

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 CO₂ and CH₄ 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 CO₂ fluxes of these soils and, inversely, for CH₄. To test this assumption, the present study analysed the C gas exchange (gross primary production – GPP, ecosystem respiration – R_{eco}, net ecosystem exchange – NEE, CH₄) 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;

28 38 kg C m⁻²); and c) Hemic Histosol (HS; 87 kg C m⁻²). Daily GWL data was used to calculate
29 dynamic SOC (SOC_{dyn}) and N (N_{dyn}) stocks.

30 Average annual NEE differed considerably among sites, ranging from 47±30 g C m⁻² y⁻¹ at AR to
31 -305±123 g C m⁻² y⁻¹ at GL and -127±212 g C m⁻² y⁻¹ at HS. While static SOC and N stocks
32 showed no significant effect on C fluxes, SOC_{dyn} and N_{dyn} and their interaction with GWL
33 strongly influenced the C gas exchange, particularly NEE and the GPP : R_{eco} ratio. Moreover,
34 based on nonlinear regression analysis, 86% of NEE variability was explained by GWL and
35 SOC_{dyn}. The observed high relevance of dynamic SOC and N stocks in the aerobic zone for plant
36 and soil gas exchange likely originates from the effects of GWL-dependent N availability on C
37 formation and transformation processes in the plant-soil system, which promote CO₂ input via
38 GPP more than CO₂ emission via R_{eco}.

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

45 **1 Introduction**

46 Peatlands are one of the most important ecosystems for the terrestrial carbon (C) and nitrogen (N)
47 cycle, storing up to 500 Mg C ha⁻¹ and – particularly in nutrient-rich fens – 120 Mg N ha⁻¹ (Yu et
48 al. 2011, MacDonald et al. 2006, Kunze 1993). Throughout the world, the drainage and
49 subsequent agricultural cultivation of peatlands has increased soil organic carbon (SOC)
50 mineralisation rates and the associated CO₂ emissions (Couwenberg et al. 2010, Kasimir-
51 Klemedtsson et al. 1997, Nykänen et al. 1995), resulting in the creation of small-scale mosaics of
52 soil types with extremely variable SOC stocks, especially in the case of fens. The respective soil
53 types range from deep peat soils to humus-rich sandy soils, which are not classified as peat soils
54 due to an SOC content of <12% (IUSS Working Group WRB 2007). These individual soil types
55 are typically found at similar relative elevations within an increasingly undulating landscape and
56 the ground water level (GWL) is often subject to considerable short-term fluctuations. As a result
57 of the tight coupling between soil types and elevation, mean GWL may differ considerably

58 between individual soil types (Aich et al. 2013, Heller and Zeitz 2012, Dawson et al. 2010, Teh et
59 al. 2011, Dexler et al. 2009, Müller et al. 2007, Schindler et al. 2003). These sites are typically
60 used as grassland or cropland (Joosten and Clark 2002, Byrne et al. 2004).

61 The relevance of these soil type mosaics originating from drained fen peatlands as a source or
62 sink for greenhouse gases like CO₂ and CH₄, especially if used for cropland, still cannot be
63 exactly determined. In particular, knowledge about the influence of variable soil C stocks on the
64 C gas exchange is still limited. In light of the extreme complexity of site conditions, it seems
65 unlikely that the common focus on interactions between C stocks and particularly relevant control
66 parameters like groundwater and temperature (Adkinson et al. 2011, Berglund et al. 2010, Kluge
67 et al. 2008, Jungkunst and Fiedler 2007, Daulat et al. 1998) will result in reliable and
68 generalizable conclusions about the C gas fluxes of degraded fens; mainly because this approach
69 fails to account for the plant-induced C gas input counteracting the C gas emissions determined
70 by soil characteristics and microorganisms.

71 Therefore, new insights are much more likely to be derived from system-oriented studies
72 analysing all interrelated C gas fluxes, e.g. CH₄ exchange, CO₂ uptake during photosynthesis and
73 CO₂ emission via respiration, together with the underlying processes and control mechanisms
74 (Chapin III et al. 2009, Schmidt et al. 2011). Indeed, there are numerous indications suggesting
75 that this approach may also be promising for the C gas exchange of drained fen sites.

76 Short- and long-term fluctuations of the GWL and its interactions with soil and plants very likely
77 also play a key role in the C cycle of other groundwater-influenced soil types, similar to true peat
78 soils (Couwenberg et al. 2011, Berglund and Berglund 2011, Flanagan et al. 2002, Augustin et al.
79 1998, Martikainen et al. 1995, Nykänen et al. 1995). For peat soils, many studies documented the
80 impact of GWL on the interactions between soil C dynamics and gaseous C emissions in the form
81 of CH₄ and CO₂, the latter originating from autotrophic root respiration and heterotrophic
82 microbial respiration. Ultimately, these GWL effects are a result of the ratio between SOC stocks
83 located in the aerobic, i.e. above-GWL, and the anaerobic, i.e. below-GWL, zone (Laine et al.
84 1996). However, very few (Leiber-Sauheitl et al. 2014, Jans et al. 2010, Jungkunst et al. 2008,
85 Jungkunst and Fiedler 2007) studies have investigated Gleysols and groundwater-influenced
86 sandy soils, which make up a significant portion of fen landscapes. It also remains unclear if the

87 impact of GWL on the gas exchange is modified by the highly variable density typical of SOC-
88 rich soil horizons of drained peatlands.

89 Knowledge gaps also limit the quantification of direct GWL effects on plant-mediated CO₂
90 uptake via photosynthesis. Site-adapted plants growing on undisturbed peat soils and perennial
91 grasses cultivated on groundwater-influenced soils can tolerate changing GWL without
92 considerable deterioration of photosynthetic performance (Farnsworth and Meyerson 2003,
93 Crawford and Braendle 1996). In contrast, GWL fluctuations likely have a particularly strong
94 impact on annual crops cultivated on drained peatlands, as most crops typically react to
95 waterlogging, i.e. anoxic soil conditions as a result of high GWL, with reduced photosynthesis,
96 plant respiration and growth (Zaidi et al. 2003, Asharf 1999, Singh 1984, Wenkert et al. 1981).
97 Other studies indicate that crops cultivated on groundwater-influenced soils feature better growth
98 when GWL are low (Glaz et al. 2008), but it is unclear if this is a direct result of improved
99 aeration or an indirect effect of increased soil volume, allowing for better root development and
100 thus increased nutrient uptake (Glaz et al. 2008, Livesley et al. 1999).

101 Despite the system-orientated approach mentioned above, it can therefore be assumed that the
102 amounts of soil C and N located above the temporally variable GWL – hereafter referred to as
103 dynamic C and N stocks – are of essential relevance to plant- and microbially mediated C gas
104 fluxes on drained peatland soils. Moreover, investigations into the effects of dynamic C and N
105 stocks may yield new insights into the mechanisms controlling the C dynamics at these sites. This
106 would be a significant advancement with respect to a comprehensive and generalizable
107 understanding of the CO₂ and CH₄ source and sink capacity of drained arable fen peatlands.

