Dynamic C and N stocks – key factors controlling the C gas exchange of maize in a heterogenous peatland

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Abstract

Drainage and cultivation of fen peatlands create complex small-scale mosaics of soils with extremely variable soil organic carbon (SOC) stocks and groundwater-level (GWL). To date, the significance of such sites as sources or sinks for greenhouse gases like CO_2 and CH_4 is still unclear, especially if used for cropland. As individual control factors like GWL fail to account for this complexity, holistic approaches combining gas fluxes with the underlying processes are required to understand the carbon (C) gas exchange of drained fens. It can be assumed that the stocks of SOC and N located above the variable GWL – defined as *dynamic* C and N stocks – play a key role in the regulation of plant- and microbially mediated CO_2 fluxes of these soils and, inversely, for CH_4. To test this assumption, the present study analysed the C gas exchange (gross primary production – GPP, ecosystem respiration – R_{eco}, net ecosystem exchange – NEE, CH_4) of maize using manual chambers for four years. The study sites were located near Paulinenaue, Germany, where we selected three soil types representing the full gradient in GWL and SOC stocks (0-1m) of the landscape: a) Haplic Arenosol (AR; 8 kg C m^{-2}); b) Mollic Gleysol (GL;

38 kg C m^{-2}); and c) Hemic Histosol (HS; 87 kg C m^{-2}). Daily GWL data was used to calculate dynamic SOC (SOC_{dyn}) and N (N_{dyn}) stocks.

Average annual NEE differed considerably among sites, ranging from 47±30 g C m^{-2} a^{-1} at AR to –305±123 g C m^{-2} a^{-1} at GL and –127±212 g C m^{-2} a^{-1} at HS. While static SOC and N stocks showed no significant effect on C fluxes, SOC_{dyn} and N_{dyn} and their interaction with GWL strongly influenced the C gas exchange, particularly NEE and the GPP : R_{eco} ratio. Moreover, based on nonlinear regression analysis, 86% of NEE variability was explained by GWL and SOC_{dyn}. The observed high relevance of dynamic SOC and N stocks in the aerobic zone for plant and soil gas exchange likely originates from the effects of GWL-dependent N availability on C formation and transformation processes in the plant-soil system, which promote CO_2 input via GPP more than CO_2 emission via R_{eco}.

The process-oriented approach of dynamic C and N stocks is a promising, potentially generalizable method for system-oriented investigations of the C gas exchange of groundwater-influenced soils and could be expanded to other nutrients and soil characteristics. However, in order to assess the climate impact of arable sites on drained peatlands, it is always necessary to consider the entire range of groundwater-influenced mineral and organic soils and their respective areal extent within the soil landscape.

1 Introduction

Peatlands are one of the most important ecosystems for the terrestrial carbon (C) and nitrogen (N) cycle, storing up to 500 Mg C ha^{-1} and – particularly in nutrient-rich fens – 120 Mg N ha^{-1} (Yu et al. 2011, MacDonald et al. 2006, Kunze 1993). Throughout the world, the drainage and subsequent agricultural cultivation of peatlands has increased soil organic carbon (SOC) mineralisation rates and the associated CO_2 emissions (Couwenberg et al. 2010, Kasimir-Klemedtsson et al. 1997, Nykänen et al. 1995), resulting in the creation of small-scale mosaics of soil types with extremely variable SOC stocks, especially in the case of fens. The respective soil types range from deep peat soils to humus-rich sandy soils, which are not classified as peat soils due to an SOC content of <12% (IUSS Working Group WRB 2007). These individual soil types are typically found at similar relative elevations within an increasingly undulating landscape and the ground water level (GWL) is often subject to considerable short-term fluctuations. As a result of the tight coupling between soil types and elevation, mean GWL may differ considerably between individual soil types (Aich et al. 2013, Heller and Zeitz 2012, Dawson et al. 2010, Teh et al. 2011, Dexler et al. 2009, Müller et al. 2007, Schindler et al. 2003). These sites are typically used as grassland or cropland (Joosten and Clark 2002, Byrne et al. 2004).

The relevance of these soil type mosaics originating from drained fen peatlands as a source or sink for greenhouse gases like CO_2 and CH_4, especially if used for cropland, still cannot be exactly determined. In particular, knowledge about the influence of variable soil C stocks on the C gas exchange is still limited. In light of the extreme complexity of site conditions, it seems unlikely that the common focus on interactions between C stocks and particularly relevant control parameters like groundwater and temperature (Adkinson et al. 2011, Berglund et al. 2010, Kluge at al. 2008, Jungkunst and Fiedler 2007, Daulat et al. 1998) will result in reliable and generalizable conclusions about the C gas fluxes of degraded fens; mainly because this approach fails to account for the plant-induced C gas input counteracting the C gas emissions determined by soil characteristics and microorganisms.

Therefore, new insights are much more likely to be derived from system-oriented studies analysing all interrelated C gas fluxes, e.g. CH_4 exchange, CO_2 uptake during photosynthesis and CO_2 emission via respiration, together with the underlying processes and control mechanisms (Chapin III et al. 2009, Schmidt et al. 2011). Indeed, there are numerous indications suggesting that this approach may also be promising for the C gas exchange of drained fen sites.

Short- and long-term fluctuations of the GWL and its interactions with soil and plants very likely also play a key role in the C cycle of other groundwater-influenced soil types, similar to true peat soils (Couwenberg et al. 2011, Berglund and Berglund 2011, Flanagan et al. 2002, Augustin et al. 1998, Martikainen et al. 1995, Nykänen et al. 1995). For peat soils, many studies documented the impact of GWL on the interactions between soil C dynamics and gaseous C emissions in the form of CH_4 and CO_2, the latter originating from autotrophic root respiration and heterotrophic microbial respiration. Ultimately, these GWL effects are a result of the ratio between SOC stocks located in the aerobic, i.e. above-GWL, and the anaerobic, i.e. below-GWL, zone (Laine et al. 1996). However, very few (Leiber-Sauheitl et al. 2014, Jans et al. 2010, Jungkunst et al. 2008, Jungkunst and Fiedler 2007) studies have investigated Gleysols and groundwater-influenced sandy soils, which make up a significant portion of fen landscapes. It also remains unclear if the impact of GWL on the gas exchange is modified by the highly variable density typical of SOC-rich soil horizons of drained peatlands.

Knowledge gaps also limit the quantification of direct GWL effects on plant-mediated CO_2 uptake via photosynthesis. Site-adapted plants growing on undisturbed peat soils and perennial grasses cultivated on groundwater-influenced soils can tolerate changing GWL without considerable deterioration of photosynthetic performance (Farnsworth and Meyerson 2003, Crawford and Braendle 1996). In contrast, GWL fluctuations likely have a particularly strong impact on annual crops cultivated on drained peatlands, as most crops typically react to waterlogging, i.e. anoxic soil conditions as a result of high GWL, with reduced photosynthesis, plant respiration and growth (Zaidi et al. 2003, Asharf 1999, Singh 1984, Wenkert et al. 1981). Other studies indicate that crops cultivated on groundwater-influenced soils feature better growth when GWL are low (Glaz et al. 2008), but it is unclear if this is a direct result of improved aeration or an indirect effect of increased soil volume, allowing for better root development and thus increased nutrient uptake (Glaz et al. 2008, Livesley et al. 1999).

Despite the system-orientated approach mentioned above, it can therefore be assumed that the amounts of soil C and N located above the temporally variable GWL – hereafter referred to as dynamic C and N stocks – are of essential relevance to plant- and microbially mediated C gas fluxes on drained peatland soils. Moreover, investigations into the effects of dynamic C and N stocks may yield new insights into the mechanisms controlling the C dynamics at these sites. This would be a significant advancement with respect to a comprehensive and generalizable understanding of the CO_2 and CH_4 source and sink capacity of drained arable fen peatlands.

The present study tests the above-mentioned assumption by means of multi-year manual chambers measurements, subsequent modeling and complex statistical analysis of all relevant C gas fluxes, i.e. the net CO_2 exchange resulting from gross primary production (plant photosynthesis) and ecosystem respiration (sum of plant and soil respiration) and the CH_4 exchange, of maize cultivated on different groundwater-dependent soil types representing a steep SOC gradient. In particular, the study focuses on answering the following research questions:

1. Are there differences among soil types regarding the dynamics and the intensity of the C (CO_2 and CH_4) gas exchange of drained arable peatland soils?

2. a) Which factors and factor interactions influence the C gas exchange of drained arable peatland soils?

   b) In particular, what is the influence of the amount and the dynamics of soil C and N stocks located in the aerobic zone above the GWL on the C gas exchange of drained arable peatland soils?

