The climate warming effect of a fen peat meadow with fluctuating water table is reduced by young alder trees

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SUMMARY

Black alder (*Alnus glutinosa* (L.) Gaertn.) occurs naturally in temperate marshes and in minerotrophic peatlands and is also suitable for paludiculture - the cultivation of biomass on wet or rewetted peatland. We investigated the effect of a newly established black alder plantation on the greenhouse gas (GHG) balance of a degraded fen in north-eastern Germany over a two-year period (August 2010–August 2012). We compared the alder plantation (A_{wet}) with an extensively used meadow (M_{wet}) and a drier reference meadow (M_{moist}). GHG fluxes were measured monthly to bi-monthly using the closed chamber method. Our results show that A_{wet} was a slight net GHG (in CO_2-eq) sink of -3.4 ± 1.7 t ha^{-1} yr^{-1}, M_{wet} was a moderate net GHG source of 9.6 ± 1.2 t ha^{-1} yr^{-1}, and M_{moist} was a strong net GHG source of 24.5 ± 1.6 t ha^{-1} yr^{-1}. This was mainly driven by CO_2 uptake at the two very moist (wet) sites and by high CO_2 release at the drier reference site. A_{wet} was a larger CO_2 sink than M_{wet}, probably due to additional CO_2 uptake by the alder stand at A_{wet} and carbon export in plant material harvested from M_{wet}. All sites were significant CH_4 sources. Substantial CH_4 emission peaks were observed at all sites following extraordinarily heavy precipitation during the summer of 2011, which accounted for up to 70 % of the accumulated two-year CH_4 emissions. However, the A_{wet} site generally emitted less CH_4, possibly due to the effective oxygen transport mechanism in black alders. N_2O emissions were negligible at all three sites. Our results indicate that the GHG balances of formerly drained fens benefit in the short term from planting of black alders, mostly due to reduced CH_4 emissions. This study highlights the importance of acknowledging extreme precipitation events and groundwater fluctuations for the derivation of reliable GHG emission factors.

KEY WORDS: *Alnus*, carbon, drained fen, extreme precipitation events, methane

INTRODUCTION

At global, regional and local scales, pristine peatlands provide many important ecosystem services such as water balance regulation, carbon (C) sequestration and biodiversity (Joosten & Clarke 2002). In addition, as either sources or sinks of the three main greenhouse gases (GHGs) carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), they play a part in climate regulation (Christensen *et al.* 2004). Peatlands store 30 % of the world's soil C, although they cover only 3 % of the global land area (Joosten & Clarke 2002). However, peatlands and their natural functioning are endangered by drainage, land use intensification and climate change (Erwin 2009) leading to peat decomposition and rising GHG emissions (Couwenberg 2011, Luthardt & Wichmann 2016). Moreover, global CO_2 emissions from drained peatlands are estimated at 0.9–1.3 Gt yr^{-1}, and the European Union is the world's second largest CO_2 emitter (Smith *et al.* 2014).

Restoration of drained peatlands is an important task which has been addressed through rewetting measures in many projects during the last 50 years (*e.g.* Pfadenhauer & Grootjans 1999, Christensen *et al.* 2004, Zerbe *et al.* 2013). In Mecklenburg-Western Pomerania (north-eastern Germany), over 18,000 ha of formerly drained peatlands were rewetted before 2008 (Ziebarth 2009). Rewetting initiatives aim to restore nutrient regulation and habitat function (Erwin 2009, Zak *et al.* 2015), and reduce CO_2 and N_2O emissions (Strack & Zuback 2013, Jurasinski *et al.* 2016). However, the new ecosystem can remain a net GHG source of similar magnitude to the prerewetted state due to increased CH_4 emissions following rewetting and subsequent colonisation by 'shunt species' (Komulainen *et al*. 1998, Waddington & Day 2007, Renou-Wilson *et al.* 2016). This effect could be amplified under inundated conditions (Wilson *et al.* 2009, Cooper *et al.* 2014).

Climate change is expected to further complicate the management of wetland restoration (Erwin 2009). As a result of global warming, the frequency of extreme weather is expected to increase (Hansen *et al.* 2012), leading to warmer winters and hotter summers in Central Europe (Bauwe *et al.* 2016). Therefore, even higher GHG emissions from peatlands in northern regions are projected for the future (Smith *et al*. 2014). Although it remains uncertain whether annual precipitation totals for northern European countries will change (Beniston *et al.* 2007), global warming may also promote the occurrence of heavy precipitation events (Ban *et al.* 2015). In addition, drained fens tend to become more frequently inundated with increasing time after drainage, due to progressive peat compaction and concomitant changes in the hydrological properties of the peat (Schindler *et al*. 2003). This leads to an overall loss of oscillation capability (Whittington & Price 2006). Because such changes are not reversible (in the short to medium term) through rewetting, restored peatlands will continue to be affected until a significant amount of new peat has been formed. Therefore, it is likely that these factors (*i.e.*, increasing frequency and severity of climate extremes such as droughts and heavy precipitation, changes in hydrological properties of the peat through water table drawdown) will cause stronger water table (WT) fluctuations and hence higher frequencies of surface flooding (inundation) in drained and rewetted peatlands under current and future climate conditions.

The concept of paludiculture offers biomass cultivation options for site-adapted plant species on wet and rewetted peat soils, with the intention of reducing GHG emissions through peatland rewetting whilst also retaining farm incomes (Oehmke & Abel 2016). Suitable species and their impact on GHG dynamics have been discussed in various studies of, for example, common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), sedges (*Carex* spp.), common bulrush (*Typha latifolia* L.) (Wild *et al.* 2001, Günther *et al.* 2015), reed canary grass (*Phalaris arundinacea* L.) (Karki *et al.* 2015, Zak *et al.* 2015) and *Sphagnum* spp. (Günther *et al.* 2017).

The cultivation of black alder (*Alnus glutinosa* (L.) Gaertn.) on waterlogged but not permanently inundated soils (where it occurs naturally) provides a promising alternative to low-intensity grazing (Claessens *et al.* 2010, Oehmke & Abel 2016). Alder woodland can be used for fuel and timber production whilst sequestering C in the medium term (Oehmke & Abel 2016). In addition, there are potential biodiversity benefits, since wet alder forests have been identified as valuable habitats for rare plant and animal species (Claessens *et al*. 2010).

In general, the GHG balances of different land use options for peatlands have received considerable attention in recent years (*e.g*. Christensen *et al.* 2004, Günther *et al.* 2015, Tiemeyer *et al.* 2016, Wilson *et al.* 2016). However, the effect of black alder plantations on the full GHG balance of minerotrophic peatland (*i.e.* fen) has not yet been studied. To date, closed-chamber GHG measurements for alder stands have usually been done for single gases, either between the trees or in incubation experiments (Mander *et al.* 2008, Eickenscheidt *et al.* 2014). Closed-chamber measurements have recently been carried out in stands of tall vegetation, for example reeds (Günther *et al.* 2015), and the same method can be applied to derive full GHG balances for young alder trees of similar stature.

The aims of the study described here were to:

i) determine the full GHG balance (CO_2, CH_4 and N_2O fluxes) of a newly established black alder plantation growing in very moist soil on a degraded fen in north-eastern Germany using manual chambers that enclosed the trees;
ii) separate the effects of the black alder plantation and WT on GHG emissions by comparing GHG balances between the alder plantation, extensively used (sedge-dominated, very moist) and intensively used (grass-dominated, moderately moist) fen meadow;
iii) estimate the responses of GHG emissions to inundation resulting from naturally occurring WT fluctuations under these three land-use options; and
iv) calculate the effect of the alder plantation on the C balance in the short term and consider how it may develop in the future.