108 The present study tests the above-mentioned assumption by means of multi-year manual
109 chambers measurements, subsequent modeling and complex statistical analysis of all relevant C
110 gas fluxes, i.e. the net CO₂ exchange resulting from gross primary production (plant
111 photosynthesis) and ecosystem respiration (sum of plant and soil respiration) and the CH₄
112 exchange, of maize cultivated on different groundwater-dependent soil types representing a steep
113 SOC gradient. In particular, the study focuses on answering the following research questions:

- 114 1. Are there differences among soil types regarding the dynamics and the intensity of the C
115 (CO₂ and CH₄) gas exchange of drained arable peatland soils?

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

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

121

122 **2 Materials and methods**

123 **2.1 Site description and land use history**

124 The study sites are located near the village of Paulinenaue, in the shallow and drained peatland
125 complex ‘Havelländisches Luch’ of NE Germany (51 km W of Berlin; 52°41`N, 12°43`E). This
126 peatland was first drained at the beginning of the 14th century (Behrendt, 1988). A systematic
127 amelioration for the entire “Luch” took place from 1718 until 1724 and included The
128 construction of ditches and dams to drain the formerly swampy terrain and to provide access to
129 the land. Grasslands with hay production dominated the “Luch” at that time. In order to prevent
130 repeated flooding and to increase grassland productivity, a second amelioration with deeper
131 drainage ditches was implemented between 1907 and 1925. A substantial increase in total ditch
132 length occurred between 1958 and 1961, when approx. 1000 km of new ditches were established
133 in the area (Behrendt, 1988). The next huge effort to increase productivity started in the early
134 1970ies by the so-called “Komplexmelioration”, which lasted until the late 1980ies. The basic
135 idea was to establish a system of pumping stations and related ditches in order to increase and
136 lower the ground water table dynamically throughout the vegetation period depending on the
137 actual plant water demand. In addition, fertilizer application rates, including organic manure,
138 increased and the acreage of arable land doubled at the expense of grassland. After the re-
139 unification of Germany in 1989, a substantial de-intensification took place, resulting in the re-
140 conversion of arable land to grassland, reduction of fertilizer input, and abandonment of
141 hydraulic technical devices for economic reasons.

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

144 The study sites are located along a representative and steep landscape gradient in terms of soil
145 organic carbon stocks ($\text{SOC}_{\text{stocks}}$; 0–1 m), which is related to topographic position (Table 1): AR
146 – a Haplic Arenosol developed from aeolian sands with low $\text{SOC}_{\text{stocks}}$ ($8 \text{ kg C m}^{-2} \text{ m}^{-1}$) at a
147 microhigh (29.6 m a.s.l.); GL – a Mollic Gleysol developed from peat overlying fluvial sands
148 with medium $\text{SOC}_{\text{stocks}}$ ($38 \text{ kg C m}^{-2} \text{ m}^{-1}$) at 29.0 m a.s.l.; and HS – a Hemic Histosol developed
149 from peat featuring high $\text{SOC}_{\text{stocks}}$ ($87 \text{ kg C m}^{-2} \text{ m}^{-1}$) at the edge of a local depression
150 (28.8 m a.s.l.). Moreover, the vertical distribution of C and N differ between sites: at AS almost
151 all SOC and N is concentrated in the plough layer (Ap horizon), whereas GL and HS show larger
152 portions of SOC and N in subsoil horizons (Fig. S1 in supplement).

153 All sites were identically managed during the study period (Table S1 in supplement), i.e.
154 cultivated with a monoculture of grain maize with annually changing varieties. The AR and HS
155 sites are located 150 m apart within the same managed field, while GL is located 1.5 km from
156 AR/HS. However, field operations such as tillage, sowing, fertilisation and harvest were
157 conducted almost concurrently at all sites. Maize was fertilised with diammonium phosphate
158 (DAP) containing 22 kg N ha^{-1} and 24 kg P ha^{-1} in the course of sowing, followed approx. 2
159 weeks later by fertilisation with calcium ammonium nitrate (CAN) containing 100 kg N ha^{-1} .
160 During harvest, total plant biomass within the measurement plots was collected, chipped, dried at
161 60°C to constant weight and weighed. Grain yield was not recorded due to technical
162 complications. Total plant biomass subsamples were analysed for C content at the ZALF Central
163 Laboratory. After harvesting, all sites were mulched and ploughed.

164 **2.2 Environmental controls**

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

172 GWL at GL and HS was measured manually every two weeks using short 1.5 m dip wells. The
173 measured piezometric heads are considered representative of the phreatic water levels in the peat

174 layer because the organic soil layer directly overlies a sand aquifer without any major low-
175 conductance soil horizons in between. At HS, GWL was additionally recorded every 15 min by a
176 data logger (Mini-diver, Schlumberger). Time series modeling was used to fill several small data
177 gaps and to obtain continuous daily GWL data for the entire study period. The applied PIRFICT
178 approach (von Asmuth et al. 2008) implemented in the *Menyanthes* software (von Asmuth et al.
179 2012a) is a physically-based statistical time series model specifically developed to model
180 hydrologic time series, including shallow GWL fluctuations. As input, the model requires
181 continuous precipitation (DWD station ‘Kleßen’) and evapotranspiration data (FAO56 Penman-
182 Monteith; DWD station ‘Kyritz’) and optional control parameters, e.g., in our case, deep GWL
183 data recorded from a local dip well (LUGV Brandenburg). The calibrated model explained 80–
184 87% of the data variance; a good result for this data and model type (von Asmuth et al. 2012b).
185 Confidence intervals of GWL time series predictions were obtained by means of stochastic
186 simulation (see von Asmuth et al. 2012a). Due to the short distance between AR and HS and the
187 highly significant correlation of GWL at these sites ($R^2 = 0.836$), daily GWL values for AR were
188 calculated by shifting the modeled time series of HS with a constant offset of 0.9 m.

189 **2.3 Concept and calculation of dynamic C and N stocks**

190 The concept of ‘dynamic’ groundwater-dependent C and N stocks was developed to account for
191 the interaction of the most important drivers of the C gas fluxes of peatlands, namely GWL and
192 soil C and N stocks. The underlying idea is to derive a quantitative, dynamic proxy for the
193 aerated, unsaturated zone which determines the actual nutrient and O₂ availability and is therefore
194 highly relevant for root and shoot growth, microbial activity, and, consequently, all C gas fluxes.
195 Using daily GWL data, it was determined for each 1-cm soil layer up to a depth of 1 m if the
196 respective layer was saturated with groundwater or not. In daily time steps, SOC and N stocks
197 were then calculated for all non-saturated 1-cm layers and cumulated over the entire non-
198 saturated soil profile, i.e. above the GWL, to generate daily dynamic SOC (SOC_{dyn}) and N (N_{dyn})
199 stocks. For further analysis, daily SOC_{dyn} and N_{dyn} values were averaged monthly and annually.

200 **2.4 Gas flux measurements**

201 Periodic trace gas measurements were carried out at three permanently installed soil collars
202 (0.75 x 0.75 m) at each site. In summer 2007, due to flooding, soil collars at the HS site had to be

203 relocated within a radius of 10 m to i) technically allow for gas flux measurements; and ii) ensure
204 that all soil collars contained flood-affected but viable plants in order to maintain comparability
205 with the GL and AR sites, where maize mortality was not increased by flooding.

