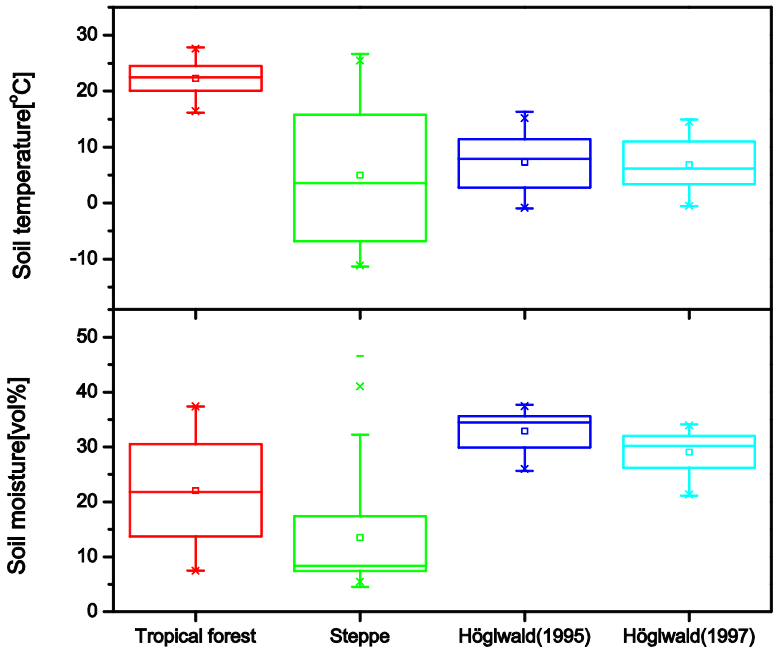

Fig. 4. Box plot of daily soil volumetric water content and soil temperature for the three investigated ecosystem types: tropical forest, semi-arid steppe, and temperate forest (Höglwald forest: data both in year 1995 and 1997). The boxes are determined by 25th and 75th percentiles. The whiskers are 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).

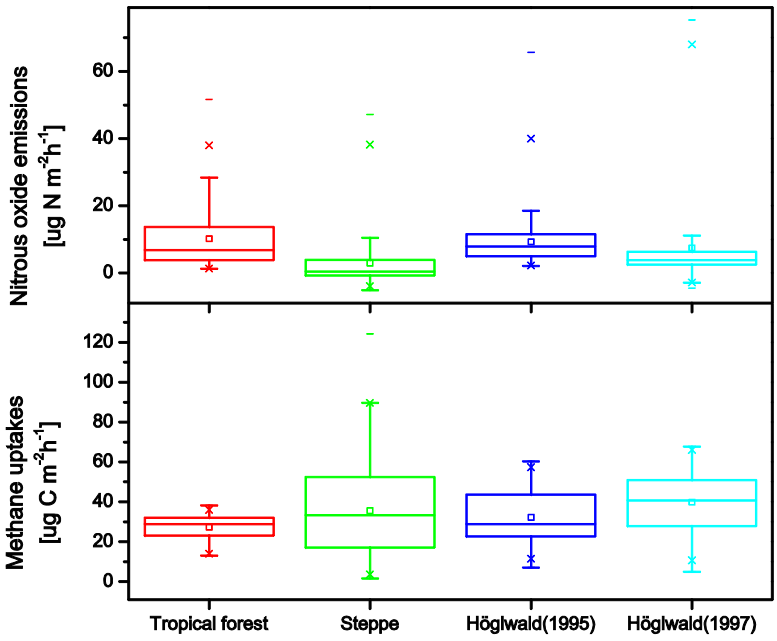

Fig. 5. Box plot of daily soil nitrous oxide and methane fluxes in tropical forest, semi-arid steppe, and temperate forest (Höglwald: data from both year 1995 and 1997). The boxes are determined by 25th and 75th percentiles. The whiskers are determined by the 5th and 95th percentiles. Additional values 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).

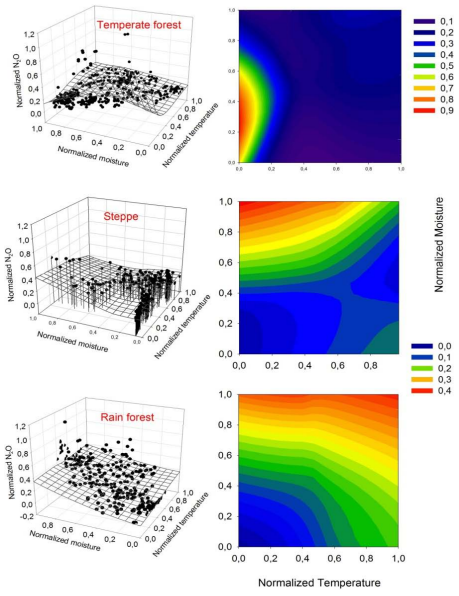

Fig. 6. Temperature and moisture effects on soil nitrous oxide fluxes for the three different ecosystems (temperate forest (Höglwald), semi-arid steppe, and tropical rain forest). Freeze and thaw periods were included. For this analysis nitrous oxide fluxes, soil temperature, and moisture data were normalized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

