

CO₂ exchange of a temperate fen during the conversion from moderately rewetting to flooding

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Received 8 December 2012; revised 4 May 2013; accepted 11 May 2013; published 20 June 2013.

[1] Year-round flooding provides a common land management practice to reestablish the natural carbon dioxide (CO₂) sink function of drained peatlands. Here we present eddy covariance measurements of net CO₂ exchange from a temperate fen during three consecutive growing seasons (May–October) that span a period of conversion from moderately rewetting to flooding. When we started our measurements in 2009, the hydrological conditions were representative for the preceding 20 years with a mean growing season water level (MWGL) of 0 cm but considerably lower water levels in summer. Flooding began in 2010 with an MWGL of 36 cm above the surface. The fen was a net CO₂ sink throughout all growing seasons (2009: -333.3 ± 12.3 , 2010: -294.1 ± 8.4 , 2011: -352.4 ± 5.1 g C m⁻²), but magnitudes of canopy photosynthesis (CP) and ecosystem respiration (Reco) differed distinctively. Rates of CP and Reco were high before flooding, dropped by 46% and 61%, respectively, in 2010, but increased again during the beginning of growing season 2011 until the water level started to rise further due to strong rainfalls during June and July. We assume that flooding decreases not only the CO₂ release due to inhibited Reco under anaerobic conditions but also CO₂ sequestration rates are constricted due to decreased CP. We conclude that rewetting might act as a disturbance for a plant community that has adapted to drier conditions after decades of drainage. However, if the recent species are still abundant, a rise in CP and autotrophic Reco can be expected after plants have developed plastic response strategies to wetter conditions.

Citation: Koebsch, F., S. Glatzel, J. Hofmann, I. Forbrich, and G. Jurasinski (2013), CO₂ exchange of a temperate fen during the conversion from moderately rewetting to flooding, *J. Geophys. Res. Biogeosci.*, 118, 940–950, doi:10.1002/jgrg.20069.

1. Introduction

[2] Although peatlands cover only 3% of the terrestrial surface [Frolking *et al.*, 2011, and references therein], they store about 20%–25% of the global organic soil carbon (C) [Gorham, 1995]. The function of peatlands to act as a sink or a source for C is mainly controlled by their hydrology [Sirin and Laine, 2008; Zaufit *et al.*, 2010]. Under wet conditions, the carbon dioxide (CO₂) release by ecosystem respiration (Reco) is lower than the CO₂ sequestration by canopy photosynthesis (CP), thus resulting in a net storage of C [Joosten and Clarke, 2002; Joosten, 2010]. Peatlands have shown to be surprisingly resilient to some level of disturbance but can rapidly shift to new states when disturbance exceeds a certain threshold [Dise, 2009]. Water table drawdown for peat extraction, forestry, or agriculture affects a variety of ecosystem functions [Turetsky and St. Louis, 2006, and references

therein]. When exposed to air, peat is decomposed rapidly; Reco exceeds CP, and the peat switches from being a net CO₂ sink to being a net CO₂ source [Joosten, 2010]. In densely populated areas such as Germany or the Netherlands, 85% of the total peatland area is drained for agricultural use [Silvius *et al.*, 2008], acting as hot spots for biological greenhouse gas emissions [Drösler *et al.*, 2008]. To stop this continuous C loss and as a first step to reestablish near-natural conditions of C accumulation, extensive rewetting projects are currently being carried out in drained peatlands across Europe and North America [Höper *et al.*, 2008; Erwin, 2009].

[3] The practical implementation of a projected water level throughout the year is complicated since the water retention capacity of degraded peat is low [Schwaerzel *et al.*, 2002]. As a result, rewetted sites often suffer peat loss when water levels decrease considerably below the surface during summer months [Aurela *et al.*, 2007; Saarnio *et al.*, 2007]. For peatland sites with sufficient water supply, inundation throughout the year is assumed to be a robust management practice to prevent continuing degradation of the remaining peat during periods of drought and to initiate the accumulation of new organic matter [Asada *et al.*, 2009; Euliss *et al.*, 2006]. However, as Dise [2009] pointed out, peatlands affected by disturbance can shift to a new state of organization, i.e., after decades of drainage, the biocenosis might have adapted to drier conditions. A sudden and distinct rise in water level might then cause a perturbation to this new level of

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organization [Coops *et al.*, 2003]. Primary effects of flooding that occur on the cell scale of the plants include oxygen deprivation up to anoxia and propagate to secondary effects on plant scale, such as stomatal closure, or reduced metabolic activity [Kozłowski, 1984; Taiz and Zeiger, 2010] with apparent consequences for photosynthesis as well as for autotrophic respiration.