206 Throughout the entire study period, CH₄ measurements were conducted 1–2 times per month
207 using static *non-flow-through non-steady-state* opaque chambers (vol. 0.296 m³; Livingston and
208 Hutchinson 1995, Drösler 2005), for a total of 51–60 campaigns per site. At HS, CH₄
209 measurements were terminated already in October 2010 due to management constraints.
210 Exchange of CH₄ was measured by taking four consecutive 100-ml gas samples from the
211 chamber headspace in 20-min intervals (closure time 60 min), subsequently analyzed using a gas
212 chromatograph (Shimadzu GC 14B, Lofffield, Göttingen, Germany) equipped with a flame
213 ionization detector.

214 CO₂ exchange was measured using dynamic *flow-through non-steady-state* transparent (net
215 ecosystem exchange – NEE); light transmission of 86%) and opaque (ecosystem respiration –
216 R_{eco}) chambers (Livingston and Hutchinson 1995, Drösler 2005) attached to an infrared gas
217 analyzer (Li-820, Lincoln, NE, USA). Full-day CO₂ measurement campaigns with repeated (30–
218 50) individual chamber measurements (closure time 3–5 min) were conducted regularly every 4–
219 6 weeks from 05/2007–04/2011, for a total of 29–37 full campaigns per site. Further details on
220 CO₂ measurement methodology are given in Hoffmann et al. (2015).

221 **2.5 Flux calculation and gap filling**

222 Flux calculation for CO₂ and CH₄ was based on the ideal gas equation accounting for chamber
223 volume and area, air pressure, and average air temperature during the measurement. CH₄ fluxes
224 were calculated with the R package ‘flux 0.2-2’ (Jurasinski et al. 2012), using linear regression
225 analysis with stepwise backward elimination of outliers based on the normalized root mean
226 square error (NRMSE \geq 0.2) up to a minimum of three data points. Fluxes with NRMSE $>$ 0.4
227 were rejected. The calculated flux rates were then averaged for the respective measurement day
228 and linearly interpolated to determine annual CH₄ exchange.

229 For CO₂, the R script of Hoffmann et al. (2015) was used for flux calculation as well as the
230 subsequent separation into and modeling of R_{eco}, gross primary production (GPP), and NEE.
231 Measurements $<$ 30 s were rejected and measurements $>$ 1 min were shortened by a death band of

232 10% at the beginning and end, respectively (Kutzbach et al. 2007). For each measurement, the
233 final flux rate was selected from all potential flux rates generated by a moving window approach
234 using a stepwise algorithm, numerous quality criteria and the Akaike information criterion (AIC;
235 for details see Hoffmann et al. 2015). For R_{eco} , gap filling between measurement campaigns was
236 performed using campaign-specific temperature-dependent Arrhenius-type models by Lloyd and
237 Taylor (1994). GPP fluxes were calculated by subtracting modeled R_{eco} fluxes from measured
238 NEE fluxes, and then modeled using campaign-specific hyperbolic PAR-dependent models
239 (Wang et al. 2013, Elsgaard et al. 2012, Michaelis-Menten 1913). Average measured flux rates
240 were used if no significant fit was achieved for campaign-specific R_{eco} or GPP models
241 (Hoffmann et al. 2015). Half-hourly NEE values were calculated from modeled R_{eco} and GPP
242 fluxes (Hoffmann et al. 2015, Drösler 2005), and cumulated from May 1st to April 30th of the
243 following year (Table S1 in supplement), resulting in four consecutive annual CO_2 balances.
244 Negative values represent a C gas flux from the atmosphere to the ecosystem; positive values a
245 flux from the ecosystem to the atmosphere. The uncertainty of the annual CH_4 and CO_2 exchange
246 was quantified using a comprehensive error prediction algorithm described in detail by Hoffmann
247 et al. (2015).

248 **2.6 Data analysis**

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

261 Subsequently, generalized linear model (GLM) analyses (SPSS GENLIN procedure) were
262 performed to determine the influence of environmental controls and their interactions on the
263 cumulated annual CH₄, R_{eco}, GPP, and NEE balances as well as the GPP : R_{eco} ratio. Models were
264 defined using a gamma probability distribution and a log link function and calculated in a
265 stepwise backward elimination procedure, dropping non-significant variables until no further
266 improvement of the AIC was achieved (correction for finite sample sizes: AIC_c). Parameter and
267 interaction effects were evaluated based on the Wald χ^2 statistic, appropriate for non-normally
268 distributed continuous variables. Prior to analysis, CH₄ data were log-transformed after adding
269 the minimum CH₄ value to each data value, in order to allow for application of the GLM log link
270 function. Analogously, absolute values of GPP were used for the analysis and NEE data were
271 transformed to positive values by adding the minimum NEE value to each data value.

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

278

279 **3 Results**

280 **3.1 Environmental controls**

281 During the study period (05/2007–04/2011), weather conditions were somewhat cooler (8.7°C)
282 and wetter (634 mm) compared to the long-term average (1982–2012; 9.2°C; 530 mm).
283 Particularly the 2010/11 measurement year considerably deviated from the long-term temperature
284 average, with an annual air temperature that was 1.5°C below the long-term average –1 SD (*data*
285 *not shown*). While PAR and air temperature showed high daily and seasonal dynamics (Fig. 2a),
286 no pronounced seasonal patterns were observed for precipitation (Fig. 1). Instead, precipitation
287 featured an extremely high interannual variability with particularly heavy rainfalls during the
288 summer months of 2007 (May–July; Fig. 1). The precipitation sum during this period (507 mm)
289 exceeded the long-term average (179 mm) by >180% (*data not shown*). Reflecting the
290 precipitation dynamics, the GWL showed similar temporal dynamics of the three sites, but at

291 different levels. In summer, GWL remained generally low, with the exception of July–August
292 2007. The HS site, which consistently featured the highest average GWL (−0.5 m; Fig. 1,
293 Table S2 in supplement), was flooded during this period (GWL +0.2 m; *data not shown*).

294 The SOC_{dyn} and N_{dyn} stocks calculated based on the modeled GWL showed the highest
295 fluctuations at the HS site (Fig. 1). During times of high GWL, such as in summer 2007, the HS
296 and GL site featured drastically lowered SOC_{dyn} and N_{dyn} values, amounting to only 6.2 kg C m^{−2}
297 and 0.5 kg N m^{−2}, respectively, with SOC_{dyn} and N_{dyn} reduced to zero during flooded periods. In
298 contrast, pronounced peak values at HS were calculated for the low-GWL summer months during
299 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
300 HS site always featured the highest annual SOC_{dyn} (52 kg C m^{−2}) and N_{dyn} (4 kg N m^{−2}) stocks,
301 except for 2007/08 (Fig. 1; Table S2 in supplement).

302 **3.2 Daily and annual carbon gas exchange**

303 All sites generally featured very low daily CH₄ fluxes (−0.01 to 0.01 g CH₄-C m^{−2} d^{−1}) throughout
304 the study period (Fig. S3 in supplement). However, considerable CH₄ emission peaks were
305 observed at the HS and GL sites during times of flooding or high GWL, e.g. during summer 2007
306 and spring 2008. At HS, this resulted in a maximum CH₄ flux of 1.2 g CH₄-C m^{−2} d^{−1} on
307 August 1st, 2007, which is approx. 60 times higher than the median flux (0.02 g CH₄-C m^{−2} d^{−1}) at
308 this site. As a result of the flooding, annual CH₄ emissions in 2007/08 at HS amounted to 28±
309 4 g CH₄-C m^{−2} y^{−1}, and were thus nearly 100 times higher than observed for HS in the following
310 years (0.3±0.5 and ±0.2 g CH₄-C m^{−2} y^{−1}) and at least 25 times higher than observed for AR and
311 GL (< 1.2±0.6 g CH₄-C m^{−2} y^{−1}; Table 2). However, as the high annual CH₄ emissions 2007/08 at
312 HS result from a peak described by three measurement campaigns during the flooded period
313 (Fig. S3 in supplement), they are also associated with a higher uncertainty (±3.7 g CH₄-C m^{−2} y^{−1}
314 in 2007/08 vs. ±0.5 and ±0.2 g CH₄-C m^{−2} y^{−1} in 2008/09 and 2009/10; Table 2).