2 Materials and methods

2.1 Site description and land use history

The study sites are located near the village of Paulinenaue, in the shallow and drained peatland complex ‘Havelländisches Luch’ of NE Germany (51 km W of Berlin; 52°41`N, 12°43`E). This peatland was first drained at the beginning of the 14th century (Behrendt, 1988). A systematic amelioration for the entire “Luch” took place from 1718 until 1724 and included The construction of ditches and dams to drain the formerly swampy terrain and to provide access to the land. Grasslands with hay production dominated the “Luch” at that time. In order to prevent repeated flooding and to increase grassland productivity, a second amelioration with deeper drainage ditches was implemented between 1907 and 1925. A substantial increase in total ditch length occurred between 1958 and 1961, when approx. 1000 km of new ditches were established in the area (Behrendt, 1988). The next huge effort to increase productivity started in the early 1970ies by the so-called “Komplexmelioration”, which lasted until the late 1980ies. The basic idea was to establish a system of pumping stations and related ditches in order to increase and lower the ground water table dynamically throughout the vegetation period depending on the actual plant water demand. In addition, fertilizer application rates, including organic manure, increased and the acreage of arable land doubled at the expense of grassland. After the re-unification of Germany in 1989, a substantial de-intensification took place, resulting in the re-conversion of arable land to grassland, reduction of fertilizer input, and abandonment of hydraulic technical devices for economic reasons.

The region is characterized by a continental climate with a mean annual air temperature of 9.2°C and a mean annual precipitation of 530 mm (1982–2012).

The study sites are located along a representative and steep landscape gradient in terms of soil organic carbon stocks (SOC_{stocks}; 0–1 m), which is related to topographic position (Table 1): AR – a Haplic Arenosol developed from aeolian sands with low SOC_{stocks} ($8\ kg\ C\ m^{-2}\ m^{-1}$) at a microhigh (29.6 m a.s.l.); GL – a Mollic Gleysol developed from peat overlying fluvial sands with medium SOC_{stocks} ($38\ kg\ C\ m^{-2}\ m^{-1}$) at 29.0 m a.s.l.; and HS – a Hemic Histosol developed from peat featuring high SOC_{stocks} ($87\ kg\ C\ m^{-2}\ m^{-1}$) at the edge of a local depression (28.8 m a.s.l.). Moreover, the vertical distribution of C and N differ between sites: at AS almost all SOC and N is concentrated in the plough layer (Ap horizon), whereas GL and HS show larger portions of SOC and N in subsoil horizons (Fig. S1 in supplement).

All sites were identically managed during the study period (Table S1 in supplement), i.e. cultivated with a monoculture of grain maize with annually changing varieties. The AR and HS sites are located 150 m apart within the same managed field, while GL is located 1.5 km from AR/HS. However, field operations such as tillage, sowing, fertilisation and harvest were conducted almost concurrently at all sites. Maize was fertilised with diammonium phosphate (DAP) containing $22\ kg\ N\ ha^{-1}$ and $24\ kg\ P\ ha^{-1}$ in the course of sowing, followed approx. 2 weeks later by fertilisation with calcium ammonium nitrate (CAN) containing $100\ kg\ N\ ha^{-1}$. During harvest, total plant biomass within the measurement plots was collected, chipped, dried at 60°C to constant weight and weighed. Grain yield was not recorded due to technical complications. Total plant biomass subsamples were analysed for C content at the ZALF Central Laboratory. After harvesting, all sites were mulched and ploughed.

2.2 Environmental controls

Half-hourly values of air temperature (20 cm height), soil temperatures (2, 5 and 10 cm depth), PAR, and precipitation were continuously recorded by a climate station installed within 1 km of the sites. Site-specific air and soil temperatures were manually measured simultaneously with CO_2 and CH_4 flux measurements. Site-specific half-hourly air and soil temperature models were derived from correlations between the respective climate station temperature records and site-specific manual temperature data. Sunshine hours and long-term climate data originate from the ‘Potsdam’ station of the German Weather Service (DWD).

GWL at GL and HS was measured manually every two weeks using short 1.5 m dip wells. The measured piezometric heads are considered representative of the phreatic water levels in the peat layer because the organic soil layer directly overlies a sand aquifer without any major low-conductance soil horizons in between. At HS, GWL was additionally recorded every 15 min by a data logger (Mini-diver, Schlumberger). Time series modeling was used to fill several small data gaps and to obtain continuous daily GWL data for the entire study period. The applied PIRFICT approach (von Asmuth et al. 2008) implemented in the *Menyanthes* software (von Asmuth et al. 2012a) is a physically-based statistical time series model specifically developed to model hydrologic time series, including shallow GWL fluctuations. As input, the model requires continuous precipitation (DWD station ‘Kleßen’) and evapotranspiration data (FAO56 Penman-Monteith; DWD station ‘Kyritz’) and optional control parameters, e.g., in our case, deep GWL data recorded from a local dip well (LUGV Brandenburg). The calibrated model explained 80–87% of the data variance; a good result for this data and model type (von Asmuth et al. 2012b). Confidence intervals of GWL time series predictions were obtained by means of stochastic simulation (see von Asmuth et al. 2012a). Due to the short distance between AR and HS and the highly significant correlation of GWL at these sites ($R^2 = 0.836$), daily GWL values for AR were calculated by shifting the modeled time series of HS with a constant offset of 0.9 m.

2.3 Concept and calculation of dynamic C and N stocks

The concept of ‘dynamic’ groundwater-dependent C and N stocks was developed to account for the interaction of the most important drivers of the C gas fluxes of peatlands, namely GWL and soil C and N stocks. The underlying idea is to derive a quantitative, dynamic proxy for the aerated, unsaturated zone which determines the actual nutrient and O_2 availability and is therefore highly relevant for root and shoot growth, microbial activity, and, consequently, all C gas fluxes. Using daily GWL data, it was determined for each 1-cm soil layer up to a depth of 1 m if the respective layer was saturated with groundwater or not. In daily time steps, SOC and N stocks were then calculated for all non-saturated 1-cm layers and cumulated over the entire non-saturated soil profile, i.e. above the GWL, to generate daily dynamic SOC (SOC_{dyn}) and N (N_{dyn}) stocks. For further analysis, daily SOC_{dyn} and N_{dyn} values were averaged monthly and annually.

2.4 Gas flux measurements

Periodic trace gas measurements were carried out at three permanently installed soil collars (0.75 x 0.75 m) at each site. In summer 2007, due to flooding, soil collars at the HS site had to be relocated within a radius of 10 m to i) technically allow for gas flux measurements; and ii) ensure that all soil collars contained flood-affected but viable plants in order to maintain comparability with the GL and AR sites, where maize mortality was not increased by flooding.

Throughout the entire study period, CH_4 measurements were conducted 1–2 times per month using static *non-flow-through non-steady-state* opaque chambers (vol. 0.296 m^3; Livingston and Hutchinson 1995, Drösler 2005), for a total of 51–60 campaigns per site. At HS, CH_4 measurements were terminated already in October 2010 due to management constraints. Exchange of CH_4 was measured by taking four consecutive 100-ml gas samples from the chamber headspace in 20-min intervals (closure time 60 min), subsequently analyzed using a gas chromatograph (Shimadzu GC 14B, Loftfield, Göttingen, Germany) equipped with a flame ionization detector.

CO_2 exchange was measured using dynamic *flow-through non-steady-state* transparent (net ecosystem exchange – NEE); light transmission of 86%) and opaque (ecosystem respiration – R_{eco}) chambers (Livingston and Hutchinson 1995, Drösler 2005) attached to an infrared gas analyzer (Li-820, Lincoln, NE, USA). Full-day CO_2 measurement campaigns with repeated (30–50) individual chamber measurements (closure time 3–5 min) were conducted regularly every 4–6 weeks from 05/2007–04/2011, for a total of 29–37 full campaigns per site. Further details on CO_2 measurement methodology are given in Hoffmann et al. (2015).

2.5 Flux calculation and gap filling

Flux calculation for CO_2 and CH_4 was based on the ideal gas equation accounting for chamber volume and area, air pressure, and average air temperature during the measurement. CH_4 fluxes were calculated with the R package 'flux 0.2-2' (Jurasinski et al. 2012), using linear regression analysis with stepwise backward elimination of outliers based on the normalized root mean square error (NRMSE ≥ 0.2) up to a minimum of three data points. Fluxes with NRMSE > 0.4 were rejected. The calculated flux rates were then averaged for the respective measurement day and linearly interpolated to determine annual CH_4 exchange.