[4] Studies addressing the state conversion of peatlands from drainage to rewetting, including its implications on ecosystem functionings, are sparse. Most of the available research is concerned with the recreation of former peat extraction sites [e.g., Bortoluzzi *et al.*, 2006; Glatzel *et al.*, 2004; Waddington *et al.*, 2010]. Since the harvest of peat is associated with a total damage of ecosystem functioning, such sites' response to rewetting might not be comparable with that of less altered, i.e., drained peatland sites [Höper *et al.*, 2008]. Komulainen *et al.* [1999] found two drained peatland sites (a minerotrophic fen and an ombrotrophic bog) to turn from CO₂ neutrality to a net CO₂ sink within 2 years after rewetting and stressed the importance of vital vegetation as a precondition for organic matter accumulation. Höper *et al.* [2008] reported an initially low net CO₂ uptake from a flooded fen site in northeastern Germany (water level 20–100 cm above surface), which was associated with the submergence of the plant community. The integrated investigation of peatland response to rewetting beyond the apparent effect of oxygen deprivation on organic matter decomposition is crucial to promote our understanding of ecosystem processes taking place during the conversion from drainage to rewetting. A comprehensive understanding of this conversion is required to advance ecosystem management toward a fast succession and the persistent reestablishment of the CO₂ sink function of peatlands.

[5] Rewetting of peatlands is known to stimulate emissions of methane (CH₄) [Hahn-Schöfl *et al.*, 2011; Wilson *et al.*, 2008], a potent greenhouse gas with a 25 times higher net radiative forcing on climate than that of CO₂ on a 100 year horizon [Forster *et al.*, 2007]. However, on a long-term perspective, pristine mires exhibit a net radiative cooling effect on the atmosphere, because the carbon fixation in peat over millennia by far exceeds the release of comparably short-lived CH₄ molecules into the atmosphere [Frolking *et al.*, 2011]. Therefore, the restoration of peatlands' effective CO₂ sink is essential to reestablish their natural net cooling effect.

[6] We monitored CO₂ exchange in a degraded coastal fen during the conversion from moderate rewetting to permanent, shallow inundation with the eddy covariance (EC) approach. The obtained data encompass the growing seasons of three consecutive years, with 2009 being the reference year before flooding (hence, years 2010–2011 are post flooding). In 2009, the fen had been moderately rewetted for 19 years (mean growing season water level (MGWL): 0 cm) and exhibited an established macrophytic community. At that time, the site was mowed annually for nature conservation purposes. The growing season spans the period from May to October, which coincides with the period from the emergence of young shoots to the senescence of plants.

[7] The eddy covariance approach provides a quasi-continuous net flux of CO₂ at the ecosystem scale [Baldocchi, 2003]. Using partitioning approaches, the net flux can be separated into its components Reco and CP, both presenting potentially flooding-sensitive ecosystem processes.

Considering the role of plants for CO₂ storage, we used the enhanced vegetation index (EVI) from Moderate Resolution Imaging Spectroradiometer (MODIS) remote sensing data [Earth Observing System (EOS), 2013] as a proxy for vegetation response at our site. EVI is derived using the reflectance properties of plant leaf tissue in the red and near-infrared spectra [Carter, 1993; Huete *et al.*, 2002] and is therefore sensitive to spatiotemporal changes in plant canopy [Li *et al.*, 2007; Sakamoto *et al.*, 2007]. It is available in 8 day frequency on a spatial resolution up to 250 m, which corresponds well with the quasi-continuous character and the ecosystem scale focus of the eddy covariance approach. Therefore, EVI has been established as a model parameter to predict net ecosystem exchange (NEE) and CP across a variety of biomes [e.g., Peng *et al.*, 2013; Xiao *et al.*, 2010, 2011]. We expect EVI to provide a reliable proxy for phenological changes within the growing season as well as for differences in plant vitality across different years and, hence, to be a good predictor for intra-annual and interannual variations in CP.

[8] We hypothesize that the peatland switches from a net CO₂ source to a net CO₂ sink after flooding due to a severe decrease in Reco, primarily caused by the reduction of heterotrophic respiration under anaerobic conditions. Further, we hypothesize that vegetation suffers from inundation, leading to decreased plant vitality and a decline in CP, resulting in a low net CO₂ sink potential in the initial phase of rewetting.

2. Site Description

[9] Measurements were conducted at the “Rodewiese,” an anthropogenically disturbed fen, which is part of the nature reserve “Heiligensee und Hütelmoor.” The site is located in northeastern Germany (latitude 54°12', longitude 12°10', Figure 1) on a transition zone between Atlantic maritime climate from the west and more continental climate effects from the east [Voigtländer *et al.*, 1996] (Table 1). The fen extends 1.59 km in the north-south direction and 1.38 km in the east-west direction. Since the northern and western parts of the fen adjoin the Baltic Sea, it had been episodically flooded with brackish waters. However, a dune dike was installed in 1963 to cut the fen off from the Sea [Voigtländer *et al.*, 1996]. According to the general attempt to intensify agricultural production in mid-Europe [van Diggelen *et al.*, 2006], the fen had been drained in the 1970s and was used as a meadow, i.e., it was mowed twice a year for hay production. As a result, the mean annual water level dropped down to 1.60 m below the ground surface. Peat decomposed rapidly and was identified as sapric histosol in 2010. In the 1990s, decreasing yields due to proceeding peat degradation promoted the shift to a more ecological focus on peatland use across mid-Europe [van Diggelen *et al.*, 2006]. Correspondingly, the study site was moderately rewetted and mown once per year to keep the vegetation relatively open. Extensive mowing supports the aims of nature conservation to preserve a resting site for migratory birds while allowing the restoration of the typical fen vegetation. The mean growing season water level (MWGL) during this time was close to the surface. However, the water level dropped down to 70 cm below the surface during summer, which raised suspicion about ongoing peat decomposition. Therefore, a ground sill was installed in the outflow of the catchment in winter 2009/2010 to initiate year-round shallow flooding of the site.