METHODS

Study area

The study area 'Kleiner Landgraben' is a typical percolation mire of the southern Baltic region (Succow 2001) located in north-eastern Germany (53° 40' N, 13° 18' E; Figure 1). The fen developed in a glacigenic tunnel valley, formed by retreating ice at the end of the Weichselian glacial about 10,000 years ago. The climate of the study region is temperate and humid, with average annual

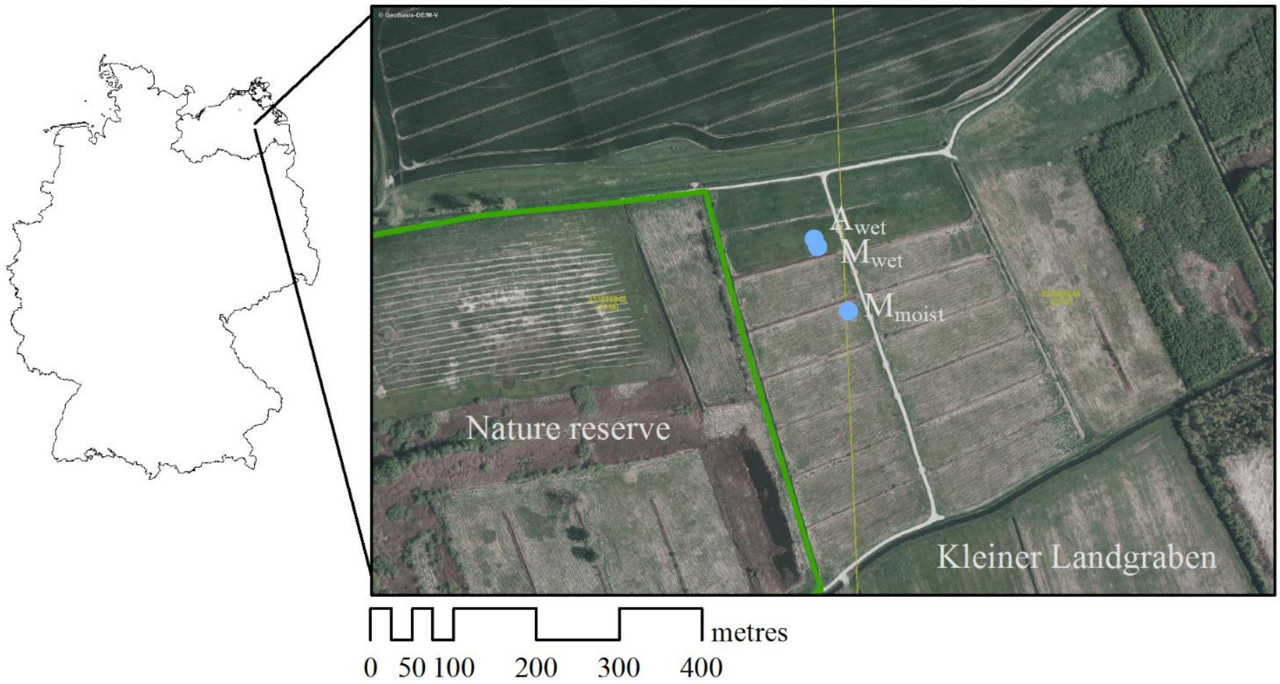

Figure 1. Map of the study area showing the three measurement locations, the adjacent nature reserve "Waidmannslust" and the river 'Kleiner Landgraben'. The inset shows the geographical position in north-east Germany (Mecklenburg-Western Pomerania).

precipitation 530 mm and air temperature 8.7 °C (1981–2010, German Meteorological Service (DWD)). The first drainage ditches were built during the Middle Ages and they were deepened regularly until intensive drainage measures during the 1970s enabled use of the land as meadows and pastures (Jeschke 2003). The present vegetation of the study area is characterised by communities of intensively used grassland with moderately moist soil conditions (Roth & Succow 2001, Couwenberg *et al.* 2008). On a few wetter areas, wetland plants typical of very moist soil conditions, such as sedges and reeds, can be found.

Experimental setup

Three measurement sites were established within the study area: a moderately moist reference site (moist meadow, M_{moist}) on drained, degraded fen with typical grassland communities; a very moist site dominated by sedges (wet meadow, M_{wet}); and a very moist site dominated by sedges, with an alder plantation (A_{wet}). The terms 'moderately moist' and 'very moist' originate from the concept of water level classes as site descriptors that integrate long-term mean annual WT and WT fluctuations and can be related to certain vegetation community types (*cf.* Roth & Succow 2001, Couwenberg *et al.* 2008, Couwenberg *et al*. 2011). In this concept, a water level class of 4+ is described as 'very moist', whereas a water level class of 2+ is described as 'moderately moist' (*cf.* Table 1). To establish a clear nominal distinction between our study sites, we indexed the ones with very moist soil conditions (water level class 4+) as 'wet' (A_{wet} and M_{wet}) and those with moderately moist soil conditions (water level class 2+) as 'moist' (M_{moist}). Since the water level classes reflect long-term site characteristics, the actual conditions observed during a short-term study period may deviate from values assigned to the class.

The sites were all within 100 m of one another (Figure 1). The vegetation of M_{moist} was classified as an intensive, polytrophic meadow community. A high abundance of meadow foxtail (*Alopecurus pratensis* L.) indicated former intensive grassland use with several harvests *per* year and an ample nutrient supply (*cf.* Appendix). Other less-abundant species included *Poa pratensis* L., *Agrostis stolonifera* L. and *Ranunculus repens* L. A lower, naturally wetter area within the degraded fen was selected to accommodate M_{wet} and A_{wet} and to mimic expected conditions for the entire fen after rewetting. Here, the vegetation was dominated by acute sedge (*Carex acuta* L.), with lower cover of brown sedge (*Carex disticha* Huds.), reed mannagrass (*Glyceria maxima* (Hartm.) Holmb.) and reed canary grass. In A_{wet}, 20 young black alders (approximately 1.5 m tall and 8 years old) were planted in June 2010 within an area of 48 m².

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Three replicate square PVC collars (0.75 m × 0.75 m × 0.15 m) *per* site were inserted next to each other, targeting similar vegetation representative of each site (*cf*. Appendix), and inserted approximately 10 cm into the peat. The collars remained on site during the whole study period (August 2010 – August 2012). Measurement campaigns with manual closed chambers were done bi-monthly for CO_2 and monthly for CH_4 and N_2O. For every measurement, wooden boards were placed on top of pre-installed wooden poles around each collar to minimise damage and disturbance to the sites, which could cause gas ebullition events and lead to bias in the measurements. The meadow sites M_{moist} and M_{wet} were harvested once *per* year in July 2011 and June/July 2012.

Measurements

Environmental conditions

Air temperature at 200 cm height (°C), soil temperature at 2, 5 and 10 cm depth (°C), air pressure (Pa), photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}), relative humidity (%) and wind velocity (m s^{-1}) were recorded at half-hourly intervals by a climate station (WXT520, Vaisala, Finland) located next to the M_{wet} site. Precipitation data (mm) were provided by a ZALF-climate station (Dedelow, 60 km south-east of the Kleiner Landgraben). WT was measured half-hourly with a groundwater data logger equipped with a high precision pressure sensor (ATP00, Aquitronic, Germany) < 10 m from the measurement sites M_{wet} and A_{wet}. The WT data were adapted for each measurement site according to their respective differences in altitude, assuming similar WT fluctuations due to homogenous site conditions and a common land use history. Negative WT values indicate WT levels below the surface.

Prior to GHG measurements, soil sampling was performed in November 2009 next to the gas measurement sites M_{wet} and A_{wet}. This indicated highly degraded peat in the uppermost 30 cm and less degraded peat at 50–70 cm depth (Table 1). Peat thickness across the whole site was mostly 100–200 cm but occasionally exceeded 200 cm (data not shown).

