Effects of experimental drying intensity and duration on respiration and methane production recovery in fen peat incubations

Cristian Estop-Aragonés*, Christian Blodau

Limmological Research Station & Department of Hydrology, University of Bayreuth, Universitätsstrasse 30, 95447, Germany

A R T I C L E   I N F O

Article history:
Received 17 October 2011
Received in revised form
6 December 2011
Accepted 11 December 2011
Available online 23 December 2011

Keywords:
Peatland
Fen
Drought/drying
Moisture
Respiration
Methanogenesis
Incubation

A B S T R A C T

Drying and rewetting to a variable extent influence the C gas exchange between peat soils and the atmosphere. We incubated a decomposed and compacted fen peat and investigated in two experiments 1) the vertical distribution of CO2 and CH4 production rates and their response to drying and 2) the effects of temperature, drying intensity and duration on CO2 production rates and on CH4 production recovery after rewetting. Surface peat down to 5 cm contributed up to 67% (CO2) and above 80% (CH4) of the depth-aggregated (50 cm) production. As CO2 production sharply decreased with depth water table fluctuations in deeper peat layers are thus not expected to cause a substantial increase in soil respiration in this site. Compared to anaerobic water saturated conditions drying increased peat CO2 production by a factor between 1.4 and 2.1. Regarding the effects of the studied factors, warmer conditions increased and prolonged drying duration decreased CO2 production whereas the soil moisture level had little influence. No significant interactions among factors were found. Short dry events under warmer conditions are likely to result in greatest peaks of CO2 production rates. Upon rewetting, CH4 production was monitored over time and the recovery was standardized to pre-drying levels to compare the treatment effects. Methane production increased non-linearly over time and all factors (temperature, drying intensity and duration) influenced the pattern of post-drying CH4 production. Peat undergoing more intense and longer drying events required a longer lag time before substantial CH4 production occurred and warmer conditions appeared to speed up the process.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

In peatlands, plant biomass production has exceeded decomposition of organic matter (OM) after the last glaciation and resulted in accumulation of a global relevant storage of terrestrial carbon (Gorham, 1991; Vasander and Kettunen, 2006). Peatlands release C both via emissions, mostly as CO2 and CH4, and via leaching in form of dissolved inorganic and organic carbon, CH4 and particulate organic carbon. Carbon dioxide and CH4 are end products of the decomposition of OM and constitute a major fraction in the C balance of the ecosystem (Worrall et al., 2007). In relation to climate change, the frequency of drying and flooding is predicted to increase in many regions (Meehl et al., 2007). Temporal shifts between aerobic and anaerobic conditions, a major control for peat accumulation and CO2 and CH4 production rates, are thus expected and raise concern about the influence of such hydrological changes on the exchange of these greenhouse gases with the atmosphere.

A key control on turnover rates is peat OM “quality”, that is, the organic chemistry of the decaying plant material, which is site specific. The type of vegetation and the associated litter were shown to be related to production rates (Moore and Dalva, 1997). The ratio of metabolic to structural carbohydrates in mosses was shown to be strongly related to their in situ decomposition as well (Turetsky et al., 2008). However, the rates of both CH4 as well as aerobic and anaerobic CO2 production do not seem to be related to a particular OM fraction (Inglett et al., 2011).