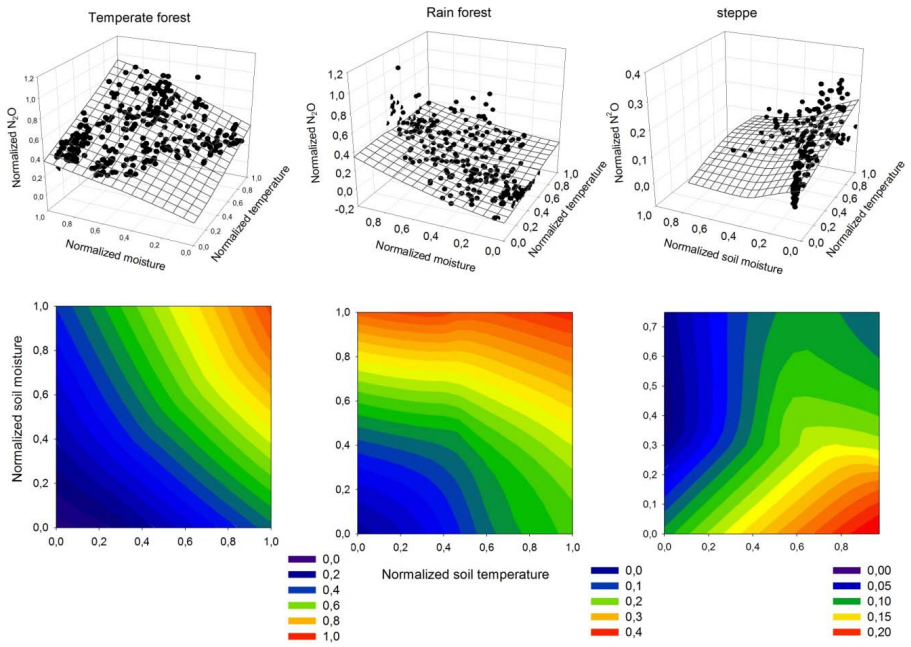

Fig. 7. Temperature and moisture effects on soil nitrous oxide fluxes for the three different ecosystems (temperate forest (Höglwald), semi-arid steppe, and tropical rain forest). For this analysis nitrous oxide fluxes, soil temperature, and moisture data were normalized at site scale to a range of 0-1 (zero: lowest observed value; 1: highest observed value). Nitrous oxide data for Höglwald Forest was randomly selected from observations in the year 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 was smoothed with the Loess algorithm (sampling proportion = 1).

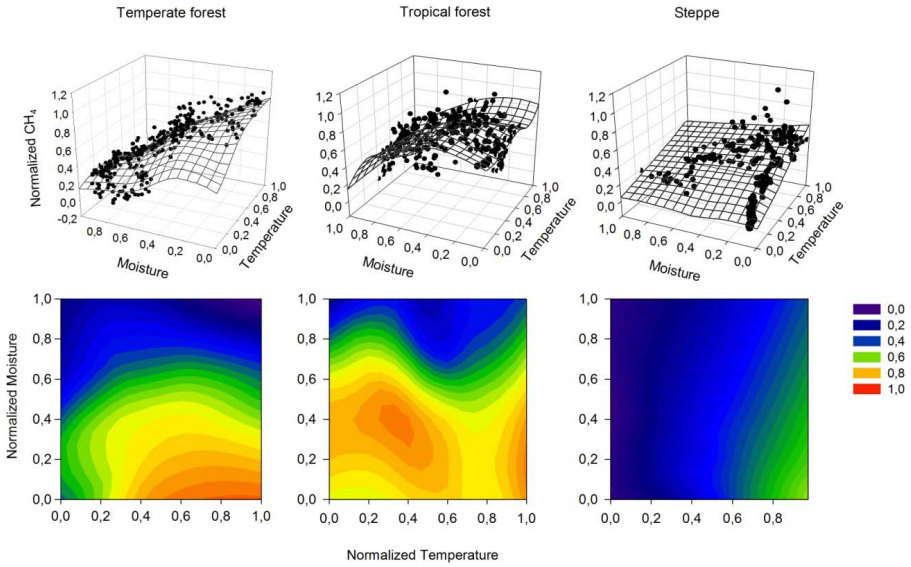

Fig. 8. Temperature and moisture effects on soil methane uptake rates for the three different ecosystems (temperate forest (Höglwald), semi-arid steppe, and tropical rain forest). For this analysis methane flux, soil temperature, and moisture data were normalized at site scale to a range of 0–1 (zero: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