For CO_2, the R script of Hoffmann et al. (2015) was used for flux calculation as well as the subsequent separation into and modeling of R_{eco}, gross primary production (GPP), and NEE. Measurements <30 s were rejected and measurements >1 min were shortened by a death band of

10% at the beginning and end, respectively (Kutzbach et al. 2007). For each measurement, the final flux rate was selected from all potential flux rates generated by a moving window approach using a stepwise algorithm, numerous quality criteria and the Akaike information criterion (AIC; for details see Hoffmann et al. 2015). For R_{eco}, gap filling between measurement campaigns was performed using campaign-specific temperature-dependent Arrhenius-type models by Lloyd and Taylor (1994). GPP fluxes were calculated by subtracting modeled R_{eco} fluxes from measured NEE fluxes, and then modeled using campaign-specific hyperbolic PAR-dependent models (Wang et al. 2013, Elsgaard et al. 2012, Michaelis-Menten 1913). Average measured flux rates were used if no significant fit was achieved for campaign-specific R_{eco} or GPP models (Hoffmann et al. 2015). Half-hourly NEE values were calculated from modeled R_{eco} and GPP fluxes (Hoffmann et al. 2015, Drösler 2005), and cumulated from May 1st to April 30th of the following year (Table S1 in supplement), resulting in four consecutive annual CO_2 balances. Negative values represent a C gas flux from the atmosphere to the ecosystem; positive values a flux from the ecosystem to the atmosphere. The uncertainty of the annual CH_4 and CO_2 exchange was quantified using a comprehensive error prediction algorithm described in detail by Hoffmann et al. (2015).

2.6 Data analysis

Daily values for CH_4 efflux, GPP, R_{eco}, NEE were cumulated monthly for a total of 48 monthly datasets per site to reduce the effects of temporal autocorrelation. The respective environmental controls were cumulated (sunshine hours, precipitation and linear modelled biomass) or averaged (for GWL, SOC_{dyn}, N_{dyn}, air and soil temperature) for each month. Gas flux balances for longer time periods may vary considerably depending on the duration of the respective cumulation period. As the wavelet analysis of daily NEE data for inherent signals revealed strong annual dynamics (Stoy et al. 2013; Fig. S2 in supplement), a 365-day cumulation period was used to calculate gas flux balances. Additional variability in annual balances can result from arbitrarily chosen starting dates of the cumulation period. To account for this uncertainty in the calculation of annual balances, a 365-day moving window was shifted in monthly time steps through the entire study period, resulting in a total of 111 datasets (37 per site) for annual NEE, GPP, R_{eco} and CH_4 efflux and the respective environmental control parameters.

Subsequently, generalized linear model (GLM) analyses (SPSS GENLIN procedure) were performed to determine the influence of environmental controls and their interactions on the cumulated annual CH_4, R_{eco}, GPP, and NEE balances as well as the GPP : R_{eco} ratio. Models were defined using a gamma probability distribution and a log link function and calculated in a stepwise backward elimination procedure, dropping non-significant variables until no further improvement of the AIC was achieved (correction for finite sample sizes: AIC_c). Parameter and interaction effects were evaluated based on the Wald χ^2 statistic, appropriate for non-normally distributed continuous variables. Prior to analysis, CH_4 data were log-transformed after adding the minimum CH_4 value to each data value, in order to allow for application of the GLM log link function. Analogously, absolute values of GPP were used for the analysis and NEE data were transformed to positive values by adding the minimum NEE value to each data value.

Multiple nonlinear regression analyses were performed to derive a model for NEE based on GWL and SOC_{dyn}, N_{dyn}, SOC_{dyn} : N_{dyn} ratio and biomass, representing the main GLM parameter groups. For model calculation, data was averaged for twelve site-specific GWL classes to account for uncertainty from GWL model data. Class number was determined using Sturges' rule, appropriate for $n < 200$ (Scott 2009). All data analyses were performed using the R (R 3.0.3) and SPSS (SPSS 19.0.1, SPSS Inc.) software.

3 Results

3.1 Environmental controls

During the study period (05/2007–04/2011), weather conditions were somewhat cooler (8.7°C) and wetter (634 mm) compared to the long-term average (1982–2012; 9.2°C; 530 mm). Particularly the 2010/11 measurement year considerably deviated from the long-term temperature average, with an annual air temperature that was 1.5°C below the long-term average –1 SD (*data not shown*). While PAR and air temperature showed high daily and seasonal dynamics (Fig. 2a), no pronounced seasonal patterns were observed for precipitation (Fig. 1). Instead, precipitation featured an extremely high interannual variability with particularly heavy rainfalls during the summer months of 2007 (May–July; Fig. 1). The precipitation sum during this period (507 mm) exceeded the long-term average (179 mm) by >180% (*data not shown*). Reflecting the precipitation dynamics, the GWL showed similar temporal dynamics of the three sites, but at different levels. In summer, GWL remained generally low, with the exception of July–August 2007. The HS site, which consistently featured the highest average GWL (–0.5 m; Fig. 1, Table S2 in supplement), was flooded during this period (GWL +0.2 m; *data not shown*).

The SOC_{dyn} and N_{dyn} stocks calculated based on the modeled GWL showed the highest fluctuations at the HS site (Fig. 1). During times of high GWL, such as in summer 2007, the HS and GL site featured drastically lowered SOC_{dyn} and N_{dyn} values, amounting to only 6.2 kg C m^{-2} and 0.5 kg N m^{-2}, respectively, with SOC_{dyn} and N_{dyn} reduced to zero during flooded periods. In contrast, pronounced peak values at HS were calculated for the low-GWL summer months during the rest of the study period, with monthly averages of 21–86 kg C m^{-2} and of 2–5 kg N m^{-2}. The HS site always featured the highest annual SOC_{dyn} (52 kg C m^{-2}) and N_{dyn} (4 kg N m^{-2}) stocks, except for 2007/08 (Fig. 1; Table S2 in supplement).

3.2 Daily and annual carbon gas exchange

All sites generally featured very low daily CH_4 fluxes (–0.01 to 0.01 g CH_4-C m^{-2} d^{-1}) throughout the study period (Fig. S3 in supplement). However, considerable CH_4 emission peaks were observed at the HS and GL sites during times of flooding or high GWL, e.g. during summer 2007 and spring 2008. At HS, this resulted in a maximum CH_4 flux of 1.2 g CH_4-C m^{-2} d^{-1} on August 1st, 2007, which is approx. 60 times higher than the median flux (0.02 g CH_4-C m^{-2} d^{-1}) at this site. As a result of the flooding, annual CH_4 emissions in 2007/08 at HS amounted to 28± 4 g CH_4-C m^{-2} y^{-1}, and were thus nearly 100 times higher than observed for HS in the following years (0.3±0.5 and ±0.2 g CH_4-C m^{-2} y^{-1}) and at least 25 times higher than observed for AR and GL (< 1.2±0.6 g CH_4-C m^{-2} y^{-1}; Table 2). However, as the high annual CH_4 emissions 2007/08 at HS result from a peak described by three measurement campaigns during the flooded period (Fig. S3 in supplement), they are also associated with a higher uncertainty (±3.7 g CH_4-C m^{-2} y^{-1} in 2007/08 vs. ±0.5 and ±0.2 g CH_4-C m^{-2} y^{-1} in 2008/09 and 2009/10; Table 2).

The modelled CO_2 exchange rates (for model evaluation statistics see Table S3 in supplement) reflected the daily and seasonal dynamics of air temperature and PAR, with generally higher fluxes in the growing season compared to fall and winter (Fig 2a, b). In summer, peak GPP fluxes considerably exceeded the amplitude of R_{eco} fluxes. At all sites, the CO_2 exchange was also influenced by management events, with particularly pronounced peaks of R_{eco} following tillage. In addition, GPP was immediately reduced to zero after maize harvest due to the removal of the photosynthetically active aboveground plant biomass. In general, the organic GL and HS sites showed the highest CO_2 exchange intensity, with maximum R_{eco} and GPP fluxes of 23 g CO_2-C m^{-2} d^{-1} and –46 g CO_2-C m^{-2} d^{-1}, respectively, observed at the HS site (Fig 2a, b). However, during the wet summer of 2007, the mineral AR site featured the highest intensity of CO_2 exchange, resulting in cumulated annual R_{eco} and GPP fluxes that were 25–44% and 52–61% higher, respectively, than in the following years (2008–2011, Table 2). In contrast, at HS, the 2007 flooding resulted in strongly reduced CO_2 flux intensites and large net annual CO_2-C losses (NEE of 493±83 g CO_2-C m^{-2}) compared to the following years. Although the CO_2 fluxes measured during the flooded period are associated with higher error values compared to periods without flooding (Table 2), the modelled results are plausible, clearly reflecting the negative effects of flooding on plant growth and thus plant C exchange. Hence, in 2007/08, cumulated annual R_{eco} and GPP fluxes at AR were 76% and 49% higher than at the HS site (Table 2).