315 The modelled CO₂ exchange rates (for model evaluation statistics see Table S3 in supplement)
316 reflected the daily and seasonal dynamics of air temperature and PAR, with generally higher
317 fluxes in the growing season compared to fall and winter (Fig 2a, b). In summer, peak GPP fluxes
318 considerably exceeded the amplitude of R_{eco} fluxes. At all sites, the CO₂ exchange was also
319 influenced by management events, with particularly pronounced peaks of R_{eco} following tillage.
320 In addition, GPP was immediately reduced to zero after maize harvest due to the removal of the

321 photosynthetically active aboveground plant biomass. In general, the organic GL and HS sites
322 showed the highest CO₂ exchange intensity, with maximum R_{eco} and GPP fluxes of 23 g CO₂-
323 C m⁻² d⁻¹ and -46 g CO₂-C m⁻² d⁻¹, respectively, observed at the HS site (Fig 2a, b). However,
324 during the wet summer of 2007, the mineral AR site featured the highest intensity of CO₂
325 exchange, resulting in cumulated annual R_{eco} and GPP fluxes that were 25–44% and 52–61%
326 higher, respectively, than in the following years (2008–2011, Table 2). In contrast, at HS, the
327 2007 flooding resulted in strongly reduced CO₂ flux intensities and large net annual CO₂-C losses
328 (NEE of 493±83 g CO₂-C m⁻²) compared to the following years. Although the CO₂ fluxes
329 measured during the flooded period are associated with higher error values compared to periods
330 without flooding (Table 2), the modelled results are plausible, clearly reflecting the negative
331 effects of flooding on plant growth and thus plant C exchange. Hence, in 2007/08, cumulated
332 annual R_{eco} and GPP fluxes at AR were 76% and 49% higher than at the HS site (Table 2).

333 Excluding 2007/08, the average NEE during the study period at the mineral AR site was close to
334 zero with 50±32 g CO₂-C m⁻² y⁻¹ (Table 2), whereas the organic sites were net CO₂-C sinks with
335 -385±133 g CO₂-C m⁻² y⁻¹ (GL) and -334 ± 61 g CO₂-C m⁻² y⁻¹ (HS). Including the flood-
336 dominated year of 2007/08 resulted in a 62% and 21% reduction of the overall NEE at the HS
337 and GL sites, respectively. In contrast, when 2007/08 is included in the overall 2007–2011
338 average for the AR site, cumulated R_{eco} and GPP increase by 63% and 67%, respectively, while
339 NEE remains unaffected.

340 **3.3 Impact of environmental controls on carbon gas exchange**

341 Despite the wide range of control parameters included in the complex analysis, site (i.e. soil) had
342 a significant (*p*- value ≤ 0.05) effect on all gas fluxes (Table 3). The generally highly significant
343 (*p*- value ≤ 0.001) interactions between site and controls like biomass, GWL and soil parameters
344 show that the selected study sites represented a wide range of the respective control parameters.
345 Especially annual CH₄-C emissions were dominated by site, suggesting the presence of additional
346 important control factors not considered in this analysis. However, little residual variability
347 indicates that most of the variability in annual R_{eco} and GPP was explained by the factors
348 included in the GLM analyses, with more residual variability remaining for NEE and the
349 GPP : R_{eco} ratio.

350 While climate played a minor role in determining annual CH₄-C emissions via the effect of
351 precipitation on GWL, climate controls were more relevant for CO₂ exchange (Table 3). There,
352 the importance of climate was higher for cumulated GPP and R_{eco} than for NEE and the
353 GPP: R_{eco} ratio. The impact of climate variability on CO₂ exchange was even more pronounced at
354 the monthly scale, as indicated by highly significant interactions between climate controls and
355 month of year (*data not shown*). Biomass was equally important as climate in determining annual
356 GPP, whereas for R_{eco} biomass and its interactions were less relevant than climate (Table 3). In
357 contrast, the derived variables NEE and GPP : R_{eco} were less influenced by biomass than the
358 individual fluxes R_{eco} and GPP.

359 Direct groundwater influence was particularly pronounced for R_{eco}, GWL by far being the most
360 important GLM parameter (Table 3). Groundwater influence on CH₄-C emissions and the
361 GPP: R_{eco} ratio was expressed mainly through the interaction between GWL and site.

362 Groundwater-dependent soil parameters and their interactions with site and GWL dominated
363 annual CH₄-C emissions (Table 3). Soil parameters were also the main controls on NEE,
364 particularly the SOC_{dyn} : N_{dyn} ratio and its interactions with site. Dynamic soil parameters and
365 their associated interactions thus were of higher relevance for the derived variables NEE and
366 GPP : R_{eco} than for the NEE flux components R_{eco} and GPP. This indicates differences between
367 R_{eco}, and GPP with respect to their reaction to changing GWL and soil parameters, i.e. a shift in
368 the ratio between R_{eco}, and GPP throughout the range of GWL, SOC_{dyn} and N_{dyn} stocks. In
369 contrast, static SOC_{stocks} and N_{stocks} showed no significant (p -value ≥ 0.05) effect on cumulated
370 annual or monthly fluxes of either R_{eco}, GPP, or NEE (*data not shown*).

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

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

381

382 **4 Discussion**

383 **4.1 Soil influence on C gas exchange**

384 As indicated in the introduction, data about the CO₂ exchange of groundwater-influenced arable
385 soils is generally scarce, particularly for maize, although some data is available for organic soils.
386 Although the maximum CO₂ fluxes observed during a 1-year study of maize cultivated on a
387 Haplic Gleysol in the Netherlands (Jans et al. 2010) are ~25% lower compared to the studied
388 Gleysol (Fig. 2), the flux dynamics and the cumulative net CO₂ exchange of the organic soil
389 types are relatively similar in both studies, with mean annual NEE of -385 g CO₂-C m⁻² y⁻¹
390 (Gleysol) and -334 g CO₂-C m⁻² y⁻¹ (Histosol) in this study (Table 2) vs. -332 g CO₂-C m⁻² y⁻¹
391 (Jans et al. 2010). Moreover, the dynamics and the intensity of the CO₂ exchange observed for
392 the groundwater-influenced soils in this study are in the same order of magnitude as reported for
393 maize cultivated on soils without groundwater influence (Gilmanov et al. 2013, Kalfas et al.
394 2011, Zeri et al. 2011, Ceschia et al. 2010). The observed biomass yield of maize (257–
395 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,
396 Verma et al. 2005). According to Gilmanov et al. (2013) and Ceschia et al. (2010), maize
397 cultivation generally resulted in a net annual CO₂ sink across a wide range of sites in America
398 and Europe, but – like in this study – with considerable variability between sites and years (+89
399 to -573 g CO₂-C m⁻² y⁻¹).