Production rates of CO2 and CH4 have typically been determined by incubating peat samples under controlled conditions. This way controls on peat respiration were identified and their effect quantified, among them presence of oxygen, temperature and peat moisture. Aerobic conditions, related to oxygen penetration in peat when the water table (WT) declines, favours CO2 and inhibits CH4 production, whereas anaerobic conditions, associated with high water content, favour lower CO2 and greater CH4 production rates.
Warmer conditions have widely been reported to raise production rates both under aerobic and anaerobic conditions (Gao et al., 2009; Hogg, 1993; Hogg et al., 1992; McKenzie et al., 1998; Moore and Dalva, 1997; Waddington et al., 2001; Wang et al., 2010; Yavitt et al., 1997). Peat moisture was shown to be an important control (Jaatinen et al., 2008) but its influence on CO2 production is more intricate. Relative to water saturated conditions CO2 production typically increases with drying up to an optimum moisture content and then decreases with further drying; such a pattern has been observed in some studies (Hogg et al., 1992; Howard and Howard, 1993; Waddington et al., 2001; Wang et al., 2010). The response is very variable among peats and CO2 production was also reported to decline as volumetric water content decreased (McNeil and Waddington, 2003). Higher moisture contents have been associated with greater CO2 production in agricultural fen peat, although the response differed greatly among horizons and temperatures indicating strong factor interactions (Kecharavi et al., 2010). Overall, these studies suggest that the response of CO2 production to drying not only differs among sites but also changes with depth within a given site. A close relation exists between WT and CH4 emissions, which typically decrease during drying events (Hurtunen et al., 2003; Moore and Dalva, 1993). Drying was also shown to cause a regeneration of the electron acceptor pool and upon rewetting CH4 production is usually delayed due to electron acceptor reducing bacteria outcompeting methanogens (Achtnich et al., 1995; Blodau and Moore, 2003; Knorr and Blodau, 2009). A greater severity of the drought event might be thus expected to lead to longer recuperation of methanogenic conditions upon rewetting. Water table decline is commonly associated with greater CO2 emissions from peat soils. Such a response generally occurs if the drawdown starts from a WT position above the peat surface (Moore and Dalva, 1997; Moore and Knowles, 1989) since anaerobic conditions prevail in the entire profile. Under field conditions, however, the WT is mostly lower, depending on the site, microtopography, and time of year. Emissions were shown to increase during WT drawdown in some sites (Silvola et al., 1996) but not in others (Chimner and Cooper, 2003; Lafleur et al., 2005; Silvola et al., 1996). Previous measurements at the Schlöppnerbrunnen site, here investigated, reported no increase in soil CO2 emissions by intensified and prolonged drought compared to natural WT decline in summer (Muhr et al., 2011). Such a response has been attributed to a strong decline in organic matter decomposability with depth. High respiration rates in the surface layers would then effectively mask changes in respiration rates in the poorly decomposable peat layers at greater depth that are exposed to changing redox conditions.

While this reasoning is intuitive, we are currently lacking clear evidence that a strong decline in OM decomposability can explain the reported lack of response of soil respiration fluxes to drought in peat soils. Furthermore, drought periods vary in duration and intensity and might occur in different seasons, i.e. under different temperature conditions. The studies discussed above provided insufficient information about the combined effect of these factors on peat respiration and specifically on the recovery of CH4 production after the drought. In light of these knowledge deficiencies, we first quantified production rates of CO2 and CH4 with depth to confirm such reasoning and also identified effects of drying on these rates. In a second experiment, we investigated the effect of combinations of temperature, drought duration and intensity on CO2 production rates and CH4 production recovery after rewetting. We specifically hypothesized that a switch from oxic to anoxic conditions in deeper peats would have little impact on total CO2 production in a peat column aggregated from CO2 production in the incubation experiments. Secondly, we expected that CO2 production in individual soil layers would be raised with drying intensity and duration and that CH4 production recovery would be substantially retarded.

2. Material and methods

2.1. Site description

The Schlöppnerbrunnen site has been previously described in a number of studies (Knorr et al., 2009; Muhr et al., 2011; Otieno et al., 2009). The site is a small (<1 ha) soligenous fen surrounded by a Picea abies forest located in the Fichtelgebirge region, north-east of Bavaria, at an elevation ~750 m above sea level. The region underwent peat extraction for glasswork approximately until 1950 (Firbas and v. Rochow, 1956) and some deteriorated but visible drainage ditches suggest this site was not an exception. Mean annual precipitation (1961–1990) was 1156 mm and mean annual temperature 5 °C. The WT fluctuated between 5 and 15 cm below peat surface during at least 50% of the year and was only above 5 cm depth for about 5% of the year in 2008–2009. Seasonal WT decline of 70 cm below surface was observed in summer. Vegetation is dominated by vascular plants mainly including Molinia caerulea, Carex rostrata, Carex canescens, Juncus effusus, Nardus stricta and Eriophorum vaginatum. The narrow hollows between plant cushions are either colonized by sparsely found Sphagnum spp. patches or covered by decaying litter from vascular plants. The peat is dense, with bulk density (BD) in this study ~0.1 g cm−3, well decomposed (H7–H9, von Post scale), has a high and variable mineral content with depth (8–80%), and forms a 50–70 cm thick deposit with a clay horizon underneath. In the upper 60 cm the C content ranged from 16 to 48% and the N content from 0.9 to 2.2% (Knorr et al., 2008a). The mean pore water pH in situ was 4.8 (2008–2009).