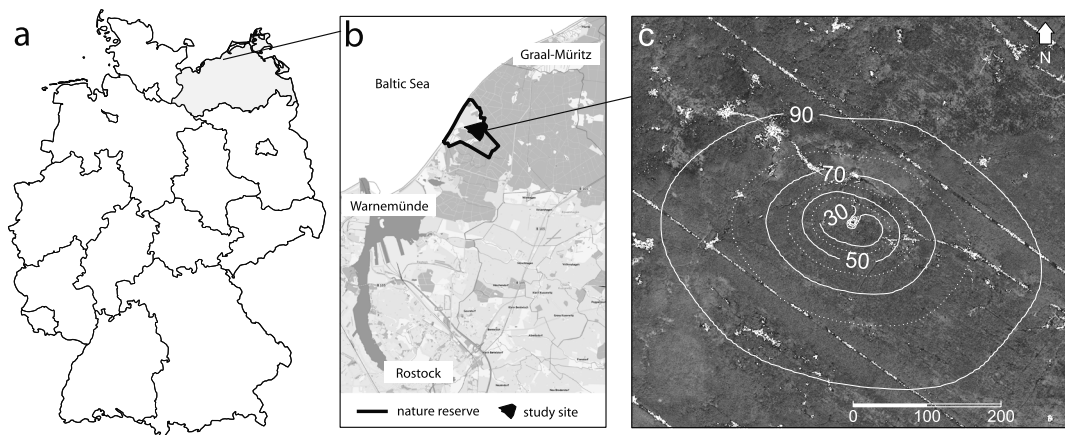


Figure 1. Location of the study site. (a) The Rodewiese is situated in northeastern Germany. (b) Due to its vicinity to the Baltic Sea, the fen had been periodically flooded in the past. Nowadays, the nature reserve is cut off from the Sea by a dike. (c) The source area consists of a patchy pattern of macrophyte species representative for the fen. Lines indicate the isopleths of the cumulative growing season footprint climatology, i.e., the area within the 0.9 contour contributes 90% to the growing season flux.

[10] Currently, the vegetation at the fen is dominated by a patchy pattern of dense Common reed stands (*Phragmites australis* (Cav.) Trin. ex Steud., leaf area index at peak growing season in August (LAI_{peak}): 3.9) that colonized around the drainage ditches and bulks of Lesser Pond sedge (*Carex acutiformis* Ehrh., LAI_{peak} : 6.9), which occur at drier areas. These species are typical for secondary succession in species-poor, rewetted fen sites of this region [Timmermann *et al.*, 2006]. Additionally, mixed stands of Sea and Grey Club-rush (*Bolboschoenus maritimus* (L.) Palla *Schoenoplectus tabernaemontani* (C. C. Gmel.) Palla, LAI_{peak} : 2.2) present relics of former brackish conditions.

3. Methods

3.1. EC and Supporting Meteorological Measurements

[11] We mounted our EC instrumentation at a height of 3.15 m above the ground surface in an accessible area which is representative for vegetation and hydrology of the fen. EC instrumentation comprised (1) an open-path infrared gas analyzer (IRGA, LI-7500, LI-COR, Lincoln, NE, USA) to measure fast fluctuations of CO₂ molar density and (2) a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA) to measure wind velocities and sonic temperature. Supporting meteorological measurements were conducted at the tower or in close proximity. These included (1) global radiation (R_g), measured with a pyranometer (CMP 3; Kipp & Zonen, Delft, the Netherlands);

(2) relative humidity, and (3) air temperature, which were both measured with an aspirated, shielded thermistor and capacitance sensor (HMP45C, Vaisala, Vantaa, Finland). All signals were recorded by a CR3000 Micrologger (Campbell Scientific, Logan, Utah) and a flash memory storage card with a scan rate of 10 Hz. The supporting meteorological variables were then averaged over 30 min to correspond to the flux averaging interval (see below).

[12] Data gaps of 30–60 min in the 30 min time series of the supporting meteorological variables were filled by linear interpolation. Longer periods with missing data were filled using data from a nearby meteorological station of the German Weather Service.

3.2. Flux Calculations and Footprint Climatology

[13] We used the EddyPro 3.0 software (LI-COR, Lincoln, Nebraska) to calculate half-hourly mean fluxes from the high-frequency data. The effect of humidity on sonic temperature was corrected by the method of van Dijk *et al.* [2004]. Spikes in the high-frequency data were removed by the method of Vickers and Mahrt [1997]. Canopy height in our site is complex, composed of patches of high reed stands, medium rushes, and open water surface. Hence, in order to minimize flow distortion effects and to align the sonic coordinate system with the mean streamline [Finnigan *et al.*, 2003], we used sector-wise [Siebicke *et al.*, 2011] planar-fit rotation following Wilczak *et al.* [2001]. Time lags of measurements resulting from the spatial distance of IRGA and anemometer