400 The results of this study demonstrate for the first time a considerable influence of groundwater-
401 influence soils on crop CO₂ exchange, particularly on cumulative NEE (Tables 3, 4, Fig. 3), thus
402 clearly affirming the research question (1) regarding the soil effect. Surprisingly, the C-rich
403 drained organic soils showed a strong net CO₂ uptake (Table 2), while the C-poor Arenosol was a
404 small net CO₂ source. This observation cannot be entirely explained by the interaction between
405 GWL and the potentially mineralizable soil C stocks. Hence, an integrated consideration of all
406 relevant C gas fluxes and their regulation within the plant-soil system is required, which is
407 discussed in detail below. We are unaware of any previous study ever reporting such an effect,

408 likely because any systematic effects may only be observed in longer-term studies due to the high
409 interannual variability of C gas fluxes. This strongly supports the high relevance of such
410 investigations for the accurate evaluation of the C dynamics of groundwater-influenced arable
411 soils.

412 **4.2 Relevance of interactions between GWL and maize ecophysiology**

413 Apart from soil type and SOC content, the study sites are mainly differentiated by different
414 average GWL, which our study results show to be a crucial factor determining the high short- and
415 long-term variability of maize C gas exchange across the entire range of groundwater-influenced
416 soils. Previous studies have mainly shown an influence of GWL on CH₄ fluxes from peat soils,
417 mainly reporting an exponential increase of CH₄ fluxes for rising GWL with particularly high
418 CH₄ losses for GWL ≥ -0.2 m (Couwenberg et al. 2011, Jungkunst & Fiedler 2007, Drösler 2005,
419 Fiedler & Sommer 2000). Annual CH₄ emissions (-0.2 to 1.2 g CH₄-C m⁻² y⁻¹) for GWL between
420 -1.6 and -0.6 m and peak fluxes during flooding (≤ 28 g CH₄-C m⁻² y⁻¹; GWL of -0.3 m)
421 observed at the HS site are similar to values of Couwenberg et al. (2011) and Drösler (2005).
422 However, for crops cultivated on groundwater-influenced mineral soils, little data is available on
423 the impact of GWL on CH₄ fluxes (e.g., Pennock et al. 2010).

424 CO₂ exchange has also been intensively studied for organic soils, but mostly for pristine
425 peatlands and grasslands on peat soils (e.g., Leiber-Sauheitl et al. 2014, Berglund and Berglund
426 2011, Couwenberg et al. 2011), while data on maize are lacking. For peatland NEE, one study
427 reports a linear decrease with rising GWL over a range of -0.4 m to -0.1 m, with maximum NEE
428 observed at -0.4 m (Leiber-Sauheitl et al. 2014). Couwenberg et al. (2011) also observed
429 decreasing NEE when GWL rose above -0.5 m, but net CO₂-C uptake was only reported for very
430 high GWL above -0.1 m. In contrast, in this study, maize NEE was largely negative across the
431 entire range of GWL recorded at the studied groundwater-influenced soils (-2.1 m to $+0.2$ m),
432 changing to positive values when GWL rose above -0.4 m to -0.6 m. Moreover, the GWL–NEE
433 relationship for maize shows a clearly nonlinear relationship to GWL, with a distinct optimum at
434 considerably lower GWL (between -0.8 m and -1.0 m; Fig. 3) than observed for grasslands.
435 Further studies are required to determine if this is a general pattern applicable to other
436 groundwater-influenced soil types and crops.

437 Our study results further indicate that R_{eco} and GPP also feature specific GWL optima (*data not*
438 *shown*). For example, maximum R_{eco} fluxes were observed for GWL of -0.8 m to -1.0 m, similar
439 to data from grassland on four GWL-influenced soil types (Fiedler et al. 1998). Similar to the
440 R_{eco} of maize at the organic HS and GL sites, R_{eco} fluxes of grasslands on organic soils typically
441 decrease with rising GWL (Leiber-Sauheitl et al. 2014, Berglund and Berglund 2011, Laine et al
442 1996, Silvola et al. 1996), particularly if GWL rises above the soil surface (Koebsch et al. 2013).
443 The impact of GWL on GPP was relatively small in this study (Table 3); except for the effect of
444 the 2007 flooding, which resulted in a drastic reduction in GPP (Table 2) as also observed by
445 Koebsch et al. (2013) after rewetting.

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

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

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

468 **4.3 Relevance of interactions between GWL and dynamic soil C and N stocks**

469 The strong effect of GWL on the C gas exchange is likely also the reason for the lack of any
470 effect of total, i.e. static, soil C and N stocks on daily, monthly or annual C gas exchange. In the
471 few existing studies on this subject, an impact of soil C and N stocks on C gas fluxes was only
472 found for if GWL was either constant (Mundel 1976) or irrelevant for the soil water regime
473 (Lohila et al. 2003). Moreover, in agreement with the results of this study, Leiber-Sauheitl et al.
474 (2014) found no relationships between static soil C and N stocks and the C gas exchange of
475 Gleysols with highly variable GWL during a 1-year study. In contrast, our study revealed a very
476 strong effect of mainly GWL-determined dynamic soil C and N stocks on C gas dynamics
477 (Table 3), thus indicating a higher relevance of SOC and N stocks located in the aerobic zone
478 above the GWL for plant and soil gas exchange than of total soil SOC_{stocks} and N_{stocks} in the soil
479 profile.

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

- 483 i) All C gas fluxes are differently and specifically influenced by the dynamic soil C and
484 N stocks (Tables 3, 4).
- 485 ii) Compared to the GWL, the effects of dynamic soil C and N stocks on NEE are
486 considerably stronger than on the individual R_{eco} and GPP fluxes, also reflected by the
487 associated shift in the GPP : R_{eco} ratio (Table 3). It must be pointed out that these two
488 parameters differ in their informational value: while NEE is the absolute difference
489 between the opposing CO_2 fluxes R_{eco} and GPP, the GPP : R_{eco} ratio reflects the
490 relative proportion of these fluxes, thus giving indications for the reasons of changing
491 NEE values. Interestingly, the dynamic C : N ratio shows a similarly strong effect on
492 these two parameters. The potential relevance of these observations for explaining the
493 study results is also discussed in section 4.2.
- 494 iii) The effects of the GWL and the dynamic soil C or N stocks on the cumulative CO_2
495 fluxes clearly differ with respect to their type and direction (Fig. 3, Table 4).

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

508 **4.4 The nature and relevance of mechanisms causing the effect of the dynamic** 509 **soil C and N stocks**

510 **4.4.1 Potential mechanisms**

511 A common observation may be used as a starting point for a comprehensive explanation: crop
512 growth on groundwater-influenced soils is mainly influenced by rooting depth, which in turn is
513 mostly influenced by GWL (e.g., for maize: Kondo et al. 2000). In this context, stress due to O_2
514 deprivation only plays a minor role, i.e. via the GWL-defined lower limit of the root-able soil
515 volume (Glaz et al. 2008, Livesley et al. 1999). More importantly, larger root systems enable
516 improved supply of plants with nutrients and water (especially at the AR site), likely resulting in
517 increased photosynthetic capacity and thus higher primary productivity. The link between
518 increasing N content and increased GPP was previously documented in studies by Flanagan et al.
519 (2002) and Ashraf et al. (1999). Interestingly, several long-term field trials with crops grown on
520 mineral soils also show that changing SOC stocks not only depend on crop rotation and organic
521 fertiliser amount, but also on the nutrient supply to the crops *per se*. In these trials, the mere
522 application of mineral fertiliser results in a significant increase of soil organic matter compared to
523 non-fertilised treatments (Jung and Lal 2011, Banger et al. 2010, Thomas et al. 2010, Christopher
524 and Lal 2007, Sainju et al. 2006,). Among other crops, this also applies to maize (Kaur et al.
525 2007).