2.2. Incubation experiments

Two different experiments were carried out with a common methodology to determine CO2 and CH4 production rates by incubating peat. All samples were collected in hollows dominated by decaying litter in absence of dense vegetation to reduce plant living tissues and root abundance in the incubations.

2.2.1. Depth distribution of CO2 and CH4 production and drying effects

Three peat cores at least 50 cm deep were obtained with a Finnish box corer on 27 August 2009. Each core was sliced in 5 cm layers using a knife. A known volume of each layer was obtained by pushing a PVC cylinder (5 cm long, 4.6 cm i.d.) through each peat segment with the aid of a knife. This procedure maintained the original peat structure during the experiment. Samples were kept in a coolbox with ice packs (~4 °C), transported to the laboratory within 4 h after collection, and submerged overnight in a N2-flushed distilled water bath to obtain water saturated conditions while minimizing exposure to oxygen. The peat material was coherent and its structure preserved after submergence. Each cylinder containing the water saturated peat was subsequently weighed (~85 g wet peat) and immediately placed in 250 mL jars, which were capped and flushed with N2 to commence the anaerobic phase. The cap contained a sealed rubber stopper with two needles allowing for N2-flush and headspace sampling. All jars were wrapped with aluminium foil to avoid exposure to light other than during the drying periods when caps were removed. An initial period under anaerobic conditions, during which peat was water saturated for 263 days, was followed by an aerobic period of up to 69 days, when peat dried and water loss was monitored gravimetrically. Production rates
were repeatedly measured using three replicates of each layer. Anaerobic and aerobic rates were determined in depth layers of 0–5, 5–10, 10–15, 15–20, 20–25, 25–30, 35–40 and 45–50 cm. Additional incubations from depths 0–5, 15–20 and 45–50 cm were kept as anaerobic controls throughout the experiment. This experiment was carried out at 11 °C.

2.2.2. Effects of temperature, drought duration and intensity on CO2 and CH4 production

In the upper peat layer (0–5 cm) the effects of 1) temperature, 2) air filled porosity (AFP, as surrogate for drying intensity) and 3) drought duration on CO2 and CH4 production rates were investigated using a factorial design with two levels for each factor in three replicates (Table 1). Each factor level represented conditions similar to those previously observed in situ in this fen peat (Estop-Aragonés, unpublished results). Additional samples served as anaerobic controls at both temperatures. Samples were collected on 24 September 2009 and randomly assigned to treatments. Soil was extracted using a saw and a small spade and sample preparation followed the described protocol using the aforementioned PVC cylinders. Samples were anaerobically incubated for 24 days at 11 or 20 °C, depending on the treatment. Caps were then removed from the jars, except for controls, to commence the drying. Initial aerobic CO2 production was quantified without delay and water loss monitored subsequently by weighing. The mean BD of 6 additional samples was determined to calculate, based on an averaged total porosity and water saturated conditions, the required loss of water to the targeted water content of each treatment (5 or 25% AFP, Table 1). Once the targeted AFP was reached, it was kept constant (±2%) for 10 or 30 days, according to treatment, by regularly adding distilled water with a syringe. Aerobic production rates were subsequently measured three times and statistically evaluated. Samples were subsequently rewetted to saturation and incubated anaerobically to monitor post-drying anaerobic CO2 production and recovery of methanogenesis.