Table 1. Climate Characteristics of the Fen Site Rodewiese^a

	Precipitation Sum (mm)						Mean Air Temperature (°C)						Sunshine Duration Sum (h)					
	30 Year Statistics			Investigation Period			30 Year Statistics			Investigation Period			30 Year Statistics			Investigation Period		
	Min	Mean	Max	2009	2010	2011	Min	Mean	Max	2009	2010	2011	Min	Mean	Max	2009	2010	2011
Annual basis	428	645	955	540	706	955*	7.4	9.2	10.4	9.6	8.1	9.8	1457	1740	2029	1897	1673	1802
Growing season	188	358	770	328	392	770*	13.0	14.7	16.6	14.9	14.6	15.2	971	1224	1464	1320	1192	1164

^aClimate variables are given as 30 year statistics (1982–2011) and specified for our investigation period. Data were provided by the German Weather Service. Growing season encompasses the months May–October of 1 year. Maxima of the 30 year statistics that occurred within our investigation period are marked with an asterisk.

were compensated by cross correlation. Spectral attenuations in the low- and high-frequency ranges were compensated by the method of *Moncrieff et al.* [1997]. Air density fluctuations were removed according to the correction of *Webb et al.* [1980].

[14] The planar-fit method requires long averaging intervals with a stable position of the anemometer relative to the surface [*Siebicke et al.*, 2011]. However, above-surface fluctuations of water level and seasonal changes of vegetation height induce changes in the effective measurement height (z_m). Therefore, averaging intervals were arranged in a way to minimize within-changes of z_m and cover periods of 4–8 weeks. The study site was mowed successively over several weeks during July 2009. Because this period was associated with strong temporal and spatial changes in vegetation height, we performed a double coordinate rotation [*Lee et al.*, 2004] for data from July 2009.

[15] In order to define the area within the fen that contributes most to the measured fluxes, we computed a footprint climatology [*Amiro*, 1998]. The shape of the footprint climatologies was similar throughout all the years. As an example, we projected the isopleths from the footprint climatology of 2011 on an aerial photograph that was taken in June of the same year (Figure 1c). The 30 min source weight functions were computed with the analytical footprint model of *Kormann and Meixner* [2001] including an iterative estimation of vegetation height and roughness length as proposed by *Göckede et al.* [2004] for heterogeneous terrain. This footprint model assumes a variety of preconditions, such as stationary conditions, horizontally homogeneous turbulent flow, and homogeneous terrain. However, their relatively easy implementation justifies the application of analytical footprint models as a routine analysis tool for long-term measurements [*Rannik et al.*, 2012]. The footprint analysis and all following computing steps were performed with the free software environment R [*R Core Team*, 2012].

3.3. Quality Assurance, Gap Filling, and Budgeting of Growing Season NEE

[16] Fluxes were quality flagged to rate stationarity and the development of the turbulent flow field [*Foken et al.*, 2004]. Quality criteria (qc) range from 1 (good quality) to 9 (bad quality). Fluxes were rejected if $qc > 5$. The remaining data were cross checked against low turbulence conditions based on thresholds of friction velocity (u^*) assigned individually for each growing season following the method of *Aubinet et al.* [2012]. We observed high negative NEE fluxes associated with large u^* values. Assuming that negative NEE fluxes (meaning CO₂ uptake by the ecosystem) during nighttime conditions are rather physically determined than having any ecological cause, we also applied maximum u^* thresholds. To minimize the effect of perturbed fluxes, filtering criteria for modeling and gap filling were even more strict, rejecting fluxes with $qc > 3$ and statistical flags of their inherent high-frequency data [*Vickers and Mahrt*, 1997]. In the end, the remaining data cover 53%, 83%, and 77% of the growing seasons 2009, 2010, and 2011, respectively. Gaps are due to instrument failure and data rejection and are in accordance with the average coverage for EC time series of 65% [*Falge et al.*, 2001]. Gap filling was performed with an enhanced lookup table approach, taking into account the temporal autocorrelation of NEE fluxes [*Reichstein et al.*,

2005; *Moffat et al.*, 2007]. The filled NEE values were derived from the average of fluxes measured under similar meteorological conditions within a time window centered ± 7 days around the gap. If there were no fluxes associated with similar meteorological conditions within the time window, the constraints were gradually relaxed, i.e., the time window was increased, and the classes of meteorological conditions were determined with broader definitions.

[17] The NEE seasonal budgets for each growing season were derived from the quality-checked and gap-filled data set integrated from 1 May to 31 October of the respective year. Uncertainty of NEE budgets is composed of (1) the measurement uncertainty and (2) the uncertainty associated with gap filling [*Dragoni et al.*, 2007]. Measurement uncertainty was estimated using a modified successive-day approach [*Dragoni et al.*, 2007] adapted to fit the assumption of *Reichstein et al.* [2005], according to which, within a ± 7 day window, the same meteorological conditions cause the same fluxes. Air temperature, global radiation, and water vapor pressure deficit are used as parameters to bin fluxes, the uncertainty of which is then computed from the standard deviation of the binned fluxes. We expect larger flux deviations caused by surface heterogeneity within our source area (Figure 1c) to contribute to uncertainty [*Richardson et al.*, 2012]. Gap-filling uncertainty was estimated congruently for each missing value. However, if the initial gap-filling constraints do not provide any results, averaging intervals are extended [*Reichstein et al.*, 2005], which increases the risk of nonstationarity [*Hollinger and Richardson*, 2005].