Excluding 2007/08, the average NEE during the study period at the mineral AR site was close to zero with 50±32 g CO_2-C m^{-2} y^{-1} (Table 2), whereas the organic sites were net CO_2-C sinks with –385±133 g CO_2-C m^{-2} y^{-1} (GL) and –334 ± 61 g CO_2-C m^{-2} y^{-1} (HS). Including the flood-dominated year of 2007/08 resulted in a 62% and 21% reduction of the overall NEE at the HS and GL sites, respectively. In contrast, when 2007/08 is included in the overall 2007–2011 average for the AR site, cumulated R_{eco} and GPP increase by 63% and 67%, respectively, while NEE remains unaffected.

3.3 Impact of environmental controls on carbon gas exchange

Despite the wide range of control parameters included in the complex analysis, site (i.e. soil) had a significant (p- value ≤ 0.05) effect on all gas fluxes (Table 3). The generally highly significant (p- value ≤ 0.001) interactions between site and controls like biomass, GWL and soil parameters show that the selected study sites represented a wide range of the respective control parameters. Especially annual CH_4-C emissions were dominated by site, suggesting the presence of additional important control factors not considered in this analysis. However, little residual variability indicates that most of the variability in annual R_{eco} and GPP was explained by the factors included in the GLM analyses, with more residual variability remaining for NEE and the GPP : R_{eco} ratio.

While climate played a minor role in determining annual CH_4-C emissions via the effect of precipitation on GWL, climate controls were more relevant for CO_2 exchange (Table 3). There, the importance of climate was higher for cumulated GPP and R_{eco} than for NEE and the GPP: R_{eco} ratio. The impact of climate variability on CO_2 exchange was even more pronounced at the monthly scale, as indicated by highly significant interactions between climate controls and month of year (*data not shown*). Biomass was equally important as climate in determining annual GPP, whereas for R_{eco} biomass and its interactions were less relevant than climate (Table 3). In contrast, the derived variables NEE and GPP : R_{eco} were less influenced by biomass than the individual fluxes R_{eco} and GPP.

Direct groundwater influence was particularly pronounced for R_{eco}, GWL by far being the most important GLM parameter (Table 3). Groundwater influence on CH_4-C emissions and the GPP: R_{eco} ratio was expressed mainly through the interaction between GWL and site.

Groundwater-dependent soil parameters and their interactions with site and GWL dominated annual CH_4-C emissions (Table 3). Soil parameters were also the main controls on NEE, particularly the $SOC_{dyn} : N_{dyn}$ ratio and its interactions with site. Dynamic soil parameters and their associated interactions thus were of higher relevance for the derived variables NEE and GPP : R_{eco} than for the NEE flux components R_{eco} and GPP. This indicates differences between R_{eco}, and GPP with respect to their reaction to changing GWL and soil parameters, i.e. a shift in the ratio between R_{eco}, and GPP throughout the range of GWL, SOC_{dyn} and N_{dyn} stocks. In contrast, static SOC_{stocks} and N_{stocks} showed no significant (p-value ≥ 0.05) effect on cumulated annual or monthly fluxes of either R_{eco}, GPP, or NEE (*data not shown*).

Nonlinear regression analysis of annual NEE versus GWL and either SOC_{dyn}, N_{dyn}, $SOC_{dyn} : N_{dyn}$ or biomass across all sites resulted in highly significant 2-parameter models (Table 4; Fig. 3). While all models explained >86% of the overall variability of annual NEE, model fit was best for GWL and SOC_{dyn}, likely because the study sites represent a wide range of SOC_{dyn}. For all sites, the model shows a negative NEE optimum for GWL of 0.8–1.0 m below the soil surface, with NEE increasing at higher or lower GWL (Fig. 3). In contrast, the model reflects a linear effect of SOC_{dyn} on NEE with more negative NEE for higher SOC_{dyn}. Depending on SOC_{dyn}, NEE changes to positive values at GWL above –0.43 m (for SOC_{dyn} = 60 kg C m^{-2}) or –0.61 m

(SOC_{dyn} = 30 kg C m^{-2}). However, the shown relations cannot be assumed as valid outside the measured ranges of SOC_{dyn} and GWL.

4 Discussion

4.1 Soil influence on C gas exchange

As indicated in the introduction, data about the CO_2 exchange of groundwater-influenced arable soils is generally scarce, particularly for maize, although some data is available for organic soils. Although the maximum CO_2 fluxes observed during a 1-year study of maize cultivated on a Haplic Gleysol in the Netherlands (Jans et al. 2010) are ~25% lower compared to the studied Gleysol (Fig. 2), the flux dynamics and the cumulative net CO_2 exchange of the organic soil types are relatively similar in both studies, with mean annual NEE of –385 g CO_2-C m^{-2} y^{-1} (Gleysol) and –334 g CO_2-C m^{-2} y^{-1} (Histosol) in this study (Table 2) vs. –332 g CO_2-C m^{-2} y^{-1} (Jans et al. 2010). Moreover, the dynamics and the intensity of the CO_2 exchange observed for the groundwater-influenced soils in this study are in the same order of magnitude as reported for maize cultivated on soils without groundwater influence (Gilmanov et al. 2013, Kalfas et al. 2011, Zeri et al. 2011, Ceschia et al. 2010). The observed biomass yield of maize (257–3117 g DM m^{-2} y^{-1}) is also in line with previous studies (500–2800 g DM m^{-2} y^{-1}; Zeri et al. 2011, Verma et al. 2005). According to Gilmanov et al. (2013) and Ceschia et al. (2010), maize cultivation generally resulted in a net annual CO_2 sink across a wide range of sites in America and Europe, but – like in this study – with considerable variability between sites and years (+89 to –573 g CO_2-C m^{-2} y^{-1}).

The results of this study demonstrate for the first time a considerable influence of groundwater-influence soils on crop CO_2 exchange, particularly on cumulative NEE (Tables 3, 4, Fig. 3), thus clearly affirming the research question (1) regarding the soil effect. Surprisingly, the C-rich drained organic soils showed a strong net CO_2 uptake (Table 2), while the C-poor Arenosol was a small net CO_2 source. This observation cannot be entirely explained by the interaction between GWL and the potentially mineralizable soil C stocks. Hence, an integrated consideration of all relevant C gas fluxes and their regulation within the plant-soil system is required, which is discussed in detail below. We are unaware of any previous study ever reporting such an effect, likely because any systematic effects may only be observed in longer-term studies due to the high interannual variability of C gas fluxes. This strongly supports the high relevance of such investigations for the accurate evaluation of the C dynamics of groundwater-influenced arable soils.

4.2 Relevance of interactions between GWL and maize ecophysiology

Apart from soil type and SOC content, the study sites are mainly differentiated by different average GWL, which our study results show to be a crucial factor determining the high short- and long-term variability of maize C gas exchange across the entire range of groundwater-influenced soils. Previous studies have mainly shown an influence of GWL on CH_4 fluxes from peat soils, mainly reporting an exponential increase of CH_4 fluxes for rising GWL with particularly high CH_4 losses for GWL ≥ –0.2 m (Couwenberg et al. 2011, Jungkunst & Fiedler 2007, Drösler 2005, Fiedler & Sommer 2000). Annual CH_4 emissions (–0.2 to 1.2 g CH_4-C m^{-2} y^{-1}) for GWL between –1.6 and –0.6 m and peak fluxes during flooding (≤ 28 g CH_4-C m^{-2} y^{-1}; GWL of –0.3 m) observed at the HS site are similar to values of Couwenberg et al. (2011) and Drösler (2005). However, for crops cultivated on groundwater-influenced mineral soils, little data is available on the impact of GWL on CH_4 fluxes (e.g., Pennock et al. 2010).

CO_2 exchange has also been intensively studied for organic soils, but mostly for pristine peatlands and grasslands on peat soils (e.g., Leiber-Sauheitl et al. 2014, Berglund and Berglund 2011, Couwenberg et al. 2011), while data on maize are lacking. For peatland NEE, one study reports a linear decrease with rising GWL over a range of –0.4 m to –0.1 m, with maximum NEE observed at –0.4 m (Leiber-Sauheitl et al. 2014). Couwenberg et al. (2011) also observed decreasing NEE when GWL rose above –0.5 m, but net CO_2-C uptake was only reported for very high GWL above –0.1 m. In contrast, in this study, maize NEE was largely negative across the entire range of GWL recorded at the studied groundwater-influenced soils (–2.1 m to +0.2 m), changing to positive values when GWL rose above –0.4 m to –0.6 m. Moreover, the GWL–NEE relationship for maize shows a clearly nonlinear relationship to GWL, with a distinct optimum at considerably lower GWL (between –0.8 m and –1.0 m; Fig. 3) than observed for grasslands. Further studies are required to determine if this is a general pattern applicable to other groundwater-influenced soil types and crops.