2.3. Analytical procedures and calculation of production rates

Production rates were calculated from the linear increase of CO2 and CH4 concentration in jars with time. During the anaerobic phase jars were flushed with N2 for 8 min prior to sampling causing a small loss in water-filled porosity from 100% up to 95% by the end of the experiment. During aerobic conditions jars were simply capped instead. In all incubations headspace samples (2 mL) were withdrawn at 1, 6, 24 and 30 h from the capped jars using a disposable syringe and CO2 and CH4 analyzed on an SRI 8610C gas chromatograph with FID and a CO2 methanizer. The calculation of production rates accounted for CO2 distribution between water and gas phase using Henry’s law constant corrected for temperature for CO2 and CH4 (Sander, 1999). Formation of HCO3− was neglected due to low pH observed in this site (mostly below 5.5). Changes in the headspace volume due to peat drying were taken into account and corrected (Hogg et al., 1992). At the end of the experiment, samples were dried (105 °C) to constant mass to determine BD and total porosity for each sample. Then, the degree of water saturation was calculated for each sample and the calculation corrected for the headspace volume change in each jar during the drying. Moisture content in this study is expressed as air filled porosity (AFP) which, analogously to water-filled porosity, is considered as index of soil aeration with relevance for the microbiological processes in soil (Linn and Doran, 1984; Schjonning et al., 1999). OM content was determined from mass loss for each sample by placing a subsample at 550 °C for 5 h. Due to the relatively high natural mineral content production rates are expressed based on dry weight of OM following Turetsky and Ripley (2005). The CO2 and CH4 production rates were calculated from the coefficient of linear regression to evaluate and remove from the data set those measurements with potential leaking during sampling or saturation in the headspace. Rates with an R²<0.9 were discarded leading to a 6% (experiment 2.2.1) and a 9% data loss (experiment 2.2.2) with respect to CO3 production rates.

2.4. Statistical analysis and other calculations

Repeated measures analysis of variance (RMANOVA) was performed using SPSS 18 for Windows to test the significance of factors and conditions, and post-hoc analyses applying the Bonferroni correction were used. This analysis was used to evaluate differences between peat depths and to test if the low and high level of each factor (temperature, drought duration and intensity, refer to Table 1) and their interactions significantly controlled aerobic CO2 production rates. Additional tests using the anaerobic CO2 rates as a covariate to remove the initial between-treatment effect were also performed but did not yield substantial changes in the significance of the factors tested. Correlation analyses were applied to determine relations among variables. Throughout the text, we refer to ‘significant’ if P < 0.01 unless otherwise specified. In the analysis of the depth distribution of production rates, the contribution of each interval depth was quantified as % relative to the aggregated production under anaerobic and aerobic conditions. With regard to effects of temperature, drying intensity and duration the main effect of each factor was quantified using the mean response of aerobic CO2 production between low (11 °C, 5% AFP, 10 days duration) and high (20 °C, 25% AFP, 30 days duration) levels (Berthouex and Brown, 2002). The effect of temperature was also quantified with Q10 values calculated as Q10 = (R2/R1)10(T2 − T1) where R1 and R2 are the production rates at temperatures T1 (11 °C) and T2 (20 °C), respectively. The recovery of methanogenesis after the rewetting was expressed as a % relative to the maximum measured CH4 rate of each jar during the initial anaerobic period, previous to drying. The same analysis using mean values, rather than the maximum CH4 production, led to the same pattern. Methanogenesis in incubated soil typically evolves non-linearly as different factors affect CH4 production rates over time (Leifseth et al., 1999; Segers and Kengen, 1998). To illustrate the CH4 production recovery lines were fitted to the data using a sigmoid function.

3. Results

3.1. Depth distribution of CO2 and CH4 production rates and drying effects

3.1.1. Anaerobic phase

Anaerobic CO2 production decreased with time between 27 and 38% compared to initial measurements. Production was fastest in
the uppermost peat layer, which contributed between 38 and 60% of the depth-aggregated anaerobic CO₂ production at rates between 15.48 and 5.55 μmol CO₂ g OM⁻¹ d⁻¹. The layer of 5–10 cm depth contributed between 14 and 20% at rates between 4.56 and 2.25 μmol CO₂ g OM⁻¹ d⁻¹. Differences between the uppermost layer and those beneath, and the second layer and those beneath 25 cm depth, were significant (RMANOVA). Production of CO₂ in deeper layers (between 15 and 50 cm) was similar and contributed between 9 and 1% each; rates were usually below 1 μmol CO₂ g OM⁻¹ d⁻¹ (see anaerobic phase in Fig. 1).