GHG exchange measurements

For GHG exchange measurements, rectangular chambers (75 cm × 75 cm basal area) were placed on the PVC collars. Airtight closure between chamber and collar was ensured by rubber gaskets at the chamber bottom and two additional elastic belts. The chamber volume was 0.296 m³ or 0.316 m³, depending on the chamber used (height 52.6 cm or 56.2 cm). Chamber extensions (75 cm × 75 cm × 52.6 cm) were used to increase the chamber height to accommodate the black alders (three extensions + chamber) and mature grassland vegetation (one extension + chamber). During the CO_2 measurements, air temperatures inside and outside the chamber, soil temperature at 2, 5 and 10 cm depth as well as PAR were recorded. During CH_4 and N_2O measurements, only air temperature outside the chamber and soil temperature at 2, 5 and 10 cm depth were recorded.

The CO_2 exchange was measured with flow-through non-steady-state manual chambers (Livingston & Hutchinson 1995) during 14 two-day measurement campaigns between August 2010 and August 2012. Opaque chambers were used for ecosystem respiration (R_{eco}) and separate transparent chambers (86 % light transmission) for net ecosystem exchange (NEE) measurements. To cover the full diurnal range of temperature and PAR, and thus of plant and microbial activity, flux measurements were performed throughout the day, starting before sunrise and ending in the afternoon (Huth *et al.* 2017). The chambers for CO_2 exchange measurements were equipped with fans to avoid air stratification. When extension chambers were used, additional fans were placed within the chamber headspace. To measure the CO_2 concentration change over time, a portable CO_2 infrared gas analyser (LI-820, Li-COR) was connected to the chamber with flexible tubes while a pump generated a continuous air flow. The CO_2 concentration was logged every five seconds with a data logger (CR1000, Campbell Scientific, USA) for five minutes *per* measurement.

Monthly measurements of CH_4 and N_2O fluxes were conducted with non-flow-through non-steady-state opaque chambers (Livingston & Hutchinson 1995). Each chamber was equipped with four vents on the top to connect evacuated gas bottles (60 ml) for air sampling. The initial sample was taken directly after chamber placement, then three more samples at 20-minute intervals over a total period of 60 minutes followed. The air samples were analysed for CH_4, N_2O and CO_2 concentrations with a gas chromatograph (GC-14A and GC-14B, Shimadzu Scientific Instruments, Japan; detectors: flame ionisation detector for CH_4, electron capture detector for CO_2 and N_2O). When the WT was above the soil surface, we used open-top chamber extensions that were carefully placed on top of the collars until the chambers could be placed on top of the extensions. The WT level was measured for each site and collar during the gas measurement campaigns and the appropriate water column volume was then subtracted from the extension-chamber volume.

Table 1. Selected characteristics of the three study sites. Water table (WT) classes follow Roth & Succow (2001) and Couwenberg *et al.* (2008) and represent long-term site characteristics (note that conditions during the study period may vary). A single core was taken within an area of 2 × 2 m, < 10 m from the measurement sites M_{wet} and A_{wet}, and the following peat properties were determined: degree of decomposition (von Post scale); dry mass content of carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), iron (Fe) and aluminium (Al) (mg g^{-1}) of the upper peat layer (10–30 cm depth) and the deeper, moderately decomposed peat layer (50–70 cm depth). Values are rounded up and represent median values and ranges (n = 3–6).

Site	M_{moist}	M_{wet}	A_{wet}
Land use/disturbance	intensive meadow	extensive meadow	black alder plantation
WT class	2+*	4+**	4+**
Dominant species	*Alopecurus pratensis*	*Carex acuta*	*Carex acuta*, *Alnus glutinosa*

	all sites	
Peat sampling depth	10–30 cm	50–70 cm
Degree of decomposition	H10	H5–H6
Dry bulk density (mg dm^{-3})	199 (190–200)	119 (116–122)
Loss on ignition (% of dry mass)	78 (77–79)	92 (91–92)
C_t	398 (393–416)	511 (503–515)
N_t	31 (29–31)	26 (26–27)
P_t	2.3 (1.8-2.7)	0.5 (0.5-0.5)
Ca_t	37 (35–45)	24 (23–25)
Fe_t	12 (10–12)	5.0 (4.6–5.3)
Al_t	2.8 (2.5–3.0)	0.5 (0.4–2.8)
C/N quotient (molar)	15.6 (14.8–15.8)	22.5 (22.4–23.5)

*winter WT -35 to -70 cm, summer WT -45 to -85 cm; **winter WT -5 to -15 cm, summer WT -10 to -20 cm.

CO_2 flux calculation and gap filling

Flux calculation, gap filling and error prediction were performed with R 2.15.2 (R Core Team 2012) using the modular R script from Hoffmann *et al.* (2015). Fluxes (F in g m^{-2} s^{-1}) were calculated using the ideal gas law:

$$F = \frac{MpV}{RTA} \cdot \frac{\mathrm{d}c}{\mathrm{d}t} \qquad [1]$$

where M is molar mass of the gas (g mol^{-1}), p is the ambient air pressure (Pa), V is chamber volume (m^3), R is the gas constant (8.314 m^3 Pa K^{-1} mol^{-1}), T is the temperature inside the chamber (K), A is inside-collar surface area (0.5625 m^2), and dc/dt is the linear CO_2, CH_4, or N_2O concentration change over time (s^{-1}).

To determine the rate of CO_2 concentration increase dc/dt in the chamber headspace, a linear regression analysis was applied to the CO_2 concentration measurements. We used a variable moving window (> 35 s) of a subset of concentration data points in order to find the best linear fit. To avoid bias due to disturbance during chamber placement and saturation or desaturation effects, 10 % of the data from the beginning and end of each measurement were discarded prior to flux calculation. All calculated fluxes were tested for normality, variance homogeneity and linearity using the Kolmogorov-Smirnov and the Breusch-Pagan tests (α = 0.1). CO_2 fluxes were, furthermore. discarded if they met any of the following criteria:

- non-significant regression slope (P-value > 0.1);
- temperature differences within the flux window > 0.75 K; and
- PAR variation within the flux window > ± 10 %.

Fluxes passing through screening according to these criteria were assumed to represent the least disturbed part of the measurement. Fluxes are reported using the atmospheric sign convention, where positive values represent GHG fluxes from the soil to the atmosphere.

To model CO_2 exchange over the two-year study period, CO_2 fluxes measured using the three collars at each site were combined following Hoffmann *et al.* (2015). For R_{eco} fluxes, temperature dependent Arrhenius type respiration models (Lloyd & Taylor 1994) were used for each measurement campaign by fitting measured R_{eco} fluxes to measured soil and air temperatures. The R_{eco} model with the lowest AIC (Akaike's Information Criterion) and statistically significant model parameters was used for further gap filling. Since gross primary production (GPP) was not measured directly, GPP fluxes were computed by subtracting the corresponding modelled R_{eco} fluxes from the measured NEE fluxes. This has been shown to be a prerequisite to avoid underestimation of GPP (see Huth *et al.* 2017 for details). To derive campaign-specific GPP models, calculated GPP fluxes were fitted to the measured PAR values using a rectangular hyperbolic light response function (Michaelis-Menten Kinetics). If no significant models could be fitted for either R_{eco} or GPP, the respective average campaign fluxes were used for interpolation.

Subsequently, half-hourly GPP and R_{eco} fluxes were modelled by applying the campaign-wise derived R_{eco} and GPP models to continuously recorded temperature and PAR values (climate station). Fluxes between two campaigns were obtained by using a temporally weighted average of the two fluxes calculated with model parameters of the neighbouring campaigns (Günther *et al.* 2015, Hoffmann *et al.* 2015). To estimate the model uncertainty, the error calculation was performed as described by Hoffmann *et al.* (2015).