Our study results further indicate that R_{eco} and GPP also feature specific GWL optima (*data not shown*). For example, maximum R_{eco} fluxes were observed for GWL of –0.8 m to –1.0 m, similar to data from grassland on four GWL-influenced soil types (Fiedler et al. 1998). Similar to the R_{eco} of maize at the organic HS and GL sites, R_{eco} fluxes of grasslands on organic soils typically decrease with rising GWL (Leiber-Sauheitl et al. 2014, Berglund and Berglund 2011, Laine et al 1996, Silvola et al. 1996), particularly if GWL rises above the soil surface (Koebsch et al. 2013). The impact of GWL on GPP was relatively small in this study (Table 3); except for the effect of the 2007 flooding, which resulted in a drastic reduction in GPP (Table 2) as also observed by Koebsch et al. (2013) after rewetting.

Most of the study results concerning the individual CO_2 fluxes can be explained by the interactions between GWL and maize plant activity, because the magnitude and the variability of GPP and R_{eco} is most pronounced during the short period from May to September, which corresponds to the growing period of maize (Fig. 2). For example, the drastic reduction of the CO_2 fluxes during the flooding in 2007 at HS and GL (Fig. 1, 2) is very likely caused by the previously mentioned negative effect of anoxic soil conditions on maize metabolism. On the other hand, the lower CO_2 fluxes during the summer of 2009 especially at the AR site probably result from an inhibition of maize gas exchange due to drought stress (Vitale et al. 2008, Jones et al. 1986), i.e. long periods of very low GWL (Fig. 1, 2). Apart from these extreme situations, GWL were mostly at soil depths which were favourable for the metabolism and the productivity of a C4 plant like maize (Tollenaar and Dwyer 1999).

For example, maize features considerably higher gas exchange activity under maximum PAR and temperature conditions than all C3 grasses and crops (Zeri et al. 2011, Kutsch et al. 2010). As a consequence, although the main growing period of maize (~2 months) is much shorter than that of most C3 plants (3–4 months), the CO_2 flux intensity of maize throughout this short active period is large enough to result in higher annual cumulative R_{eco} and GPP values compared to C3 crops (Beetz et al. 2013, Klumpp et al. 2011, Zeri et al. 2011, Flanagan et al. 2002). It is very likely that the GWL optima of GPP and R_{eco} can be traced back to this fact, e.g., as indicated by the enhanced amplitudes of the GPP as well as the R_{eco} fluxes at the AR site during the wet summer 2007 compared to years with lower GWL (Fig. 2). However, the interactions between

GWL and maize growth do not offer explanations for the observed differences in cumulative NEE among sites and the functional relationship between NEE and GWL.

4.3 Relevance of interactions between GWL and dynamic soil C and N stocks

The strong effect of GWL on the C gas exchange is likely also the reason for the lack of any effect of total, i.e. static, soil C and N stocks on daily, monthly or annual C gas exchange. In the few existing studies on this subject, an impact of soil C and N stocks on C gas fluxes was only found for if GWL was either constant (Mundel 1976) or irrelevant for the soil water regime (Lohila et al. 2003). Moreover, in agreement with the results of this study, Leiber-Sauheitl et al. (2014) found no relationships between static soil C and N stocks and the C gas exchange of Gleysols with highly variable GWL during a 1-year study. In contrast, our study revealed a very strong effect of mainly GWL-determined dynamic soil C and N stocks on C gas dynamics (Table 3), thus indicating a higher relevance of SOC and N stocks located in the aerobic zone above the GWL for plant and soil gas exchange than of total soil SOC_{stocks} and N_{stocks} in the soil profile.

However, the functional GWL-related mechanisms mentioned in the introduction cannot fully explain the results of this study. Several observations indicate that the influence of the dynamic soil C and N stocks on the C gas exchange extends beyond the mere GWL effect:

i) All C gas fluxes are differently and specifically influenced by the dynamic soil C and N stocks (Tables 3, 4).

ii) Compared to the GWL, the effects of dynamic soil C and N stocks on NEE are considerably stronger than on the individual R_{eco} und GPP fluxes, also reflected by the associated shift in the GPP : R_{eco} ratio (Table 3). It must be pointed out that these two parameters differ in their informational value: while NEE is the absolute difference between the opposing CO_2 fluxes R_{eco} and GPP, the GPP : R_{eco} ratio reflects the relative proportion of these fluxes, thus giving indications for the reasons of changing NEE values. Interestingly, the dynamic C : N ratio shows a similarly strong effect on these two parameters. The potential relevance of these observations for explaining the study results is also discussed in section 4.2.

iii) The effects of the GWL and the dynamic soil C or N stocks on the cumulative CO_2 fluxes clearly differ with respect to their type and direction (Fig. 3, Table 4).

Despite a limited number of sites, clustering of sites with respect to GWL range, and a single crop, the results of this study are considered consistent and plausible for the range of measured GWL and soil C stocks, as the results from several very different statistical methods point to the same conclusions. Still, subsequent studies which consider other sites and plants are required to determine if the discussed conclusions regarding the type and intensity of the effect of dynamic soil C and N stocks on cumulative NEE, their differentiated effects on GPP and R_{eco} as well as their interactions with GWL are generally valid. A reassessment of data from previous studies using continuous GWL data (if available) for the calculation of dynamic soil C and N stocks could be helpful to determine if similarly strong effects of dynamic soil C and N stocks on C gas dynamics exist for other sites and plants. System-oriented investigations, which are aiming to understand the underlying processes and mechanisms, might reveal if and how the observed phenomena are related and from which underlying processes they originate.

4.4 The nature and relevance of mechanisms causing the effect of the dynamic soil C and N stocks

4.4.1 Potential mechanisms

A common observation may be used as a starting point for a comprehensive explanation: crop growth on groundwater-influenced soils is mainly influenced by rooting depth, which in turn is mostly influenced by GWL (e.g., for maize: Kondo et al. 2000). In this context, stress due to O_2 deprivation only plays a minor role, i.e. via the GWL-defined lower limit of the root-able soil volume (Glaz et al. 2008, Livesley et al. 1999). More importantly, larger root systems enable improved supply of plants with nutrients and water (especially at the AR site), likely resulting in increased photosynthetic capacity and thus higher primary productivity. The link between increasing N content and increased GPP was previously documented in studies by Flanagan et al. (2002) and Ashraf et al. (1999). Interestingly, several long-term field trials with crops grown on mineral soils also show that changing SOC stocks not only depend on crop rotation and organic fertiliser amount, but also on the nutrient supply to the crops *per se*. In these trials, the mere application of mineral fertiliser results in a significant increase of soil organic matter compared to non-fertilised treatments (Jung and Lal 2011, Banger et al. 2010, Thomas et al. 2010, Christopher and Lal 2007, Sainju et al. 2006,). Among other crops, this also applies to maize (Kaur et al. 2007).

In particular, the N supply plays a key role: up to a threshold, the gradual increase of mineral N fertiliser amount generally results in higher SOC and SON stocks (e.g., for maize: Kaur et al. 2007, Blair et al. 2006a, Blair et al. 2006b). Pot experiments with maize indicate that N fertilisation increases the input of newly assimilated C more than CO_2 emissions from root respiration and mineralisation of soil organic matter (Gong et al. 2012, Conde et al. 2005), thus resulting in the accumulation of SOC. Moreover, in field trials, mineral N fertilisation reduced the decomposition rate of maize residues in the soil (Grandy et al. 2013). Therefore – apart from the impact of C export (removal during harvesting) and import (input through organic fertilisation) on the soil C budget – it seems highly likely that the N fertilisation of arable crops contributes to an increase of SOC stocks by promoting C input through gross and net primary productivity more than C loss via ecosystem respiration. Although this has not yet been experimentally confirmed in its entirety, scientific evidence on the individual effects of N fertilisation on the SOC stocks of arable soils without groundwater influence makes this hypothesis plausible.

4.4.2 Indications for similar mechanisms on groundwater-influenced soils

Several results of this study suggest a strong N impulse on C gas fluxes. All sites received a total of 122 kg N ha^{-1} y^{-1} throughout the entire study period, providing sufficient N for plant growth. The dynamic soil N stocks and the SOC_{dyn} : N_{dyn} ratio had strong effects on cumulative NEE and the GPP : R_{eco} ratio (Table 3). Formally, this also holds true for the dynamic SOC stocks, but – unlike for N – this effect results from the tight correlation of soil C and N contents rather than from direct effects of organic matter production or decomposition. The large influence of GWL on dynamic soil N stocks, reflected by a strong interaction, indicates that both parameters control N mineralisation. It has been repeatedly observed both for organic and mineral soils that the lowering of the GWL, i.e. an increase of the dynamic N stocks due to improved soil aeration, increases N mineralisation, while a rising GWL, i.e. decreasing dynamic N stocks, results in the opposite (Eickenscheid et al. 2014, McIntyre et al. 2009, Venterink et al. 2002; Hacin et al. 2001, Goettlich 1990, Reddy and Patrick 1975).