Methanogenic conditions were not favourable at the time of sample collection due to the seasonal WT decline to about 30 cm below surface and usually no CH₄ was detected during the initial measurements; the maximum rate was only 0.17 μmol CH₄ g OM⁻¹ d⁻¹. The anaerobic incubation was thus extended and measurements resumed between day 250 and 263. By then, CH₄ production had substantially increased only in the upper 5 cm, which contributed between 83 and 88% to the depth-aggregated CH₄ produced at rates between 2.32 and 1.41 μmol CH₄ g OM⁻¹ d⁻¹. Methane was also produced in the next depth interval of 5–10 cm and contributed between 6 and 15%. However, despite the long anaerobic incubation time, at least one replicate per depth below 10 cm did not produce methane at detectable levels. Such incapacity for CH₄ production in layers below 10 cm depth was also confirmed by the anaerobic control incubations from 20 to 50 cm depth for up to 320 days under anaerobic conditions (Supplementary data S1). Rates in control jars did not differ to the other samples during the anaerobic phase for a given depth (Supplementary data S2) and decreased over time (Supplementary data S1).

### 3.1.2. Aerobic phase

Aerobic CO₂ production rates were on average between 110 and 44% higher than anaerobic ones depending on depth and AFP (Fig. 1). Rates at 0–5 cm contributed between 48 and 67% of the depth-aggregated CO₂ produced and ranged from 38.81 to 13.87 μmol CO₂ g OM⁻¹ d⁻¹. The following layer (5–10 cm) contributed between 10 and 19% with rates ranging from 6.77 to 3.08 μmol CO₂ g OM⁻¹ d⁻¹. The contribution of deeper layers (between 15 and 50 cm) ranged between 10 and 1%. Statistical differences followed the same pattern as during the anaerobic phase. The effects of soil moisture on CO₂ production were not apparent; as peat became drier rates varied randomly and no consistent direction of change was observed under the investigated moisture range.

During the aerobic period, CH₄ production was inhibited in the peat. This inhibition did not occur immediately though, as up to 1.27 μmol CH₄ g OM⁻¹ d⁻¹ were produced in samples of the upper 5 cm-thick layer exposed to air for 6 days at ~5% AFP.

Changes of BD, ash content and total porosity values with depth are given in supplementary information (Supplementary data S3). There were positive significant correlations between BD and ash content and between ash content and total porosity, and significant negative correlation between BD and total porosity.

#### 3.2. Effects of temperature, drought duration and intensity on CO₂ and CH₄ production

##### 3.2.1. Initial anaerobic phase

Anaerobic CO₂ production was initially 35.68 ± 4.83 at 11 °C and 60.38 ± 4.56 μmol CO₂ g OM⁻¹ d⁻¹ at 20 °C and slowed over time by an average factor of 2 (20 °C) and up to 3 (11 °C) during the final measurements in this phase, as illustrated in Fig. 2. In contrast, CH₄ production accelerated during this phase from 1.23 ± 1.66 to 2.21 ± 1.60 μmol CH₄ g OM⁻¹ d⁻¹ at 11 °C and from 6.72 ± 4.65 to 14.92 ± 2.68 μmol CH₄ g OM⁻¹ d⁻¹ at 20 °C. Accordingly CO₂/CH₄ ratios decreased over time to 9.76 ± 9.81 at 11 °C, and 1.66 ± 0.25 at 20 °C. Anaerobic CO₂ production and methanogenesis were positively correlated at both temperatures and were significantly greater at 20 °C than at 11 °C. Mean Q₁₀ values were 4.51 for methanogenesis and 2.32 for anaerobic CO₂ production. At a given temperature anaerobic CO₂ production did not differ among treatments (P = 0.99 at 11 °C and P = 0.16 at 20 °C). At 11 °C, CH₄ production rates were similar (P = 0.84) but at 20 °C, rates did significantly differ among treatments. The variability among treatments and the effects of temperature on CH₄ production rates during this initial phase are shown in Fig. 3.