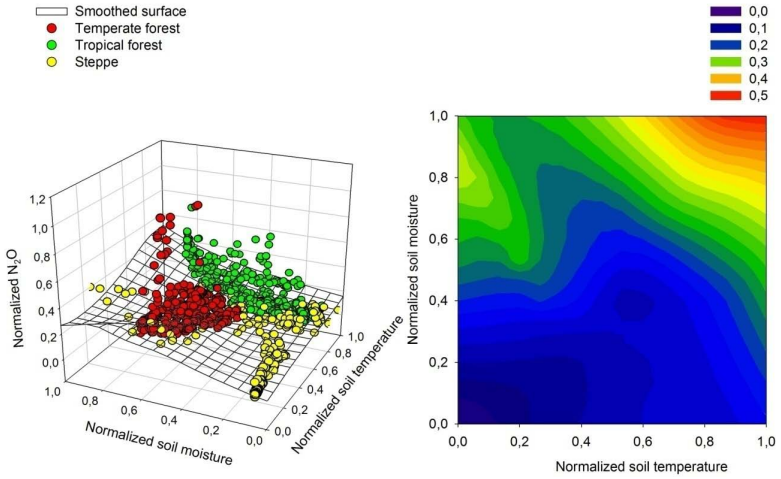

Fig. 9. Temperature and moisture effects on nitrous oxide fluxes (all data) across all three ecosystems (temperate forest, semi-arid steppe, and tropical forest). For this analysis soil moisture and soil temperature as well as nitrous oxide fluxes were first normalized across ecosystems to a range of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

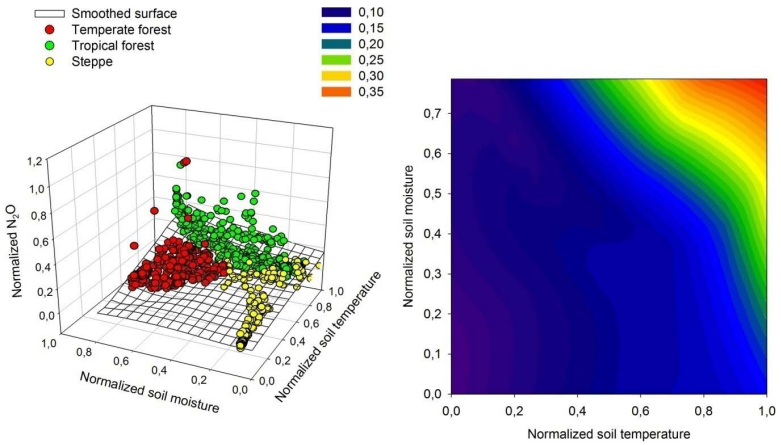

Fig. 10. Temperature and moisture effects on nitrous oxide fluxes (data for freeze-thaw periods at the temperate forest and steppe sites excluded) across all three ecosystems (temperate forest, semi-arid steppe, tropical forest). For this analysis soil moisture and soil temperature as well as nitrous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

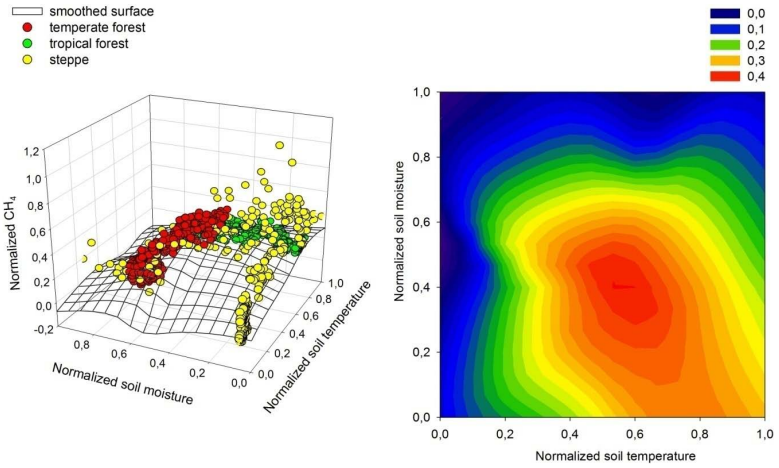

Fig. 11. Temperature and moisture effects on methane uptake fluxes across all three ecosystems (temperate forest, semi-arid steppe, and tropical forest). For this analysis, soil moisture and soil temperature as well as methane uptake flux data were normalized across ecosystem (see Fig. 9). Prior to the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