Increased dynamic soil N stocks are equivalent to an improved N supply to plants and microorganisms, which should be similar in effect to the N fertilisation in the above-mentioned long-term field trials. In this study, the tight correlation between the dynamic soil N stocks and the maize biomass development during the vegetation period ($r^2 = 0.817$; *data not shown*) indicates that most of the N mineralised when GWL were low and root systems deep likely played a significant role in plant N supply and thus plant development – regardless of the fertilisation-induced N impulse and the fact that the monthly biomass values where not measured but calculated using a simple linear approach. Similarly strong biomass and dynamic C and N stocks effects on cumulative NEE (Table 3) further support this line of thought, as an increased biomass production stimulated by higher N availability is always associated with increased CO_2 input into the plant-soil system via gross primary production.

In other words: the N supply in the plant-soil system and its effects on C formation and transformation processes likely also play a key role in the C gas exchange of groundwater-influenced soils, by promoting CO_2 input via gross primary production more than CO_2 emission via ecosystem respiration. The observed effects of the dynamic soil C and N stocks on cumulative NEE can thus be plausibly explained. However, the relatively low optimum GWL for minimizing NEE (Fig. 3) likely requires additional explanatory mechanisms. For example, an improved plant water and nutrient supply, e.g. with macro-nutrients like P and K, could increase root and shoot growth and thus CO_2 input, as observed for soils without groundwater influence (Ladha et al. 2011, Poirier et al. 2009, Al-Kaisi et al. 2008, Reay et al. 2008, Kaur et al. 2007).

4.4.3 Future improvements of the dynamic stocks concept

Most of the functional mechanisms discussed above are somewhat speculative and require subsequent validation by means of experiments which consider all mentioned processes of the plant-soil system and their respective regulating factors. Special attention should be paid to the determination of the scope of all relevant processes, as several studies state that the input of N and other nutrients does not always have only positive effects on net CO_2 exchange and the C sink function of arable soils (Thangarajan et al. 2013, Hoffmann et al. 2009, Mulvaney et al. 2009, Al-Kaisi et al. 2008, Khan et al. 2007).

Moreover, the concept of dynamic soil C and N stocks is only an indicator of real dynamic stocks, because in this study dynamic stocks were modeled exclusively based on GWL dynamics. Further developments might include precipitation-related topsoil water dynamics or soil hydraulic properties (e.g., capillary fringes), which might considerably reduce dynamic soil C and N stocks. The concept of dynamic stocks could also be expanded to other plant nutrients like plant-available P or K. However, these suggested refinements require very detailed high-resolution data on soil and plant properties and processes, including their vertical variability in the soil profile, and were thus beyond the scope of this study.

5 Conclusions

Results clearly showed that the studied soils differ considerably with respect to the intensity and dynamics of C gas exchange. In order to accurately assess the climate impact of arable sites on drained peatlands, it is therefore necessary to consider the entire range of groundwater-influenced mineral and organic soil types and their respective areal extent within a heterogeneous soil landscape.

While climatic controls like PAR, temperature and precipitation mainly have short-term effects on C gas fluxes, the effects of dynamic soil C and N stocks are clearly observable at all temporal scales. It is to be determined by future studies in how far this also applies to i) crops other than maize, ii) other land use forms like grasslands, and iii) other groundwater-influenced sites. Dynamic soil C and N stocks may be major controlling factors of C gas fluxes and the CO_2 source or sink function of the entire range of wetlands, potentially of higher and more global relevance than GWL and vegetation, which are the main factors favoured to date (Couwenberg et al. 2011, Byrne et al. 2004). The insight, that the effect of the dynamic soil C and N stocks very likely results from the regulation of C formation and transformation processes by N and – potentially – nutrient and water supply as such, may be of particular importance. This mechanism would be a favourable prerequisite for the development of generalizable process-based models, which would be very useful in providing more precise estimates of the impact of important factors like climate, site conditions and land use on the C gas fluxes of wetlands.

Overall, the presented results and subsequent analyses show the enormous potential of combining long-term measurements of C gas fluxes with process-oriented analyses of the functional mechanisms and their regulation within the soil-plant system when aiming for an improved understanding of the biogeochemistry of wetlands.

The Supplement related to this article is available online at doi: XXX.

Acknowledgements

Funding for this study was provided by the German Federal Ministry of Education and Research (BMBF, project: “Climate protection by peatland protection – Strategies for peatland management”, 01LS05049), the Thünen Institute for Climate-Smart Agriculture (TI, joint research project “Organic soils”), the European Union (project “EU-IP NitroEurope”, 017841) and the Leibniz Centre for Agricultural Landscape Research (ZALF) e.V. (interdisciplinary research project “CarboZALF”). We thank M. Bechtold (Thünen-Institute of Climate-Smart Agriculture, Braunschweig, Germany) for calculation of groundwater models and discussions. Additionally we thank A. Behrendt and the other employees of the ZALF research station in Paulinenaue and G. Goßmann for assistance in the field, M. Schmidt for technical support and N. Jurisch, N. Pehle, M. Sanchez, E. Mendez, A. Fuertes, M. Minke, A. Burlo, H. Chuvashova, R. Juszczak, T. Yarmashuk and numerous international and national students for measurement support, in particular E. Halle, E. Leithold, B. Ehrig, M. Mees, M. Liebe, J. Acebron, and J. Jäger.

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Tables

Table 1. Characteristics of study sites: soil type, elevation, and 0–1 m stocks of soil organic C and total N.

Site	Soil type[†]	Elevation	SOC_{stocks}	total N_{stocks}
		[m a.s.l.]	[kg SOC m^{-2}][‡]	[kg N_t m^{-2}] [‡]
AR	Haplic Arenosol	29.6	8.0	0.7
GL	Mollic Gleysol	29.0	37.8	3.1
HS	Hemic Histosol	28.8	86.9	5.4

[†] WRB 2006; [‡] 0–1 m soil depth

Table 2. Annual fluxes of CO_2 (R_{eco}, GPP and NEE) and CH_4 by site and year (± model error; 95 % confidence interval); and average fluxes (± 1 SD) for the entire study period (2007/08-2010/11) and excluding the flooded year 2007/08.

	C flux	Year				Periodic average	
Site	[g C m^{-2} y^{-1}]	2007/08	2008/09	2009/10	2010/11	2007/08-2010/11	2008/09-2010/11
AR	CH_4	0.17 (0.07)	0.15 (0.32)	-0.10 (0.06)	0.00 (0.04)	0.06 (0.06)	0.01 (0.07)
	R_{eco}	2880 (183)	1729 (32)	1267 (21)	1547 (40)	1856 (354)	1514 (134)
	GPP	-2889 (52)	-1670 (34)	-1143 (34)	-1534 (58)	-1810 (377)	-1449 (158)
	NEE	-9 (190)	59 (47)	125 (40)	13 (70)	47 (30)	66 (32)
GL	CH_4	1.19 (0.61)	-0.10 (0.03)	-0.04 (0.10)	-0.17 (0.08)	0.22 (0.32)	-0.10 (0.04)
	R_{eco}	1733 (191)	2131 (30)	1288 (51)	1409 (36)	1640 (189)	1609 (263)
	GPP	-1799 (43)	-2279 (43)	-1895 (97)	-1809 (40)	-1946 (113)	-1994 (144)
	NEE	-65 (196)	-148 (52)	-607 (110)	-400 (54)	-305 (123)	-385 (133)
HS	CH_4	27.57 (3.70)	0.26 (0.51)	0.30 (0.20)	n.a.[†]	n.a.[†]	n.a.[†]
	R_{eco}	1479 (55)	1853 (33)	2131 (68)	1995 (52)	1864 (141)	1993 (80)
	GPP	-985 (62)	-2065 (61)	-2535 (53)	-2382 (122)	-1992 (350)	-2327 (139)
	NEE	493 (83)	-212 (70)	-404 (86)	-387 (133)	-127 (212)	-334 (62)

[†] Data not available

Table 3. Summary statistics of generalized linear model (GLM) analysis describing the influence of site and environmental controls (GWL, climate, soil, plants) on cumulative annual CH$_4$ efflux, R$_{eco}$, GPP, NEE and the ratio of GPP : R$_{eco}$.