CH_4 and N_2O flux calculation and gap filling

Similarly to the CO_2 fluxes, CH_4 and N_2O fluxes were calculated using Equation 1, assuming a linear concentration increase over the measurement time. For flux calculations we used an adaptation of the modular R script for CO_2 flux calculation (Hoffmann *et al.* 2015). Prior to flux calculation, the GC analysis of CH_4 and N_2O concentrations was checked for reliability using the expected CO_2 concentration increase (R_{eco}; opaque chamber) over the measurement time as an indicator (Jurasinski *et al.* 2014). Biased measurements (< 7 %) were excluded from further analysis. In order to increase the robustness of flux calculation, concentration measurements from all three collars *per* site and measurement campaign were combined into one dataset and later used for flux calculation ($n = 12$). Aggregated concentration data were checked for outliers, using a multiple of the inter-quartile range (6 × IQR) of the regression residues as a threshold criterion. The measured CH_4 and N_2O fluxes were interpolated linearly between campaigns to obtain annual estimates.

Error calculation for the fluxes from the measurement campaigns was performed using a step-wise bootstrapping algorithm. Firstly, one concentration measurement was randomly left out before calculating the flux. This procedure was repeated 100 times. From the distribution of fluxes we derived a confidence interval for each flux. Subsequently, the bootstrapped fluxes were randomly sampled again 100 times for each campaign within the confidence interval from the computed distribution of fluxes. These were then used for gap filling *via* linear interpolation between the campaigns. We estimated the uncertainty of the inter-campaign period from the distribution of the interpolated emissions between two consecutive measurement campaigns. The accumulated error for each site was then derived according to the law of error propagation and the respective inter-campaign errors.

Net GHG and C balance

The annual net GHG balances were calculated in CO_2 equivalents (CO_2-eq) for accumulated CO_2, CH_4 and N_2O fluxes, using conversion factors for a 100-year time horizon ($CO_2 = 1$, $CH_4 = 28$, $N_2O = 265$; Myhre *et al.* 2013). Changes in the ecosystem C stock (plants and soil) were determined by a simple C balance composed of gaseous C exchange (CO_2 and CH_4) and C export due to harvest removals. Lateral C fluxes (dissolved organic and inorganic C) were not considered because a minor contribution of less than 10 g m^{-2} yr^{-1} can be assumed (Tiemeyer & Kahle 2014). Mixed samples of the plant material from each site and harvest were analysed for C content using elementary analysis ($n = 2$, TruSpec CNS, Leco Instruments GmbH, Germany).

RESULTS

Environmental conditions

During the two-year study period, a total of 1358 mm of precipitation was recorded (climate station Dedelow, ZALF, Figure 2). Mean annual precipitation was 651 mm yr^{-1}, which is 23 % more than the 30-year average (1981–2010, Neubrandenburg, DWD).

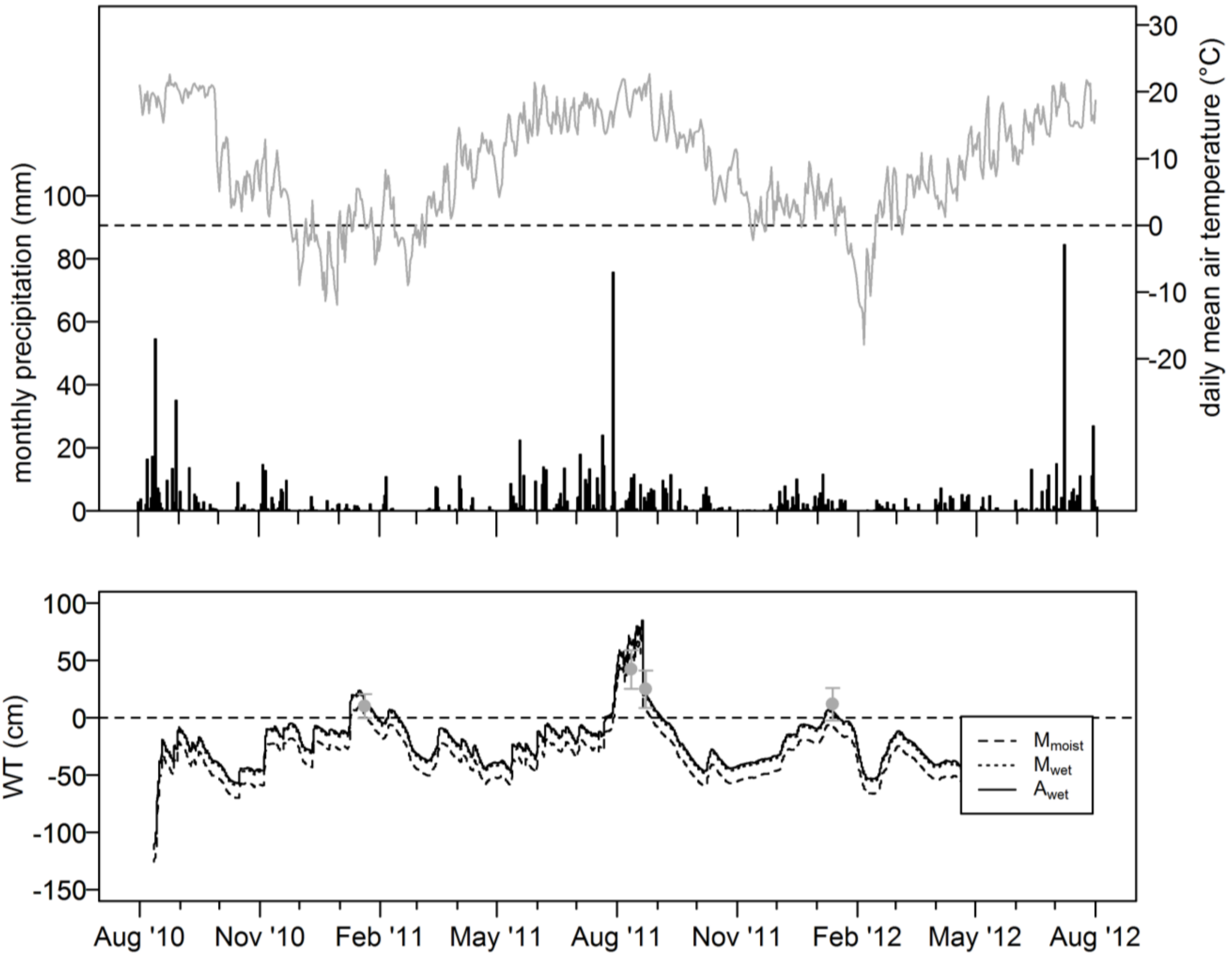

Figure 2. Environmental conditions of the study area 'Kleiner Landgraben'. Daily mean air temperature (°C) and monthly precipitation (mm) at the nearby climate station Dedelow (upper panel), and water table level (WT; cm) dynamics (lower panel) at the study sites M_{moist}, M_{wet}, A_{wet}. Grey dots show manually measured WT at the nine collars during the different inundation periods (mean ± standard deviation).

July 2011 was exceptionally wet with a total precipitation of 198 mm, which is > 350 % of the 30-year average for July (53 mm, Neubrandenburg, DWD). Since this extreme event fell right in the middle of the study period, separation of the results into two years in order to compare a first year (from August 2010 to July 2011) with a second year (from August 2011 to July 2012) would be arbitrary, due to the possibility of a time-delayed response in GHG emissions. Therefore, annual values were calculated as averages based on the total number of measurement days.

Mean WT levels were -34 cm for M_{moist}, -23 cm for M_{wet} and -21 cm for A_{wet} (Table 2). During most of the study period, the water table remained below the peat surface (Figure 2). The highest WT level was measured following the heavy precipitation in July 2011, which caused inundation of all three sites in August 2011 (M_{moist}: 34 cm, M_{wet}: 45 cm, A_{wet}: 47 cm above peat surface). Surface flooding peaked on 20 and 21 August when WT levels reached 72 cm (M_{moist}), 83 cm (M_{wet}) and 85 cm (A_{wet}).