526 In particular, the N supply plays a key role: up to a threshold, the gradual increase of mineral N
527 fertiliser amount generally results in higher SOC and SON stocks (e.g., for maize: Kaur et al.
528 2007, Blair et al. 2006a, Blair et al. 2006b). Pot experiments with maize indicate that N
529 fertilisation increases the input of newly assimilated C more than CO₂ emissions from root
530 respiration and mineralisation of soil organic matter (Gong et al. 2012, Conde et al. 2005), thus
531 resulting in the accumulation of SOC. Moreover, in field trials, mineral N fertilisation reduced
532 the decomposition rate of maize residues in the soil (Grandy et al. 2013). Therefore – apart from
533 the impact of C export (removal during harvesting) and import (input through organic
534 fertilisation) on the soil C budget – it seems highly likely that the N fertilisation of arable crops
535 contributes to an increase of SOC stocks by promoting C input through gross and net primary
536 productivity more than C loss via ecosystem respiration. Although this has not yet been
537 experimentally confirmed in its entirety, scientific evidence on the individual effects of N
538 fertilisation on the SOC stocks of arable soils without groundwater influence makes this
539 hypothesis plausible.

540 **4.4.2 Indications for similar mechanisms on groundwater-influenced soils**

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

553 Increased dynamic soil N stocks are equivalent to an improved N supply to plants and
554 microorganisms, which should be similar in effect to the N fertilisation in the above-mentioned
555 long-term field trials. In this study, the tight correlation between the dynamic soil N stocks and

556 the maize biomass development during the vegetation period ($r^2 = 0.817$; *data not shown*)
557 indicates that most of the N mineralised when GWL were low and root systems deep likely
558 played a significant role in plant N supply and thus plant development – regardless of the
559 fertilisation-induced N impulse and the fact that the monthly biomass values were not measured
560 but calculated using a simple linear approach. Similarly strong biomass and dynamic C and N
561 stocks effects on cumulative NEE (Table 3) further support this line of thought, as an increased
562 biomass production stimulated by higher N availability is always associated with increased CO₂
563 input into the plant-soil system via gross primary production.

564 In other words: the N supply in the plant-soil system and its effects on C formation and
565 transformation processes likely also play a key role in the C gas exchange of groundwater-
566 influenced soils, by promoting CO₂ input via gross primary production more than CO₂ emission
567 via ecosystem respiration. The observed effects of the dynamic soil C and N stocks on
568 cumulative NEE can thus be plausibly explained. However, the relatively low optimum GWL for
569 minimizing NEE (Fig. 3) likely requires additional explanatory mechanisms. For example, an
570 improved plant water and nutrient supply, e.g. with macro-nutrients like P and K, could increase
571 root and shoot growth and thus CO₂ input, as observed for soils without groundwater influence
572 (Ladha et al. 2011, Poirier et al. 2009, Al-Kaisi et al. 2008, Reay et al. 2008, Kaur et al. 2007).

573 **4.4.3 Future improvements of the dynamic stocks concept**

574 Most of the functional mechanisms discussed above are somewhat speculative and require
575 subsequent validation by means of experiments which consider all mentioned processes of the
576 plant-soil system and their respective regulating factors. Special attention should be paid to the
577 determination of the scope of all relevant processes, as several studies state that the input of N
578 and other nutrients does not always have only positive effects on net CO₂ exchange and the C
579 sink function of arable soils (Thangarajan et al. 2013, Hoffmann et al. 2009, Mulvaney et al.
580 2009, Al-Kaisi et al. 2008, Khan et al. 2007).

581 Moreover, the concept of dynamic soil C and N stocks is only an indicator of real dynamic
582 stocks, because in this study dynamic stocks were modeled exclusively based on GWL dynamics.
583 Further developments might include precipitation-related topsoil water dynamics or soil
584 hydraulic properties (e.g., capillary fringes), which might considerably reduce dynamic soil C
585 and N stocks. The concept of dynamic stocks could also be expanded to other plant nutrients like

586 plant-available P or K. However, these suggested refinements require very detailed high-
587 resolution data on soil and plant properties and processes, including their vertical variability in
588 the soil profile, and were thus beyond the scope of this study.

589

590 **5 Conclusions**

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

596 While climatic controls like PAR, temperature and precipitation mainly have short-term effects
597 on C gas fluxes, the effects of dynamic soil C and N stocks are clearly observable at all temporal
598 scales. It is to be determined by future studies in how far this also applies to i) crops other than
599 maize, ii) other land use forms like grasslands, and iii) other groundwater-influenced sites.
600 Dynamic soil C and N stocks may be major controlling factors of C gas fluxes and the CO₂
601 source or sink function of the entire range of wetlands, potentially of higher and more global
602 relevance than GWL and vegetation, which are the main factors favoured to date (Couwenberg et
603 al. 2011, Byrne et al. 2004). The insight, that the effect of the dynamic soil C and N stocks very
604 likely results from the regulation of C formation and transformation processes by N and –
605 potentially – nutrient and water supply as such, may be of particular importance. This mechanism
606 would be a favourable prerequisite for the development of generalizable process-based models,
607 which would be very useful in providing more precise estimates of the impact of important
608 factors like climate, site conditions and land use on the C gas fluxes of wetlands.

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

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614

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629

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938

939 **Tables**

940

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

941

Table 2. Annual fluxes of CO₂ (R_{eco}, GPP and NEE) and CH₄ by site and year (\pm model error; 95 % confidence interval); and average fluxes (\pm 1 SD) for the entire study period (2007/08-2010/11) and excluding the flooded year 2007/08.