#### 3.2.2. Aerobic phase

Rates of CO₂ production were significantly faster than in the anaerobic phase and at the high compared to the low temperature (Fig. 4). Drying duration significantly lowered mean CO₂ production but AFP had a minor effect (Table 2). No important interactions among the factors were found and only the three way interaction (Temperature × AFP × Duration) was almost significant (P = 0.057). Based on averaged data of each treatment, the effect of AFP, duration, and temperature, was quantified. Changing from the low to the high level (refer to Table 1) raised CO₂ production by a factor of 1.03 (AFP) and 2.12 (temperature) and lowered it by a mean factor of 1.24 (duration), respectively. Mean Q₁₀ value was 2.99 for aerobic CO₂ production.

As observed in the profile experiment, CH₄ production rates ceased during aerobic conditions but not immediately as methane production (0.05 μmol CH₄ g OM⁻¹ d⁻¹) was still detected 15 days after air exposure at 11 °C.

#### 3.2.3. Final anaerobic phase

After rewetting and under anaerobic conditions, methane production restarted after some lag time and increasingly and non-linearly recovered. To make the recovery quantifiable and

---

**Fig. 1.** CO₂ production rates from different peat depths measured in incubations during anaerobic conditions (−water saturation) and along different soil moisture during a drying process under aerobic conditions at 11 °C. Moisture is expressed as % air filled porosity (AFP). Bars represent the mean of three replicates measured at different times under a given condition and error bars indicate one standard deviation around the mean.
comparable among treatments, rates were standardized to pre-drying levels, regressed against time and lines were fitted to the mean values using a sigmoid function (Fig. 5). Post-drying rates were usually lower than pre-drying for the monitored period, except for the cold — wet — short treatment. At both temperatures, wet treatments recovered initially on average faster than dry treatments, although such differences were not maintained over time (Fig. 5). At 11 °C, the initial CH4 production recovery ranked wet — short >> wet — long > dry — short ~ dry — long. This pattern was also maintained at 20 °C based on the available data for the short treatments. The fitted lines illustrate that cold treatments required more time for substantial CH4 production and thus reached the “final” production conditions later than at warmer conditions (Fig. 5).
4. Discussion

4.1. Depth distribution of production rates and drying effects on peat respiration

Our experiments demonstrate that both CO₂ and CH₄ were mostly produced in the upper 5 cm layer of this fen peat (Fig. 1), where fresh plant litter was provided and root activity and exudation were likely at a maximum prior to sampling, as demonstrated by ¹³C-labelling in an earlier paper (Knorr et al., 2008a). This depth distribution of production rates has consequences for in situ respiration related to WT position. In previous work it was found that experimental changes in WT deeper in the peat, which broadly serves as a boundary between oxic and anoxic conditions, had little influence on CO₂ fluxes at the site (Knorr et al., 2008b; Muhr et al., 2011). Similar findings have been reported also from other sites (Chimner and Cooper, 2003; Lafleur et al., 2005; Silvola et al., 1996). To relate such findings to our results, we aggregated the determined aerobic and anaerobic production rates using a hypothetical WT as control for both modes of respiration, and then plotted CO₂ emission from soil respiration against WT (Fig. 6). According to this exercise and in agreement with our hypothesis the increase of CO₂ production due to a switch from anaerobic to aerobic respiration with hypothetical WT decline would have little effect below a depth of 5 cm because of the subordinate contribution of these layers to soil respiration (Fig. 6). As the mean annual WT position at this site was 15 cm below peat surface in 2008 and 2009, drought events with WT falling deeper than 15 cm are thus unlikely to raise production and CO₂ flux substantially. Such an interpretation is in agreement with the previously mentioned experiments at this site reporting no major effect of CO₂ exchange during experimental drying (Knorr et al., 2008b; Muhr et al., 2011), and also with diminished CO₂ emissions during flooding conditions (S. Wunderlich, pers. communication).