		CH$_4$ [g CH$_4$-C m^{-2} y^{-1}]		R$_{eco}$ [g CO$_2$-C m^{-2} y^{-1}]		GPP [g CO$_2$-C m^{-2} y^{-1}]		NEE [g CO$_2$-C m^{-2} y^{-1}]		GPP : R$_{eco}$	
		Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*	Wald χ^2	*p*
	Intercept	1.312	*0.252*	7.626	**_0.006*_**	14.311	**_≤0.001*_**	96.005	**_≤0.001*_**	29.743	**_≤0.001*_**
	Site	72.812	**_≤0.001*_**	25.571	**_≤0.001*_**	26.040	**_≤0.001*_**	90.685	**_≤0.001*_**	65.869	**_≤0.001*_**
Climate	Air temperature	11.218	**_0.001*_**	33.135	**_≤0.001*_**	18.706	**_≤0.001*_**	30.960	**_≤0.001*_**	17.566	**_≤0.001*_**
	Soil temperature	1.666	*0.197*	14.456	**_≤0.001*_**	5.927	**_0.015*_**	36.618	**_≤0.001*_**	18.096	**_≤0.001*_**
	Precipitation	19.008	**_≤0.001*_**	9.093	**_0.003*_**	4.827	**_0.028*_**	11.562	**_0.001*_**	17.588	**_≤0.001*_**
	Sunshine hours	10.201	**_0.001*_**	21.158	**_≤0.001*_**	9.646	**_0.002*_**	†		†	
	Year	†		6.004	**_≤0.001*_**	8.210	**_0.004*_**	7.629	**_0.006*_**	4.650	**_0.031*_**
	Year * Air temp.	†		50.403	**_≤0.001*_**	37.758	**_≤0.001*_**	†		9.919	**_0.002*_**
	Year * Sunshine hours	†		37.816	**_≤0.001*_**	24.348	**_≤0.001*_**	†		†	
	Soil temp. * Air temp.	12.791	**_≤0.001*_**	†		†		29.049	**_≤0.001*_**	12.913	**_≤0.001*_**
	Soil temp. * Sunshine h.	11.667	**_0.001*_**	20.182	**_≤0.001*_**	11.059	**_0.001*_**	29.049	**_≤0.001*_**	†	
Plants	Biomass	†		17.810	**_≤0.001*_**	23.071	**_≤0.001*_**	49.537	**_≤0.001*_**	7.361	**_0.007*_**
	Biomass * Site	†		72.633	**_≤0.001*_**	70.273	**_≤0.001*_**	80.039	**_≤0.001*_**	33.074	**_≤0.001*_**
	Biomass * Sunshine h.	†		16.733	**_≤0.001*_**	23.268	**_≤0.001*_**	†		†	
GWL	GWL	3.173	*0.075*	273.627	**_≤0.001*_**	13.516	**_≤0.001*_**	2.667	*0.102*	38.940	**_≤0.001*_**
	GWL * Site	27.256	**_≤0.001*_**	†		17.779	**_≤0.001*_**	†		61.005	**_≤0.001*_**
	GWL * Precipitation	†		†		†		6.653	**_0.010*_**	23.737	**_≤0.001*_**
Soil	SOC$_{dyn}$	5.843	**_0.016*_**	15.668	**_≤0.001*_**	8.330	**_0.004*_**	32.101	**_≤0.001*_**	18.340	**_≤0.001*_**
	N$_{dyn}$	8.683	**_0.003*_**	26.541	**_≤0.001*_**	8.479	**_0.004*_**	23.224	**_≤0.001*_**	†	
	SOC$_{dyn}$: N$_{dyn}$	0.869	*0.351*	†		13.120	**_≤0.001*_**	106.424	**_≤0.001*_**	4.146	**_0.042*_**
	SOC$_{dyn}$ * Site	24.005	**_≤0.001*_**	93.546	**_≤0.001*_**	25.348	**_≤0.001*_**	†		13.538	**_0.001*_**
	N$_{dyn}$ * Site	†		93.868	**_≤0.001*_**	25.267	**_≤0.001*_**	8.349	**_0.004*_**	†	
	SOC$_{dyn}$: N$_{dyn}$ * Site	73.365	**_≤0.001*_**	†		26.078	**_≤0.001*_**	92.340	**_≤0.001*_**	66.370	**_≤0.001*_**
	SOC$_{dyn}$ * GWL	17.551	**_≤0.001*_**	†		†		†		†	
	N$_{dyn}$ * GWL	22.532	**_≤0.001*_**	†		9.169	**_0.002*_**	64.724	**_≤0.001*_**	†	

* Asterisks denote significant factors (α = 0.05).

† Redundant parameter/parameter interaction.

Table 4. Summary statistics of multiple nonlinear regression analysis of the form NEE = poly (GWL) + lin y $^{(1;\ 2;\ 3\ \text{or}\ 4)}$ describing the influence of GWL and one environmental parameter, either 1) SOC_{dyn}, 2) N_{dyn}, 3) $SOC_{dyn} : N_{dyn}$ or 4) biomass, on cumulative annual NEE: mean absolute error (MAE), RMSE-observations standard deviation ratio (RSR), adjusted coefficient of determination (R^2), modified index of agreement (md), percent BIAS (PBIAS) and Nash-Sutcliffs model efficiency (NSE), Akaike Information Criterion (AIC) and Bayesian information criterion (BIC).

Summary statistic	Environmental parameter			
	^{1} SOC_{dyn}	^{2} N_{dyn}	$^3SOC_{dyn}:N_{dyn}$	^{4} Biomass
MAE [g m^{-2} y^{-1}]	80.99	83.86	78.99	**84.78**
RSR	**0.353**	0.362	0.355	0.354
adj. R^2	**0.869**	0.862	0.867	0.868
md	0.847	0.842	**0.850**	0.840
PBIAS [%]	**0.000**	0.000	0.000	0.000
NSE	**0.872**	0.866	0.871	0.871
AIC	**503.38**	505.37	503.88	503.67
BIC	**515.20**	517.20	515.70	515.49

Note: bold values highlight the best value for each summary statistic across the four models; all models significant at *p*- value ≤ 0.001

Figures

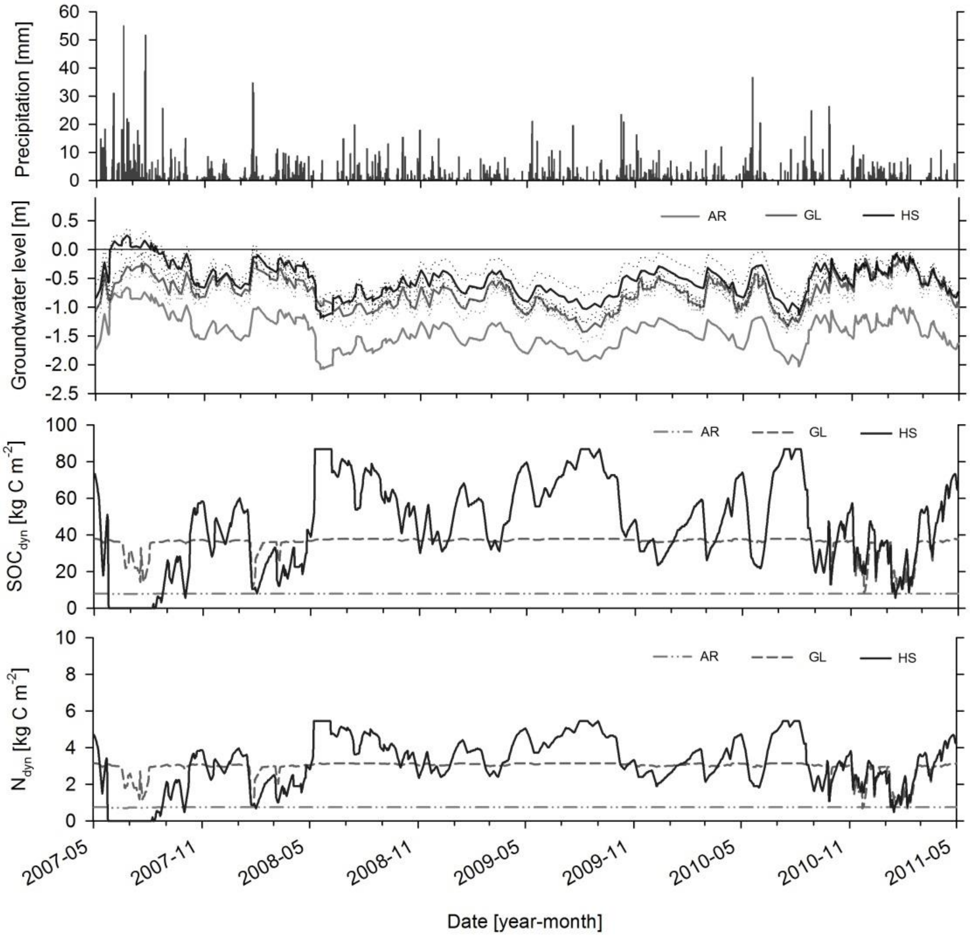

Figure 1. Seasonal dynamics of (from top to bottom) daily precipitation, average daily GWL including 95% confidence intervals (dotted lines), and daily dynamic SOC$_{dyn}$ and N$_{dyn}$ stocks by site (for 0–1 m depth).