The study period was cooler (7.4 °C) than the reference period (8.7 °C, 1981–2010, Trollenhagen, DWD). The winter of 2010/11 (November to February) was very cold with an average temperature of -0.1 °C (reference period: 1.5 °C). The coldest month was December 2010 with an average temperature of -5 °C (reference period: 1 °C). In contrast, the winter of 2011/12 was similar to the reference period (1.6 °C and 1.5 °C, respectively), and only February 2012 was colder than the long-term average (-2.3 °C and 0.7 °C, respectively). The sites were covered with ice and snow during the months of December 2010, February 2011 and February 2012.

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Table 2. Environmental variables and greenhouse gas (GHG) fluxes during the study period. Average water table level (WT), average annual precipitation (mm) and average air temperature (°C) are given. Cumulative GHG fluxes and carbon (C) balances are standardised to annual values. The net GHG balance (in CO_2-eq) was calculated using the conversion factors 28 for methane (CH_4) and 265 for nitrous oxide (N_2O) (100-year horizon, no climate–carbon feedback, Myhre *et al.* 2013). The full GHG balance includes C export as harvest calculated according to Couwenberg *et al*. (2011) and IPCC (2014). The C balance is the sum of NEE (CO_2-C), the C content of the biomass removed as harvest (± one standard error for the three respective collars) and $F_{CH4\text{-}C}$ (all in g m^{-2} yr^{-1}). Estimation of errors in gas flux measurements is described in the Methods section. Error estimation for the GHG balance and the C balance follows the law of error propagation.

		M_{moist} moist meadow	M_{wet} wet meadow	A_{wet} black alder
average WT (cm)		-34	-23	-21
average precipitation (mm yr^{-1})			651	
average air temperature (°C)			7.4	
	GPP	-1158 ± 14	-1213 ± 18	-1993 ± 29
$F_{CO2\text{-}C}$ (g m^{-2} yr^{-1})	R_{eco}	1471 ± 25	1144 ± 20	1819 ± 35
	NEE	314 ± 29	-69 ± 27	-175 ± 46
$F_{CH4\text{-}C}$ (g m^{-2} yr^{-1})		18.2 ±2.7	17.8 ± 0.7	8.2 ± 0.5
$F_{N2O\text{-}N}$ (g m^{-2} yr^{-1})		0.06 ± 0.03	0.10 ± 0.05	-0.02 ± 0.02
GHG balance (t ha^{-1} yr^{-1})		18.5 ± 1.5	4.5 ± 1.0	-3.4 ± 1.7
GHG balance (in CO_2-eq) incl. harvest (t ha^{-1} yr^{-1})		**24.5 ± 1.6**	**9.6 ± 1.2**	-
C biomass harvest (g m^{-2} yr^{-1})		166 ± 11	143 ± 17	-
C balance (g m^{-2} yr^{-1})		498 ± 31	92 ± 32	-167 ± 46

Net CO_2 exchange

The gap-filled R_{eco} models were generally better than the gap-filled NEE models (Table 3). The flux curves for the three sites showed clear seasonal patterns in CO_2 emissions, with near-zero GPP and low R_{eco} in winter and highest activity during the growing season (Figure 3). Annual R_{eco} was higher and annual GPP was lower at the M_{moist} site than at the M_{wet} site, resulting in NEE values (expressed as CO_2-C) of 314 ± 29 g m^{-2} yr^{-1} for M_{moist} and -69 ± 27 g m^{-2} yr^{-1} for M_{wet} (Table 2). Annual R_{eco} and GPP were approximately 50 % higher at A_{wet} than at M_{wet}. However, A_{wet} was the strongest annual CO_2-C sink (-175 ± 46 g m^{-2} yr^{-1}).

CH_4 and N_2O emissions

All of the experimental sites were small CH_4-C sources with daily fluxes below 0.02 g m^{-2} d^{-1} during most of the study period. The highest daily CH_4-C flux (0.73 g m^{-2} d^{-1}) was measured at M_{moist} during the flood, on 23 August 2011 (Figure 4). Similar CH_4-C emission peaks were observed at M_{wet} (0.47 g m^{-2} d^{-1}) and A_{wet} (0.28 g m^{-2} d^{-1}) in August 2011. The duration of elevated CH_4 emissions was longest in M_{wet} (starting in July 2011), while the peak period at A_{wet} and M_{moist} was limited to August and September 2011. Site A_{wet} emitted significantly less CH_4-C (16 ± 1.0 g m^{-2}) over the two-year study period than the other two sites, which showed similar overall CH_4-C emission rates of 35 ± 1.3 g m^{-2} (M_{wet}) and 32 ± 4.6 g m^{-2} (M_{moist}) (Figure 4).

In order to quantify the effect of the naturally induced inundation, the cumulative CH_4 fluxes were recalculated to exclude the flux measurements that were acquired during the flood in August 2011 (grey numbers in Figure 4). The recalculated emissions were lower at all sites, by 69 % at M_{moist}, 19 % at M_{wet} and 58 % at A_{wet}. At M_{wet}, emissions in July and

Table 3. Nash-Sutcliffe model efficiency (NSE), coefficient of determination multiplied by the slope of the linear regression (bR^2), single values for b and R^2, and root-mean-square error (RMSE, g m^{-2} half-hour^{-1}) of the 1:1 relationships of measured *versus* modelled (R_{eco}) and calculated (NEE) half-hourly CO_2 fluxes used for gap filling.

	NSE		bR^2		b		R^2		RMSE	
Site	NEE	R_{eco}	NEE	R_{eco}	NEE	R_{eco}	NEE	R_{eco}	NEE	R_{eco}
M_{moist}	0.69	0.71	0.60	0.66	0.82	0.92	0.73	0.72	0.04	0.05
M_{wet}	0.56	0.78	0.66	0.79	0.96	0.99	0.69	0.80	0.03	0.11
A_{wet}	0.76	0.82	0.67	0.78	0.87	0.95	0.77	0.82	0.04	0.12