3.4. NEE Partitioning

[18] The half-hourly averaged net CO₂ fluxes are the sum of two opposed fluxes that originate from two major ecosystem processes: ecosystem respiration (Reco), representing the release of CO₂ into the atmosphere, and canopy photosynthesis (CP), representing the uptake of atmospheric CO₂ in the plant biomass, (equation (1)). According to the meteorological convention, a negative NEE flux indicates net CO₂ uptake into the ecosystem.

$$NEE = Reco - CP \quad (1)$$

According to the meteorological convention, a negative NEE flux indicates a net CO₂ uptake into the ecosystem.

[19] At first, we tried a functional modeling approach following *Lasslop et al.* [2010] that is based on the partitioning of the daytime NEE flux into a hyperbolic light-response curve, representing CP, and an exponential temperature response term, representing Reco. With this approach, we could not predict fluxes properly during growing season 2010. Therefore, we used a more robust NEE partitioning approach for all 3 years. This approach assumes Reco to be constant throughout a ± 2 day moving window and CP to be constant during daytime conditions ($R_g > 20 \text{ W m}^{-2}$) of the same time window. Mean Reco for a certain date was derived by averaging the quality-filtered, measured nighttime NEE fluxes within the ± 2 day moving window. For mean CP, we averaged the quality-filtered, measured daytime NEE fluxes within the same time window and subtracted the averaged Reco value. If data gaps exhibited a skewed distribution throughout daytime conditions, we could not identify a representative mean CP value. Then, the CP flux was

derived by linear interpolation from the CP fluxes of the previous and successive days. Reco fluxes were scaled on a daily basis by multiplying the mean half-hourly flux with 48 (equation (2)). For daily CP, multiplication of the mean half-hourly CP flux was performed with the number of half hours with $R_g > 20 \text{ W m}^{-2}$ ($n_{R_g > 20}$) per day (equation (3)).

$$\text{Reco}_{\text{daily}} = 48 \times \text{nighttimeNEE}_{\text{half-hourly}} \quad (2)$$

$$\text{CP}_{\text{daily}} = n_{R_g > 20} \times (\text{daytimeNEE}_{\text{half-hourly}} - \text{nighttimeNEE}_{\text{half-hourly}}) \quad (3)$$

3.5. Additional Parameters

[20] From 2009 to 2010, we measured water levels within nine wells distributed over the study site in biweekly intervals. Data were interpolated linearly between measurement dates. From 2011, water levels were recorded hourly with two HOBO U20 Water Level Data Loggers (Onset, Bourne, MA, USA) installed in wells at positions representing the conditions at the study site. Water level measurements were spatially extrapolated with a digital elevation model, derived from 64 spots of a 25 m raster within our area of interest using a Leica RTK GPS 2 1200 (Leica Geosystems AG, Heerbrugg, Switzerland). We report spatially averaged water level relative to ground surface, with positive values indicating inundation. To assess a potential impact of water level on CP and Reco, respectively, we sought the line of best fit from a scatterplot, including all growing seasons. In advance, we processed our variables as biweekly averages, which minimizes scatter and corresponds to the biweekly measurement frequency of water level in 2009 and 2010. Hourly water levels from growing season 2011 were selected accordingly to fit these measurement intervals, and Reco and CP values were averaged over the corresponding 14 day periods.

[21] MODIS EVI data for use as a proxy for plant phenology and vitality were obtained from the Land Processes Distributed Active Archive Center (<https://lpdaac.usgs.gov/>), which is part of NASA's Earth Observing System Data and Information System [EOS, 2013]. Among a 16 day interval set of atmospherically corrected, surface-gridded reflectance data, the MODIS maximum value compositing approach provides the reflectance value with the view angle closest to nadir [Huete *et al.*, 2011]. According to a rule of thumb, the extent of the footprint approximates 100 times the measurement height [Businger, 1986], which corresponds to an area within 315 m distance to our tower. Thus, from a $1200 \times 1200 \text{ km}$ tile unit, we selected four $250 \times 250 \text{ m}$ pixels which were congruent to this area. EVI values of these pixels were filtered according to pixel reliability and pixel-wise quality assessment. We chose EVI data from the Aqua satellite since these provided a better data coverage after quality filtering. The relationship between EVI and CP was assessed using linear regression for each growing season separately. To do so, daily CP values were averaged over the corresponding 16 day intervals.

4. Results

4.1. Meteorological, Hydrological, and Remote Sensing Variables

[22] The years 2009–2011 were similar to the 30 year climate statistics (Table 1 and Figure 2) in terms of air

temperature and sunshine duration. In contrast, growing season 2011 was extraordinarily wet with precipitation totalling 770 mm, 550 mm of which fell during July and August, which is nearly the long-term annual average at the study site. These rainfalls exceeded all records within the last 30 years on a yearly as well as on a growing season reference period.