Site	C flux [g C m ⁻² y ⁻¹]	Year				Periodic average	
		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 CH₄ 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	<i>p</i>	Wald χ^2	<i>p</i>	Wald χ^2	<i>p</i>	Wald χ^2	<i>p</i>	Wald χ^2	<i>p</i>	
Intercept	1.312	0.252	7.626	0.006*	14.311	$\leq 0.001^*$	96.005	$\leq 0.001^*$	29.743	$\leq 0.001^*$	
Site	72.812	$\leq 0.001^*$	25.571	$\leq 0.001^*$	26.040	$\leq 0.001^*$	90.685	$\leq 0.001^*$	65.869	$\leq 0.001^*$	
Climate	Air temperature	11.218	0.001*	33.135	$\leq 0.001^*$	18.706	$\leq 0.001^*$	30.960	$\leq 0.001^*$	17.566	$\leq 0.001^*$
	Soil temperature	1.666	0.197	14.456	$\leq 0.001^*$	5.927	0.015*	36.618	$\leq 0.001^*$	18.096	$\leq 0.001^*$
	Precipitation	19.008	$\leq 0.001^*$	9.093	0.003*	4.827	0.028*	11.562	0.001*	17.588	$\leq 0.001^*$
	Sunshine hours	10.201	0.001*	21.158	$\leq 0.001^*$	9.646	0.002*	†	†	†	
	Year	†		6.004	$\leq 0.001^*$	8.210	0.004*	7.629	0.006*	4.650	0.031*
	Year * Air temp.	†		50.403	$\leq 0.001^*$	37.758	$\leq 0.001^*$	†	†	9.919	0.002*
	Year * Sunshine hours	†		37.816	$\leq 0.001^*$	24.348	$\leq 0.001^*$	†	†	†	
	Soil temp. * Air temp.	12.791	$\leq 0.001^*$	†		†		29.049	$\leq 0.001^*$	12.913	$\leq 0.001^*$
	Soil temp. * Sunshine h.	11.667	0.001*	20.182	$\leq 0.001^*$	11.059	0.001*	29.049	$\leq 0.001^*$	†	
	Plants	Biomass	†		17.810	$\leq 0.001^*$	23.071	$\leq 0.001^*$	49.537	$\leq 0.001^*$	7.361
Biomass * Site		†		72.633	$\leq 0.001^*$	70.273	$\leq 0.001^*$	80.039	$\leq 0.001^*$	33.074	$\leq 0.001^*$
Biomass * Sunshine h.		†		16.733	$\leq 0.001^*$	23.268	$\leq 0.001^*$	†	†	†	
GWL	GWL	3.173	0.075	273.627	$\leq 0.001^*$	13.516	$\leq 0.001^*$	2.667	0.102	38.940	$\leq 0.001^*$
	GWL * Site	27.256	$\leq 0.001^*$	†		17.779	$\leq 0.001^*$	†	†	61.005	$\leq 0.001^*$
	GWL * Precipitation	†		†		†		6.653	0.010*	23.737	$\leq 0.001^*$
Soil	SOC _{dyn}	5.843	0.016*	15.668	$\leq 0.001^*$	8.330	0.004*	32.101	$\leq 0.001^*$	18.340	$\leq 0.001^*$
	N _{dyn}	8.683	0.003*	26.541	$\leq 0.001^*$	8.479	0.004*	23.224	$\leq 0.001^*$	†	
	SOC _{dyn} : N _{dyn}	0.869	0.351	†		13.120	$\leq 0.001^*$	106.424	$\leq 0.001^*$	4.146	0.042*
	SOC _{dyn} * Site	24.005	$\leq 0.001^*$	93.546	$\leq 0.001^*$	25.348	$\leq 0.001^*$	†	†	13.538	0.001*
	N _{dyn} * Site	†		93.868	$\leq 0.001^*$	25.267	$\leq 0.001^*$	8.349	0.004*	†	
	SOC _{dyn} : N _{dyn} * Site	73.365	$\leq 0.001^*$	†		26.078	$\leq 0.001^*$	92.340	$\leq 0.001^*$	66.370	$\leq 0.001^*$
	SOC _{dyn} * GWL	17.551	$\leq 0.001^*$	†		†		†	†	†	
	N _{dyn} * GWL	22.532	$\leq 0.001^*$	†		9.169	0.002*	64.724	$\leq 0.001^*$	†	

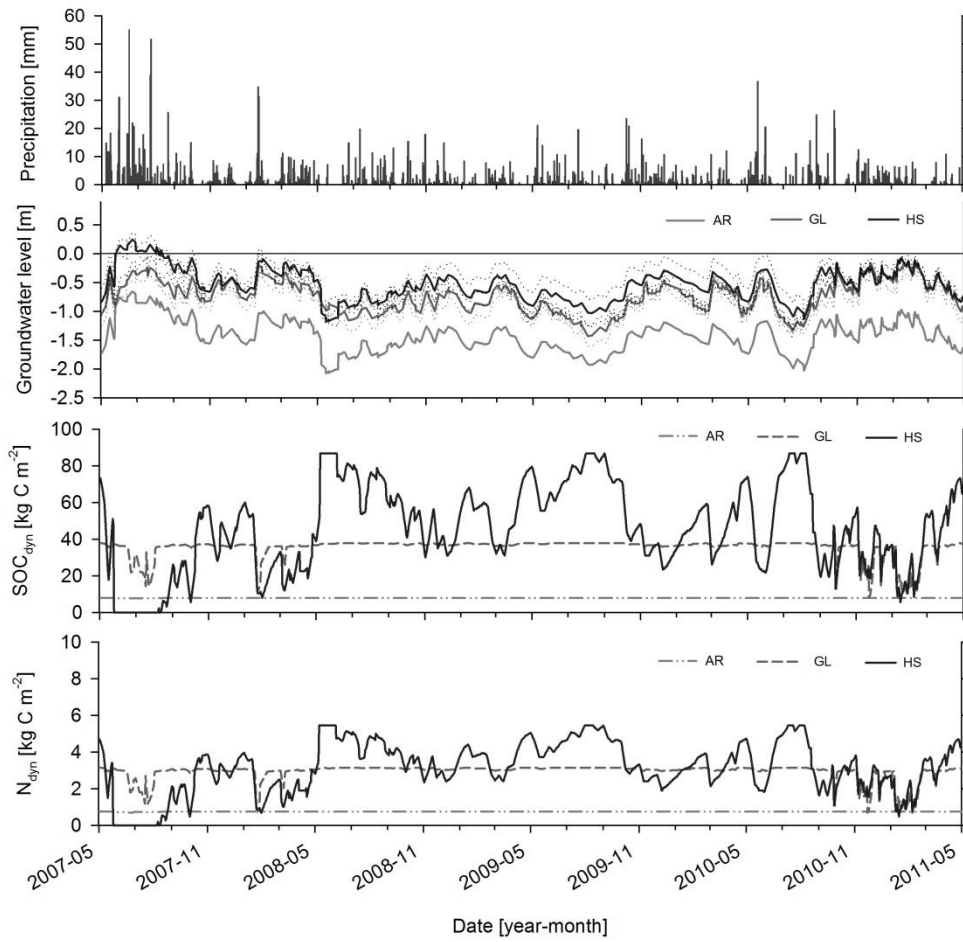
* Asterisks denote significant factors ($\alpha = 0.05$).

† Redundant parameter/parameter interaction.

Table 4. Summary statistics of multiple nonlinear regression analysis of the form $NEE = \text{poly}(\text{GWL}) + \text{lin } y^{(1; 2; 3 \text{ or } 4)}$ describing the influence of GWL and one environmental parameter, either 1) SOC_{dyn} , 2) N_{dyn} , 3) $\text{SOC}_{\text{dyn}} : \text{N}_{\text{dyn}}$ 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}	³ $\text{SOC}_{\text{dyn}} : \text{N}_{\text{dyn}}$	⁴ Biomass
MAE [$\text{g m}^{-2} \text{y}^{-1}$]	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