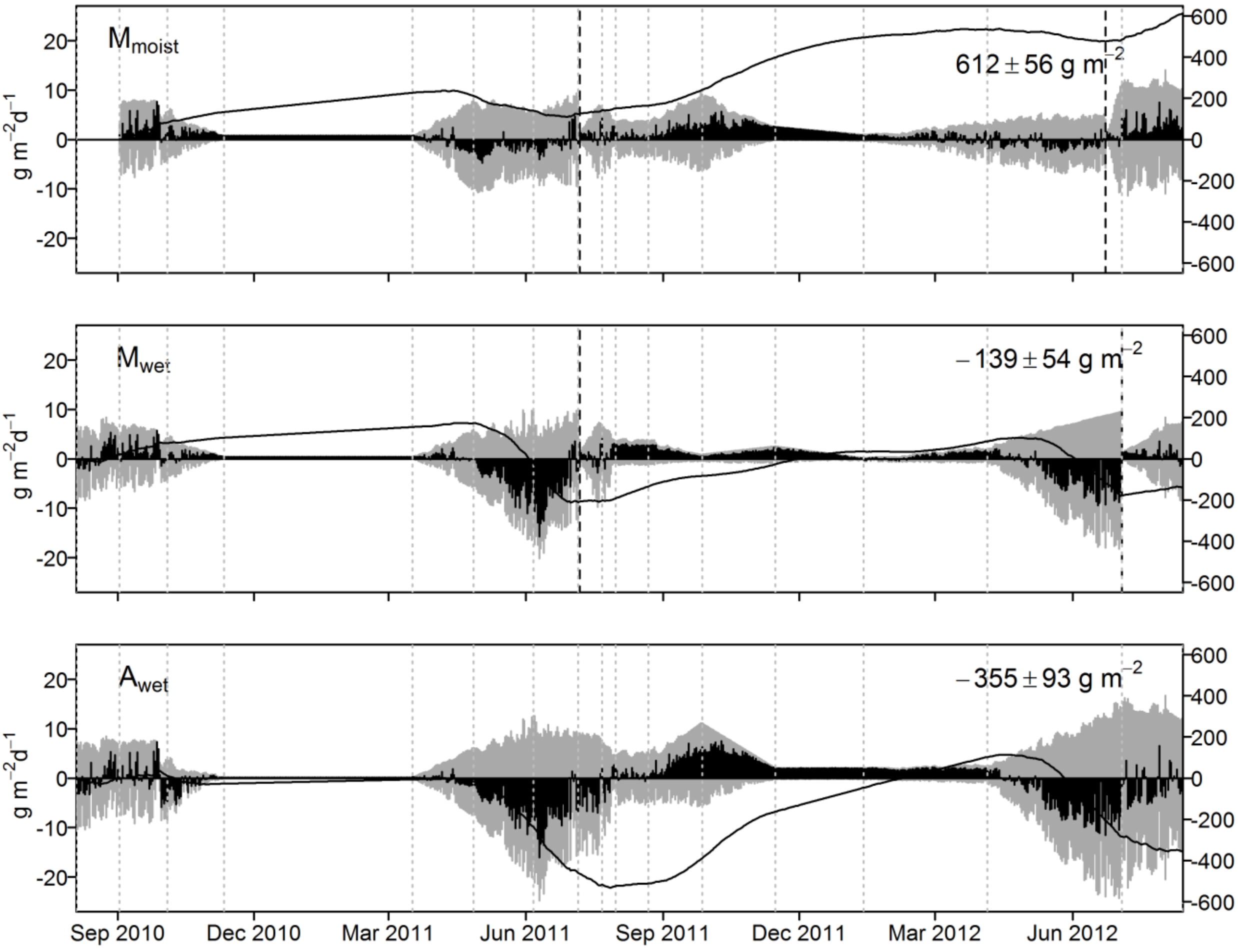

Figure 3. Time series of CO_2-C exchange (g m^{-2} d^{-1}) at the sites M_{moist}, M_{wet} and A_{wet}. Positive grey bars represent modelled daily R_{eco} fluxes, negative grey bars represent modelled daily GPP fluxes, and black bars show the calculated daily NEE (all in g m^{-2} d^{-1}). Cumulative NEE (g m^{-2}) is shown by the solid black line (right-hand y-axes) and the numbers (± standard error) at upper right of each pane. Vertical dashed lines indicate harvest dates, and vertical grey dotted lines indicate gas measurement dates. Mean CO_2 fluxes at the sites during the winter of 2010/2011 were derived by simultaneously sampling CO_2, methane (CH_4) and nitrous oxide (N_2O), using opaque chambers and subsequent gas chromatograph measurements. Note that the CO_2 measurements at M_{moist} in July and August 2012 were carried out on two collars only, because one collar was accidentally destroyed by local farming practices.

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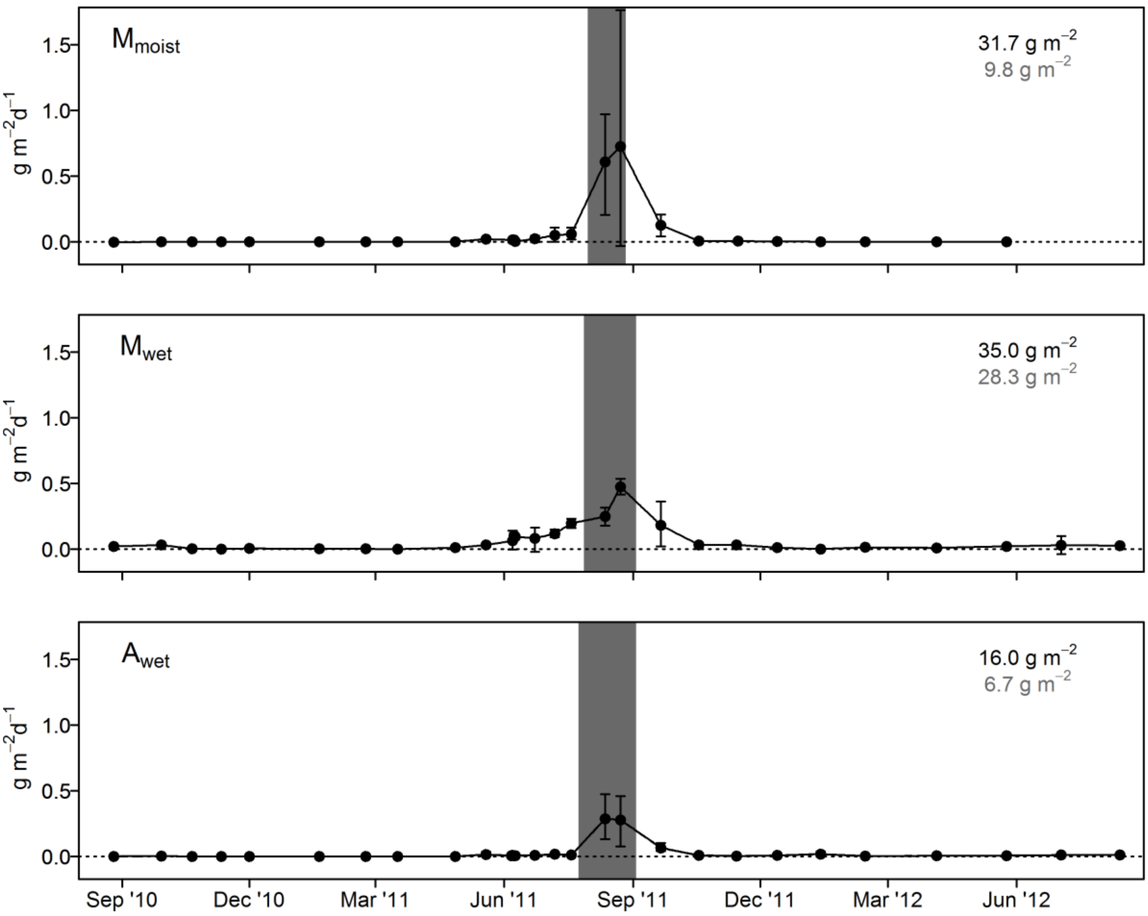

Figure 4. Methane (CH_4-C) fluxes (g m^{-2} d^{-1}) at the study sites M_{moist}, M_{wet} and A_{wet}. Dots represent measured campaign fluxes with calculated standard errors (bars). Numbers indicate cumulative CH_4 fluxes (black = all measurements, grey = August 2011 measurements excluded). Grey areas indicate the period of surface flooding (WT > 0 cm) that followed heavy precipitation in the summer if 2011. Note that the last measurement before August was on 19 July and the first measurement after the flood had receded was on 21 September. Also note that July and August 2012 measurements of M_{moist} are missing due to destruction of the vials (July) and faulty GC measurements (August).

August accounted for 29 % of total emissions because the CH_4 emissions increased earlier than in the other sites. The absolute effect of the flood event was highest at M_{moist}, where the August 2011 measurements contributed 22 g m^{-2} of CH_4-C, while the event added only 6.7 and 9.3 g m^{-2} to overall CH_4-C emissions at the two wet sites.

In contrast, N_2O fluxes were very low throughout the study period, except for single measurement days on 20 Jan 2011, 07 June 2011 and 03 March 2012. Overall, the cumulative N_2O emissions were not significantly different from zero (Table 2).