[23] In 2009, hydrological conditions were representative for the Rodewiese during the last decade with an MGWL of 6 cm (Table 2). The driest conditions occurred in June with a spatially averaged water level of 11 cm below surface. However, terrain elevation in the study site has high spatial variability due to former use of heavy machinery and the deposition of excavated material from the ditches. Hence, there were spots with water levels down to 60 cm below surface. The MGWL of 2010 was considerably higher (Table 2), causing inundation for most parts of the study site throughout the year, which resulted from the installation of the ground sill at the outflow of the catchment and not from the relatively slight change in precipitation rates (Table 1). Following the strong precipitation events in summer 2011, the fen experienced a further rise in water level. At this time, the fen was completely inundated with water levels up to 120 cm at some spots.

[24] EVI showed a clear seasonal pattern with peaks between July and late August throughout all growing seasons (Figures 2g–2j). EVI was highest in 2009, which applies for the start of the growing season in May (0.39) and for the peak value in mid-August (0.67), and decreased considerably in the first year of flooding. At the start of growing season 2010, the EVI was lowest among all EVI data (0.21) and increased slowly up to a maximum of 0.54 at the end of August. In contrast, EVI started with higher values in May 2011 (0.31) but stopped increasing after the further rise in water level in July (0.46).

4.2. Seasonal Development of CO₂ Fluxes

[25] Daily NEE and its components Reco and CP showed a similar seasonal development during all growing seasons (Figures 2j–2l). Fluxes increased during spring, peaked in summer, and decreased during autumn. Reco and CP were highest in 2009, and Reco peaked in July and August, coincident with peaks in CP. During spring, the increase of CP exceeded the increase of Reco, resulting in a consistently negative NEE until August. Afterward, there were periods with $\text{Reco} > \text{CP}$, resulting in more frequent occurrences of positive NEE values, despite high CP magnitudes. The seasonal pattern of NEE and its components was severely dampened throughout growing season 2010. Peaks of Reco and GEP both occurred in mid-July. For most days, CP exceeded Reco, resulting in a negligible number of days with positive NEE. Growing season 2011 was split into a period with moderately high rates of CP and Reco associated with negative NEE fluxes until mid-July and a period governed by reduction of CP and Reco afterward (Figure 2l). Up to September, there were single days with low positive NEE fluxes.

4.3. Growing Season NEE, Reco, and CP Budgets

[26] The Rodewiese was a net CO₂ sink throughout all three growing seasons (Table 2). Uncertainties of the annual budgets were low (<4%) and mostly dominated by gap-filling uncertainty (2009: 2.4%, 2010: 1.6%, and 2011: 0.1%). Higher gap-filling uncertainties in 2009 are due to lower data