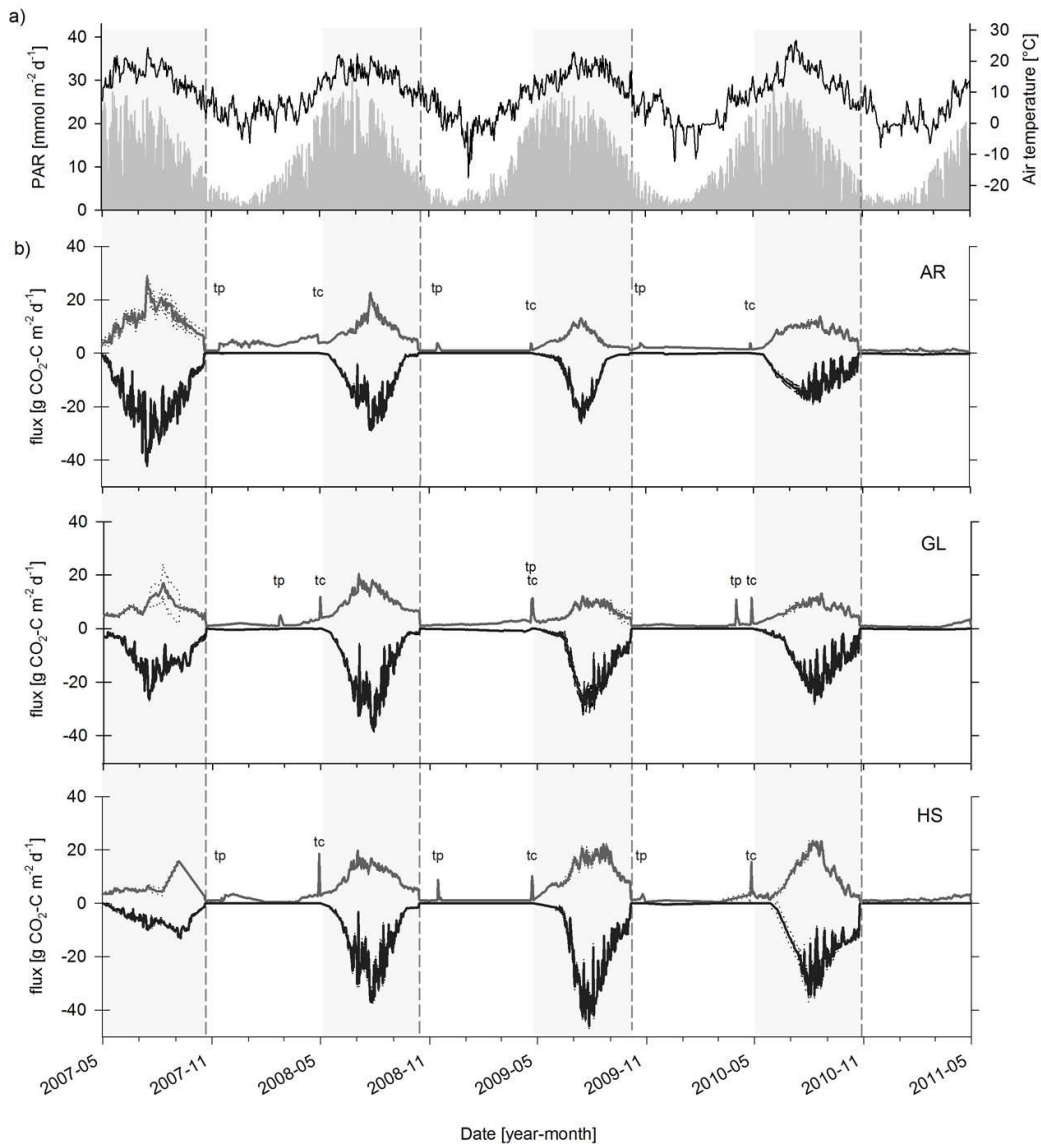


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947 **Figure 1.** Seasonal dynamics of (from top to bottom) daily precipitation, average daily GWL
 948 including 95% confidence intervals (dotted lines), and daily dynamic SOC_{dyn} and N_{dyn} stocks
 949 by site (for 0–1 m depth).

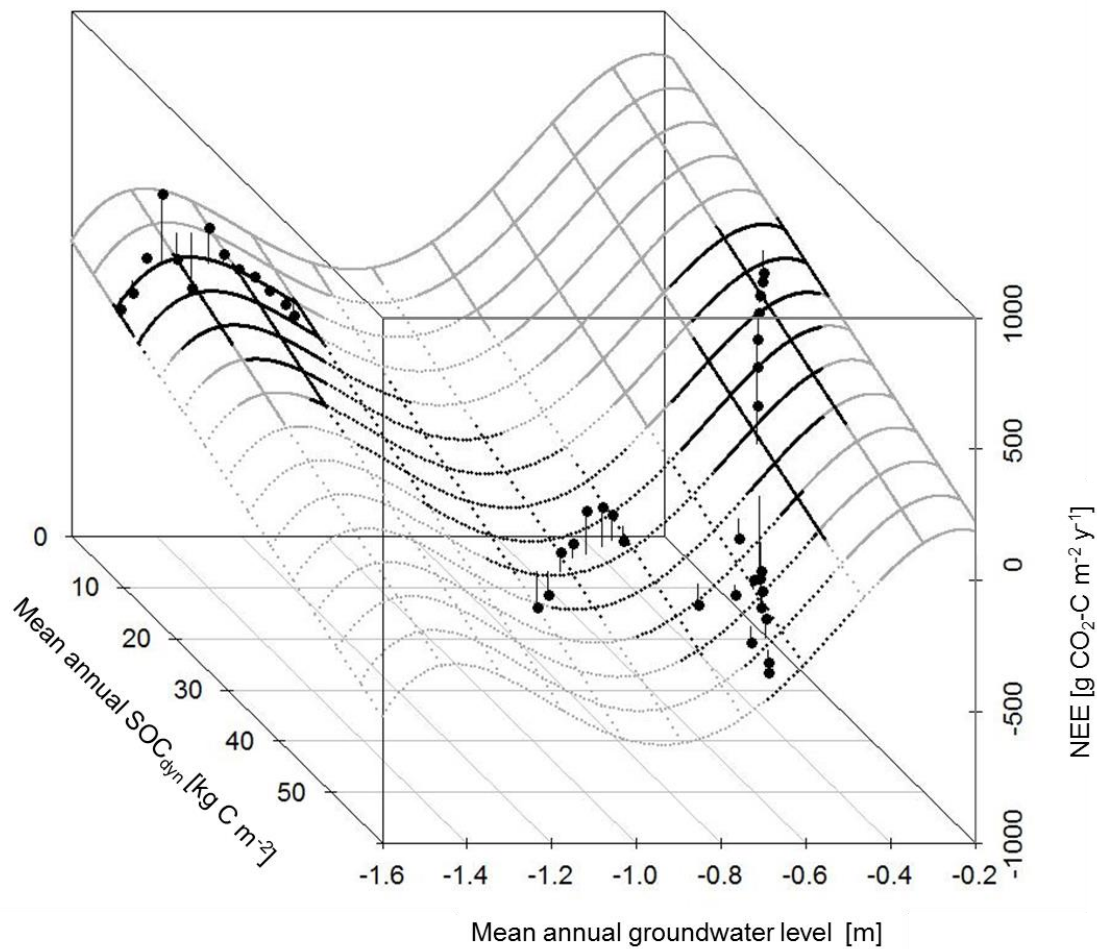
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952 **Figure 2.** Dynamics of daily a) cumulated PAR (grey vertical bars) and average air
 953 temperature at 20 cm height (black line); and b) modeled CO₂-C fluxes (grey line: R_{eco}; black
 954 line: GPP) including 95% confidence intervals (dotted lines) by site. Shaded areas indicate the
 955 period between maize sowing and harvest (dashed vertical line); tp – ploughing, tc –
 956 cultivation (sowing, fertilization).

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958

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