The results are also in agreement with the well-known fact that peat material becomes more recalcitrant against decomposition with depth, i.e. with increasing age of the peat (Hogg, 1993). Extensive evidence has been presented that CO₂ production rates in incubations are highest near the peatland surface and decrease with depth (Basiliko et al., 2005; Hogg et al., 1992; Jaatinen et al., 2007; McKenzie et al., 1998; Waddington et al., 2001; Yavitt et al., 1997). Regarding the response of peat respiration to WT position and drying and rewetting, the decline in CO₂ production with depth is thus critical. Our results indicate a small contribution of depths >10 cm and such pattern has also been reported elsewhere (Jaatinen et al., 2007).
et al., 2007, 2008; Waddington et al., 2001), whereas in other studies this decrease of CO₂ production with depth was not as sharp (Basiliko et al., 2005; Hogg et al., 1992; Waddington et al., 2001). Such differences likely mirror the long-term conditions under which peat decay has occurred, in particular with respect to the average position of the WT (Laiho, 2006). Sites with a deeper long-term WT allow for a longer exposure of buried OM to aerobic decay. The zone of high peat decomposability is then shallow and often well above the zone where WT typically fluctuates. Our results are in agreement with the broader hypothesis that “dry peatlands” show little response of CO₂ flux to temporary drought, whereas a greater increase in CO₂ production will occur in sites with a WT closer to the surface (Lafleur et al., 2005).

Regarding CH₄ production the contribution of the upper 5 cm of peat was even greater than that of CO₂ as methanogenesis was irrelevant or not detectable in layers below 10 cm. These results are roughly in agreement with previous measurements in mesocosms showing a more rapid potential for recovery of methanogenesis in the surface peat after rewetting (Knorr et al., 2008b). Previous studies in wet grasslands also found the greatest CH₄ production in the upper surface peat after rewetting (Knorr et al., 2008a) but the distribution of CH₄ production in peats was generally more variable than that of CO₂ production (Watthei et al., 2009). McKenzie et al. (2004) showed that the uppermost reactive peat layer have little or no effect on CO₂ production with increasing temperature was also observed in knowledge of soil structure parameters, such as pore size and connectivity, that influence the fraction of a soil exposed to anaerobic conditions at low AFP (Schjønning et al., 1999) and the soil surface area affected by desiccation at higher AFP (Richards and Kump, 2003). Relative to initial water saturation conditions, CO₂ production is expected to increase during peat dehydration up to an optimum when further drying leads to a decrease. Under aerobic conditions, CO₂ production in our incubations was consistently lower at the beginning of the drying when peat was near water saturation compared to drier conditions (note marked cross in Fig. 2). Aerobic CO₂ production increased at AFP > 0%, but randomly varied up to AFP values < 50% (Fig. 1) without an apparent pattern for the tested conditions. Therefore “optimum” moisture for CO₂ production in this peat seems to cover a broad range of unsaturated conditions. This insensitivity of respiration to soil moisture may be related to site disturbances such as drainage; CO₂ production was shown to stay lower and relatively constant for even a wider range of AFP conditions in drained compared to natural sites (Waddington et al., 2001). Such response is in agreement with our findings in the Schlöppnerbrunnen fen as the site is known to have been drained in the past.

4.2. Drought effects on CH₄ and its production recovery upon rewetting

In both experiments, we observed CH₄ to be produced for a few days following exposure to air during the drying period. This phenomenon suggests that O₂ did not penetrate uniformly in the peat matrix, which apparently provided anaerobic microniches, a trait that has been previously postulated for this fen soil (Knorr et al., 2008b). Activity of methane oxidizing bacteria might have also contributed to the decline in methane release after venting of the incubation flasks (Jaatinen et al., 2005). Otherwise the response to drought and oxygen exposure was expected and can be related to impact on methanogens, strict anaerobes (Petzer et al., 1993; Kiener and Leisinger, 1983; Kim et al., 2008). The fairly short delays observed for a marginal recovery of methanogenesis especially at higher temperature (Fig. 5), that have been also reported from mesocosms experiments with these peats (Knorr et al., 2008b), may be related to an adaption of the communities to oxygen stress (Öquist and Sundh, 1998). In agreement with field measurements in peat from grasslands (Van den Pol-Van Dasselaar et al., 1999) production patterns among samples remained consistent over time; samples with high rates of methanogenesis before drying usually also recovered first, particularly at low temperature.