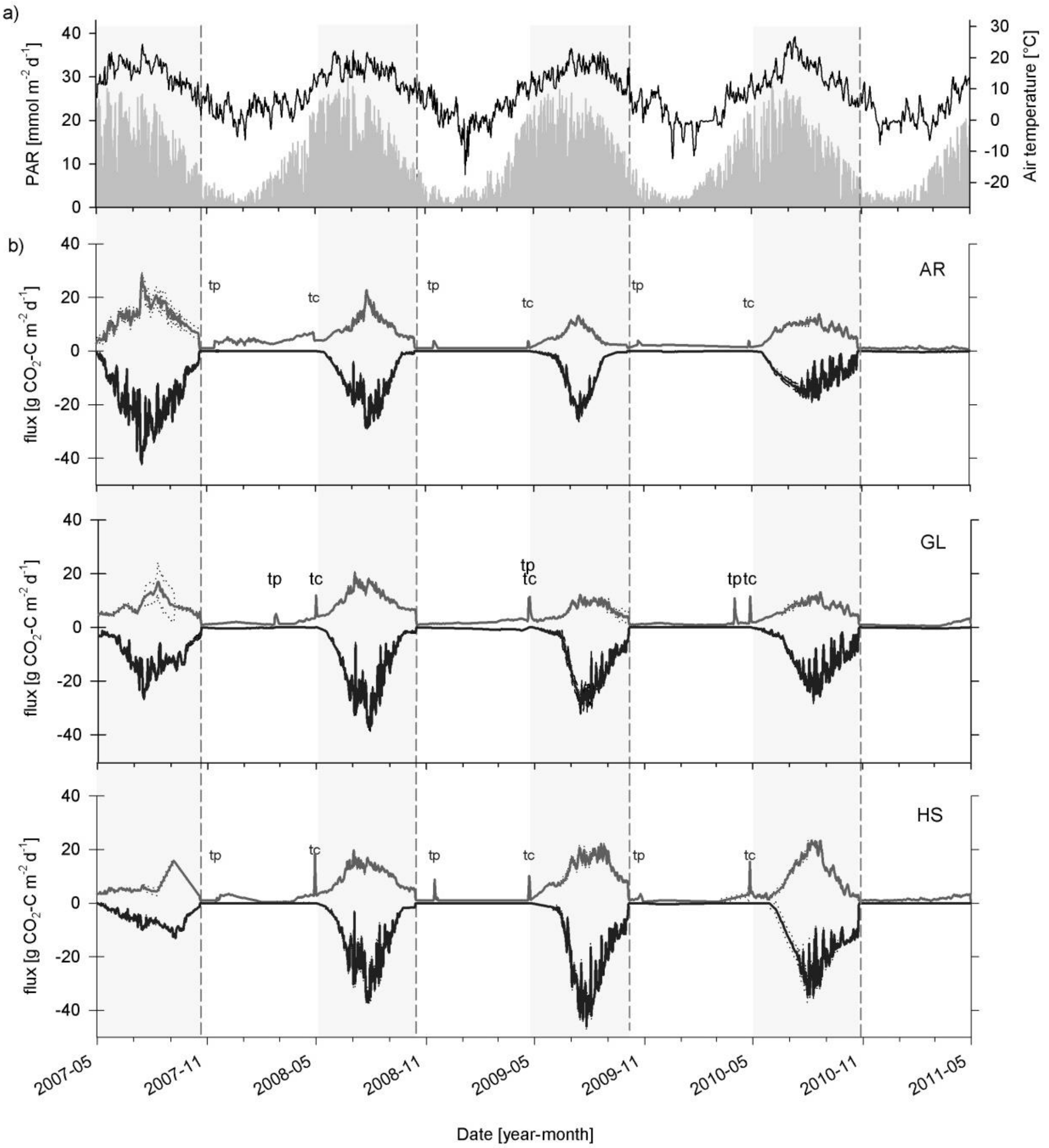

Figure 2. Dynamics of daily a) cumulated PAR (grey vertical bars) and average air temperature at 20 cm height (black line); and b) modeled CO_2-C fluxes (grey line: R_{eco}; black line: GPP) including 95% confidence intervals (dotted lines) by site. Shaded areas indicate the period between maize sowing and harvest (dashed vertical line); tp – ploughing, tc – cultivation (sowing, fertilization).

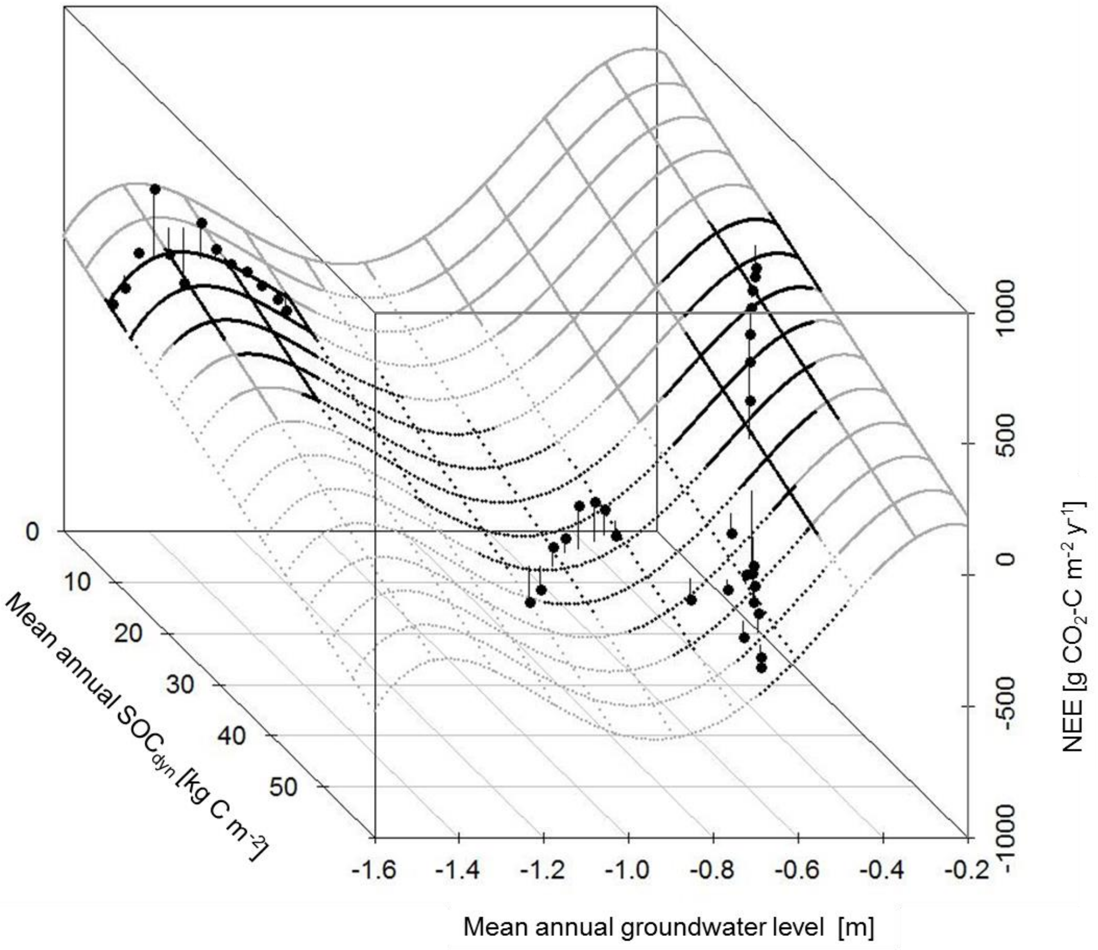

Figure 3. Result of nonlinear regression analysis between NEE, GWL and SOC$_{dyn}$ originating from 365-day moving-window analysis averaged over twelve GWL classes per site (for model statistics see Table 4). Displayed grid represents the derived model surface with i) estimated model area covered by direct measurements (solid black) and ii) non-empirically approved model area computed by extrapolation (grey). Modelled NEE is separated according to positive (solid lines) and negative (dashed lines) values.