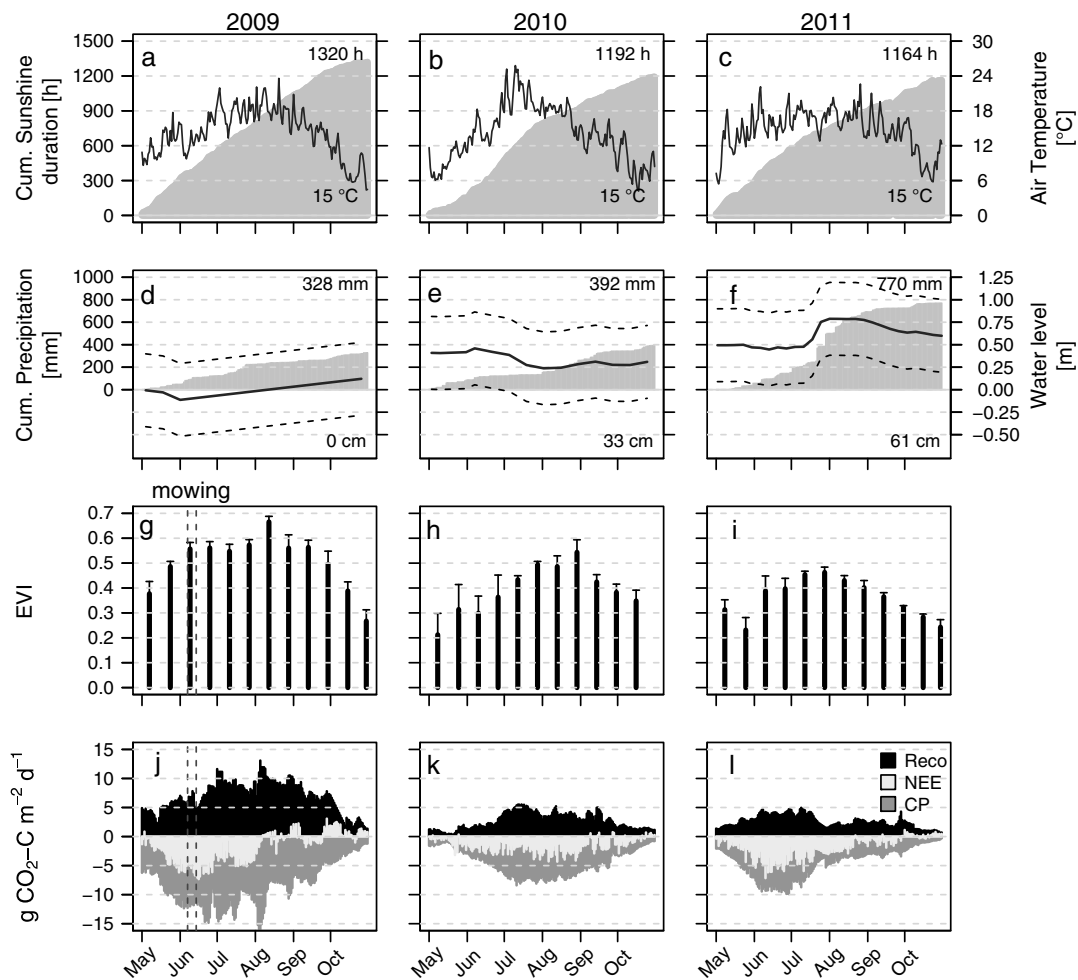


Figure 2. Seasonal development of environmental parameters and daily CO₂ fluxes. (a–f) Cumulative meteorological variables are presented as grey bars. In Figures 2d–2f, water level is depicted by a solid line (spatially averaged water level) and two dashed lines (corresponding minimum and maximum of water level due to spatially variable terrain elevation). Water level was measured in biweekly intervals in 2009 and 2010 and logged in 1 h frequency in 2011. Missing values were filled by linear interpolation. (g–i) Error bars of the enhanced vegetation indices (EVIs) indicate the standard deviation of $n=4$ EVI pixel values. Values in the top right from Figures 2a–2f represent the total growing season sums of sunshine duration or precipitation, respectively. Values in the bottom right represent growing season averages for air temperature or water level. (j–l) CO₂ fluxes are represented on a daily basis. Daily net ecosystem exchange (NEE) was derived from the gap-filled data set. Ecosystem respiration (Reco) and canopy photosynthesis (CP) were modeled with the robust partitioning approach, assuming constant Reco and CP fluxes during a ± 2 day moving window.

Table 2. Mean Water Level, Enhanced Vegetation Index, and CO₂ Fluxes of the Fen Site Rodewiese During Growing Seasons 2009–2011^a

	MGWL (cm)			EVI			NEE (g CO ₂ -C m ⁻²)				CP (g CO ₂ -C m ⁻²)				Reco (g CO ₂ -C m ⁻²)			
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Sum	Min	Mean	Max	Sum	Min	Mean	Max	Sum
2009	-11	6	24	0.27	0.50	0.67	-7.3	-1.8	3.1	-333.3 (3.6%)	1.2	8.5	16.8	1572.1	1.3	6.9	16.8	1273.4
2010	24	37	51	0.21	0.39	0.54	-4.3	-1.6	0.8	-294.1 (2.9%)	0.7	4.6	8.4	841.9	0.3	2.7	5.5	500.5
2011	47	57	79	0.23	0.35	0.46	-7.2	-1.9	1.1	-352.4 (1.4%)	0.3	4.6	9.9	827.9	0.6	2.6	5.0	477.1

^aMean growing season water level (MWGL), presented as spatial average, negative MWGLs, indicates water tables below the surface. The enhanced vegetation index (EVI) is derived from MODIS remote sensing data. CO₂ flux minima, means, and maxima are presented as daily fluxes, while sums refer to the growing season (May–October). Fluxes of net ecosystem exchange (NEE) indicate measured values, while canopy photosynthesis (CP) and ecosystem respiration (Reco) are derived from NEE partitioning approaches. Following the meteorological sign convention, a negative NEE indicates a net CO₂ uptake into the ecosystem. Percentages in parentheses provide the uncertainty associated with the NEE budget, composited by measurement and gap-filling uncertainty.

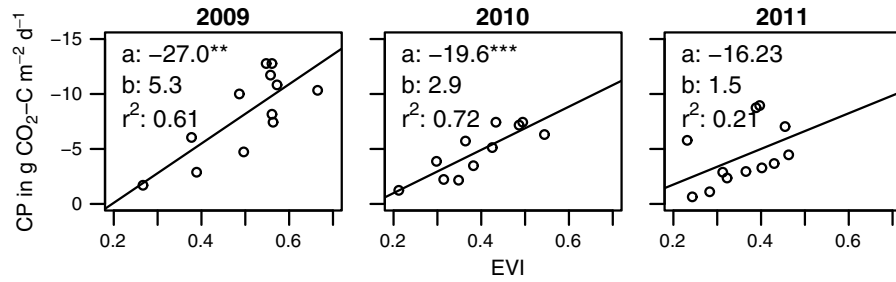


Figure 3. Linear regressions between enhanced vegetation index (EVI) and canopy photosynthesis (CP) for each growing season. EVI values cover 16 day intervals. CP data are derived from modeled daily CP values averaged over the corresponding time period. Coefficients a and b present slope and intercept of the regression line. Asterisks indicate levels of significance ($***p < 0.001$, $**p < 0.01$).

coverage. Budgets of Reco and CP were high during growing season 2009, but both decreased markedly in 2010 and remained low in growing season 2011, respectively.