Net GHG and C balances

The GHG fluxes of the two-year study period were aggregated and averaged on an annual basis (Table 2). The M_{moist} site was a strong net GHG source of (in CO_2-equivalents) 24.5 ± 1.6 t ha^{-1} yr^{-1}, while the the M_{wet} site was a moderate GHG source of 9.6 ± 1.2 t ha^{-1} yr^{-1}, and the A_{wet} site was a net GHG sink of -3.4 ± 1.7 t ha^{-1} yr^{-1}. However, C accumulation and potential C export at A_{wet} were not considered in these calculations. At the M_{moist} site, NEE accounted for the major part of the GHG balance (47 %). The relative contribution of CH_4 emissions was highest for A_{wet} (89 %, compared to 69 % for M_{wet} and 28 % for M_{moist}), whereas N_2O emissions contributed only 1 % (M_{moist}), 3 % (M_{wet}) and 2 % (A_{wet}) to the full GHG balance.

The C balances indicate that the M_{moist} site was a significant C source whereas M_{wet} was a minor C source and A_{wet} was a C sink of -167 ± 46 g m^{-2} yr^{-1} during the study period (Table 2). Harvesting approximately 143–166 g m^{-2} yr^{-1} of C in biomass leads to additional C losses in the case of the two meadows.

DISCUSSION

GHG emissions

The frequency of NEE measurements in this study was rather low. The measurements were centred around the growing season when changes in plant phenology occur within rather short periods of time. Long gaps during critical changes in plant phenology have been shown to affect estimates of annual NEE (in CO_2-C) with an uncertainty of more than ± 150 g m^{-2} (Huth *et al*. 2017, Moffat *et al*. 2018). This means that, although measurements were conducted in parallel at the three sites, the difference in NEE between A_{wet} and M_{wet} may be within the uncertainty resulting from filling long gaps. However, despite similar values of NEE and GPP/R_{eco}, GPP and R_{eco} fluxes were higher (~ 48 %) for A_{wet} than for M_{wet} indicating the additional activity of the young alders. Both sites are likely to be similar net CO_2 sinks when the harvest at M_{wet} is not taken into account. In contrast, M_{moist} was a net CO_2 source even without C export and gap-filling uncertainty (Huth *et al*. 2017, Moffat *et al*. 2018). These results are in accordance with the literature (Strack & Zuback 2013, Karki *et al*. 2015) and show that even a slight decrease in mean annual WT can lead to substantially increased aeration of the upper peat layers, peat mineralisation and CO_2 release (Christensen *et al*. 2004, Couwenberg *et al*. 2011, Tiemeyer *et al*. 2016).

All three measurement sites were CH_4 sources throughout the entire study period. Disregarding the inundation-induced CH_4 emission peak in 2011, annual emissions from A_{wet} were lower than those from pristine or rewetted peatlands (e.g., Saarnio *et al.* 2009, Huth *et al.* 2013, Wilson *et al.* 2016). However, the periods of low CH_4 emissions were counterbalanced by pronounced CH_4 release during the flood in August 2011, when measurements were conducted with WT levels 43 cm and 23 cm above the ground surface. For these measurements we took special care to place the open-top chamber extensions on the collars before chamber deployment, in order to reduce the potential for raising gas bubbles through over-pressurisation during chamber deployment (Chanton & Whiting 1995) and hence over-estimating CH_4 emissions (see Methods).

WT has been shown to be a major control on CH_4 emissions (Couwenberg *et al.* 2011, Tiemeyer *et al.* 2016). A specific WT threshold of -10 cm, above which CH_4 emissions are promoted, was introduced by Jungkunst & Fiedler (2007). This is confirmed in our study by the enhanced CH_4 emissions following the summer flood of 2011. Although other heavy precipitation events occurred in August 2010 and July 2012, WT remained below -10 cm, most probably due to an even lower initial WT (Figure 2). Therefore, no CH_4 emission peaks were observed after these precipitation events.

Plant species also affect CH_4 emissions (Couwenberg *et al.* 2011, Günther *et al.* 2015). Different wetland species present in M_{wet} and A_{wet} significantly altered annual CH_4 emissions during the present study. Firstly, sedges may transport CH_4 from anoxic layers to the atmosphere (Noyce *et al.* 2014), which could add to the higher CH_4 emissions from the M_{wet} site compared to the M_{moist} site outwith the period of inundation. Secondly, due to their aerenchyma tissues and their ability to actively induce mass flow, black alders are assumed to influence CH_4 emissions in two ways. On the one hand, CH_4 produced in the anaerobic zone reaches the atmosphere by plant-mediated transport, bypassing the aerobic zone (Rusch & Rennenberg 1998, Gauci *et al.* 2010, Pangala *et al.* 2015). On the other hand, oxygen is actively transferred into the rhizosphere, producing aerobic conditions (Kozlowski 1997) under which CH_4 can be oxidised. In contrast, sedges admit oxygen to the rhizosphere by diffusion only (Ding *et al.* 2004). Our data showed reduced CH_4 emissions from A_{wet} compared to M_{wet} both during and outwith the period of inundation. Therefore, it is likely that more active oxygen transport in the black alders promoted CH_4 oxidation and countered CH_4 transport through the trees and sedges more strongly than at the site dominated by sedges only (M_{wet}). This is further supported by Mander *et al.* (2008), who reported a CH_4-C sink value of up to -0.2 g m^{-2} yr^{-1} for an alder marsh forest.

The measured N_2O-N fluxes were negligible at all three sites, which is rather typical for pristine and rewetted fens (Nykänen *et al.* 1995, Günther *et al.* 2015). Drained fens with WT below -20 cm usually emit significant amounts of N_2O (Nykänen *et al.* 1995), which suggests that significant N_2O emissions could be expected at M_{moist}. However, N_2O fluxes are dependent on an ample nutrient supply (Maljanen *et al.* 2009) and behave erratically in space and time (Folorunso & Rolston 1984). Therefore, it is possible either that the nutrient supply was not sufficient to promote N_2O formation or that our choice of sampling intervals meant that we simply missed short-term N_2O emission peaks. However, other authors (*e.g*. Augustin 2001, Mander *et al.* 2008, Eickenscheidt *et al.* 2014) have reported comparable values to those of this study. In addition, black alders are a nitrogen-fixing species and intensify nitrogen transformation processes in ecosystems (Augustin 2001). They provide readily decomposable nitrogenous compounds (Eickenscheidt *et al.* 2014) that could lead to enhanced N_2O production (Carter *et al.* 2012). However, this effect could not be verified in our study. Therefore, the dependency of N_2O production on the age of the alder trees should be considered in future research.

Net GHG and C balances

CO_2 emissions (including harvested C) were the main contributor to the full net GHG balance of the M_{moist} site. This supports the findings of other peatland studies that have emphasised the importance of CO_2 in total GHG emissions from degraded peatlands (Jungkunst & Fiedler 2007, Carter *et al.* 2012, Tiemeyer *et al.* 2016). The M_{moist} site was a substantial GHG and C source compared to A_{wet} and M_{wet}. This could have been amplified if lateral C losses were taken into account, because elevated DOC concentrations have been demonstrated in the peat profiles of drained peatlands under intensive grassland use (Frank *et al.* 2014). Since the M_{moist} and M_{wet} sites had similar C export in harvested biomass, this outcome highlights the importance of WT influence on peat C stock conservation. This should be given priority in terms of climate protection (Couwenberg *et al.* 2011).

Since CH_4 emissions were substantially reduced at A_{wet}, and N_2O emissions were generally negligible, the young black alders reduced the GHG balance relative to M_{wet}, when C export by harvesting was ignored. However, because C stored in alder wood is regarded as a short-term pool (due to potential removal), M_{wet} and A_{wet} can be directly compared only if C storage in the alder trees is accurately estimated. This is not a simple task, but we can estimate the GHG and C balance of the young alders by making some coarse assumptions as follows:

1) a C content for young black alders of around 51 % (Chow & Rolfe 1989), and
2) mean annual increases in dry black alder biomass C of 317 (152–535) g m^{-2} based on a mean stand age of 48 (21–91) years (numbers derived from Johansson 1999).