We monitored post-drying CH₄ rates and standardized the recovery to pre-drying rates (Fig. 5), which indicates a relative rather than absolute recovery of the process and a relative impact on the methanogenic population. The non-linear shape of the curves agrees with the evolution of CH₄ production in incubated peats (Leffelaar et al., 1999 and references therein). The authors argued that CH₄ production follows three distinct temporal phases (1 – low initially, II – high in the middle, III – “stable” finally) each controlled by different factors (1 – electron acceptors, II – growth of methanogens, III – anaerobic carbon mineralization). We observed the delay for the onset of CH₄ production (Phase I) to be related to the drought event with more severe drying requiring a longer lag for an initial recovery. More intense drought events lead to higher concentrations of electron acceptors in this fen peat (Knorr et al., 2009 and Estop-Aragonés, unpublished results). Such renewal of electron acceptors is thus very likely to have occurred in a similar manner in our incubations and may explain the observed pattern in the lag time for the onset of CH₄ production recovery. The data also suggest higher temperature to shorten this initial recovery phase compared to the colder treatments. A shorter delay on methane production with increasing temperature was also observed in...
incubations from drained fen soils undergoing water saturation (Jerman et al., 2009). The faster depletion of electron acceptors substrates under warmer conditions argues for such finding as increasing temperatures are expected to speed up the onset of all phases (Leffelaar et al., 1999). According to this reasoning, colder treatments required longer to reach full recovery (Phase III). At this final stage and assuming that the monitored period after rewetting was long enough, CH4 production was on average lower at 20 °C compared to that at 11 °C. Considering the previously mentioned substrate limitation, the greater rates associated with the high temperature must have led to faster substrate depletion, which could explain the lower final CH4 production observed at the high temperature treatment. Previous experiments supplying amendments to slurries from this fen also showed that methanogenesis rates were substrate limited (Hamberger et al., 2008; Wust et al., 2009). In this respect, it must be again remarked that during the initial anaerobic phase, the highest CH4 rates at 11 °C were observed at the end of the phase whereas they occurred earlier at 20 °C; it is possible that methanogenic substrate depletion already occurred during that phase. Overall, we suggest that CH4 production recovery under warmer conditions occurred faster because of more rapid electron acceptor consumption and levelled off at a lower level because of substrate limitation in the incubations.

5. Conclusions

The frequency of drying and flooding is predicted to increase in many regions with substantial peatland cover (Meehl et al., 2007) and more frequent and intense shifts in WT position and between aerobic and anaerobic conditions in peats are expected. The depth distribution of production rates, the degree of change upon shift from anaerobic to aerobic conditions and the mean WT position in situ were considered to assess the impact of temporary drought on peat respiration. As documented in many studies, we observedoxic conditions to substantially raise CO2 production, by up to 110%, and to inhibit production of CH4 even for considerable time periods after rewetting. The effect of drying on aggregated soil respiration was limited, however, because CO2 production rates sharply decreased with depth; the upper 5 cm-thick peat layer contributed about 50% to the total CO2 production in this fen soil. Water table fluctuations and associated shifts in oxygen availability and the mode of respiration below this depth had thus only a small impact in our model system. Therefore, the study lends further credibility to observations and experimental findings that changes of in situ WT position have a smaller impact on soil CO2 efflux in dry bogs and degraded fens than previously thought. Within individual soil layers impacts may already occur from short and moderate drought, because more intense or longer drying did not raise CO2 production further, within the limits of soil physical conditions applied and observed in situ at the site. The lack of response to more intense and longer drying may be attributed to adequate oxygen availability at relatively low AFP and an evolving substrate limitation soon after drying begins. In contrast, drying intensity and duration more substantially influence the recovery of CH4 production, which took longer after more intense drying and at the lower experimental temperature. Given an unchanged frequency, more intense and longer drought will thus probably suffice to lower methane emissions after rewetting in electron acceptor-rich peatlands. This should especially be the case when soil temperatures are low, such as in early summer, because electron acceptor stores then need longer time to be depleted.

Acknowledgements

We thank Katarzyna Zajac for assisting in the field and Polina Bam for support in the laboratory. This study was funded by the Deutsche Forschungsgemeinschaft (DFG) grant BL 563/7-3 to Christian Blodau as part of the Research Group FOR 562 — Dynamics of soil processes under extreme meteorological boundary conditions.

Appendix. Supplementary material


References