This would result in C uptake by the trees of 162 (78–273) g m^{-2} yr^{-1}, which is in the same order of magnitude as C export from the M_{wet} site. If we assumed that all of this uptake entered storage in alder wood biomass, the C balance of A_{wet} would change to -5 (-89–106) g m^{-2} yr^{-1}, making A_{wet} slightly closer to C neutral than M_{wet} (92 g m^{-2} yr^{-1}; small C loss). This is in accordance with C balance estimates for similar WT classes (Couwenberg *et al.* 2008) and suggests that the mean annual WT depth at A_{wet} and M_{wet} was almost too low to ensure peat conservation. Including C export in harvested alder wood, the full GHG balance (in CO_2-equivalents) would then be 2.5 (-0.6–6.6) t ha^{-1} yr^{-1}. This suggests that black alder can reduce the full GHG balance in the short term, most probably due to reduced CH_4 emissions. It also shows that short-term uptake estimated through gaseous C measurements has to be corrected for its long-term context (Hommeltenberg *et al*. 2014).

In addition, estimates for large areas need to take account of the fact that the tree-stem density of young alder plantations is lower than the footprint covered by the chambers in our study (e.g. Claessens *et al.* 2010, < 0.8 *versus* 1.8 m^{-2}). Therefore, it is likely that a real black alder plantation will have a smaller effect than quantified here. Whether and to what extent a large alder plantation could reduce net GHG emissions in the long term will require further research and must incorporate a number of other approaches (e.g., eddy covariance, growth rings, *etc*.).

Response of CH_4 emissions to inundation

A number of heavy precipitation events during the summer of 2011 resulted in prolonged inundation of the study sites from the end of July 2011 until the end of August 2011 (M_{moist}) or beginning of September 2011 (M_{wet} and A_{wet}). Both relatively and absolutely, M_{moist} emitted the most CH_4 during that period. The site was dominated by meadow foxtail, which is sensitive to flooding. A number of studies have reported high CH_4 emissions from formerly drained fens in the temperate climate region as a result of inundation and related vegetation dieback (Huth *et al.* 2013, Günther *et al.* 2015, Hahn *et al.* 2015). Dieback of non-adapted vegetation provides an easily decomposable substrate for methanogenesis that, in combination with high WT and warmer summer temperatures, enhances CH_4 production potential (Hahn-Schöfl *et al.* 2011, Hahn *et al.* 2015).

At the M_{wet} site, the CH_4 emissions induced by inundation in August 2011 explained only 19 % of the total CH_4 emissions, which were also relatively high outwith the period of inundation. Therefore, it is likely that flooding induced no more than partial dieback of the sedges. This indicates that a sedge-dominated stand is more likely to withstand inundation than conventional grassland because sedges are adapted to higher WT levels (Roth & Succow 2001, Couwenberg *et al.* 2008). This response to inundation was also shown in a similar ecosystem by Huth *et al.* (2013).

In general, CH_4 emissions from the A_{wet} site were significantly lower than from the M_{wet} site. However, the absolute CH_4 emissions from A_{wet} and M_{wet} during inundation in August 2011 were similar. This indicates that the additional August emissions were related to a partial die-back of sedges at both sites.

Therefore, it seems that the black alders did not contribute to the inundation-induced CH_4 emissions and they withstood short-term flooding better than the sedges. Due to this site-specific and erratic behaviour, it is difficult to make landscape-level predictions of the duration and extent of increased CH_4 emissions following inundation (Jurasinski *et al.* 2016).

Our results show that drained fens can emit significant quantities of methane during flooding induced by heavy precipitation (Tiemeyer *et al.* 2016). In the future, this could create a need for adjustment of the CH_4-C emission factors provided by Drösler *et al.* (2014) for fen peatlands with deep drainage (~2 (0.2–3) g m^{-2} yr^{-1}) and shallow drainage (~4 (-0.3–8) g m^{-2} yr^{-1}) (mean emissions and 95 % confidence interval). Because the frequency of extreme weather events is likely to increase (Beniston *et al.* 2007), short-term observations of CH_4 emissions in drained fens may produce increasingly biased results. Thus, a need for longer observation periods is indicated (Günther *et al.* 2014).

CONCLUSIONS

Our results indicate that a young black alder plantation on rewetted peat grassland can improve the GHG balance and reduce C losses in the short term. In our study, CO_2 emissions were mainly linked to differences in WT - the moist site was a stronger CO_2 source than the very moist (wet) sites (with higher WT). It is likely that the alders improved the net GHG balance of the very moist peat meadow because of their ability to reduce CH_4 emissions even under inundated conditions, as seen during the summer of 2011. At all sites, flooding led to significant CH_4 emission peaks which contributed up to 70 % of the two-year CH_4 emissions. This indicates a need to regulate water levels on degraded peatlands to prevent high GHG emissions. It also highlights the importance of including periods of extreme weather in GHG field studies on degraded peatlands, in the context of refining GHG emission factors. We conclude that both rewetting and planting with young black alders can redirect degraded fen towards becoming a net GHG sink in the short term. However, the long-term GHG sink function of peatlands can only be maintained by keeping the water table close to the peat surface. In addition, the effect of black alders on the ecosystem GHG and C balances (including C export in alder biomass) should be tested at larger scales and, ideally, throughout complete alder rotations.

DATA AVAILABILITY

The data collected during this study are publicly accessible at doi:10.4228/ZALF.2012.329 (Huth *et al*. submitted). See also http://open-research-data.ext.zalf.de/SitePages/DatasetInformation.aspx?ord=10_4228-ZALF_2012_329.

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Appendix. Vegetation assessment of the study sites using a modified Londo-scale (Londo 1976) at the end of the study period (May 2012). Water level classes follow Roth & Succow (2001) and Couwenberg *et al*. (2008).

Site	A_{wet}			M_{wet}			M_{moist}		
Collar	1	2	3	1	2	3	1	2	3
Water level class	4+	4+	4+	4+	4+	4+	2+	2+	2+
Type of water regime[1]	t	t	t	t	t	t	g	g	g
Trophic state[2]	p	p	p	r	r	r	p	p	p
Land use/degree of disturbance[3]	e	e	e	e	e	e	i	i	i
Vegetation height (cm)	55	55	55	30	35	25	75	95	85
WT (cm)	-15	-15	-15	-15	-15	-15	-20	-20	-20
Total plant cover (%)	70	70	70	60	60	75	65	65	65
Straw cover (%)	90	95	95	85	95	90	85	75	85
Number of species	4	4	7	7	8	7	7	3	6
Phalaris arundinacea	b		+				b		
Glyceria maxima		a		a	1	a			
Agropyron repens	a		a		+			+	+
Carex disticha	a	+	2	+	2	+	+		+
Carex acuta	7	7	5	5	3	7			
Symphytum officinale		+							
Galium palustre			a						
Polygonum amphibium			+	+		+			
Alnus glutinosa			b						
Agrostis stolonifera				a	b		a	b	+
Equisetum palustre				+	+	+			
Ranunculus sceleratus									
Calliergonella cuspidata									
Glyceria fluitans									
Ranunculus repens				+	+	a	+		b
Potentilla anserina					+	+			
Juncus articulatus									
Rorippa amphibia									
Atriplex prostrata									
Schoenoplectus tabernaemontani									
Juncus subnodulosus									
Alopecurus pratensis							6	9	8
Poa pratensis							1		
Taraxacum officinale							+		
Carex hirta									+

[1] t – topogenous, g – groundwater
[2] p – polytrophic, r – rich (eutrophic)
[3] e – extensive, i - intensive

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