4.4. Controls on CP and Reco

[27] There was a strong, significant ($r^2 = 0.61$, $p < 0.05$) relation between CP and EVI during growing season 2009 (Figure 3). The relation was even stronger in 2010 ($r^2 = 0.72$, $p < 0.001$) but could only be identified as a vague trend in 2011 ($r^2 = 0.21$, $p = 0.13$). When aggregated over all three growing seasons, Reco and absolute values of CP were decreasing exponentially with increasing water levels (Figure 4).

5. Discussion

5.1. CO₂ Fluxes Associated With 20 Years of Stable, Moderate Rewetting

[28] From May to June 2009, the Rodewiese was highly productive. CP and Reco fluxes developed parallel throughout most parts of the growing season and followed a seasonal pattern, interrupted from a mowing event in June. Both plant phenology and mowing impact were well represented by the EVI, which, therefore, was a good predictor for CP (Figure 3). High rates of CO₂ sequestration in spring and summer compensated for periods of net CO₂ release during senescence (Figure 2). Therefore, the site was a net CO₂ sink throughout growing season 2009. Growing season budgets of the NEE components were close to those of other rewetted, productive wetlands. Rocha and Goulden [2008] reported Reco sums of 1090–1639 g CO₂-C m⁻² a⁻¹ and CP sums of 1313–1632 g CO₂-C m⁻² a⁻¹ from a restored cattail (*Typha*) marsh. A grazed, restored peatland exhibited rates of 1493–1765 g CO₂-C m⁻² a⁻¹ for Reco and 1182–1557 g CO₂-C m⁻² a⁻¹ for CP [Hatala et al., 2012]. Note that these budgets are on a yearly basis, while our budgets refer to the growing season only (183 days from 1 May to 31 October).

[29] Mowing in June interrupted the springtime increase of Reco and CP. During the following 2 weeks, the Rodewiese remained a net CO₂ sink with constant CO₂ sequestration rates. Contrastingly, many studies report that the loss of leaf area associated with mowing causes a decrease of CP and thus turns the respective ecosystems to net CO₂ sources [e.g., Veenendal et al., 2007; Schmitt et al., 2010]. In our case, EVI did not decrease, but levelled off. Since the cut biomass was left on site, there was no sudden net loss of plant tissue contributing to the infrared reflectance band. This suggests that

the cut biomass had contributed to CP for some more days. Moreover, the decomposition of dead plant material left on site likely provides a substantial source for Reco [Waddington et al., 2010]. CP and Reco started to increase a few days after mowing, indicating the regrowth of vegetation [Veenendal et al., 2007]. If mowing is conducted early in the growing season, it can extend the growing season into periods with optimal growth conditions (radiation, temperature) and consequently increase CO₂ sequestration [Sonnentag et al., 2011].

[30] Management practices at the Rodewiese in 2009 were representative for the land use and hydrological conditions of the last 20 years. Therefore, our first measurement year provides the reference state for a moderately rewetted fen with an established macrophyte community that is mowed once a year with water levels fluctuating around the surface, but being distinctively lower (down to 60 cm below surface) during the summer months. Extensive mowing is a common land management strategy for moderately rewetted fens in Europe [Mälson et al., 2010]. Therefore, these values are representative for other fens in this region.

5.2. Effects of Inundation

[31] In 2010, the water level was raised to reinitiate peat growth at the Rodewiese. This had little effect on the total

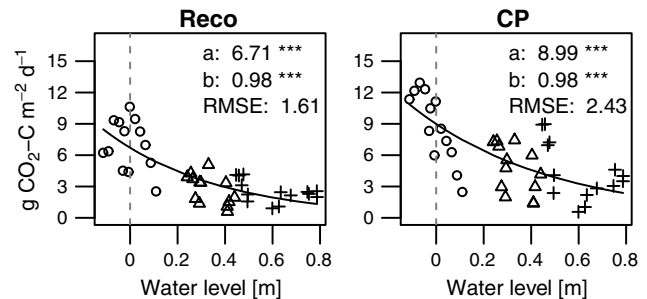


Figure 4. Exponential relation between water level and Reco and CP, respectively, aggregated for growing seasons 2009–2011. Water level was processed as biweekly values. Reco and CP data are derived from modeled, daily Reco and CP values averaged over the correspondent time period. Plotting characters represent different growing seasons (circles: 2009, triangles: 2010, crosses: 2011). Coefficients a and b present parameters of the exponential model ($f(x) = a \cdot b^x$). Root mean square error (RMSE) is used as measure for goodness of fit. Asterisks indicate levels of significance ($***p < 0.001$).

growing season net CO₂ storage that was only slightly lower compared to the 2009 budget (Table 2). However, compared to 2009, CP and Reco decreased by 46% and 61%, respectively. A drop of Reco due to more anaerobic conditions has been shown by many studies [Komulainen *et al.*, 1999; Waddington *et al.*, 2010; Hatala *et al.*, 2012]. However, in contrast to our results, these studies either report no change [Hatala *et al.*, 2012] or even an increase in CP [Komulainen *et al.*, 1999; Waddington *et al.*, 2010]. This discrepancy might be explainable by the high range of water levels in our site which exceeded those reported in these studies by far. Flooding can cause considerable stress to plants, and we assume that this was one reason for the decreased CP and Reco rates. Decreased plant vitality was reflected by lower EVI throughout growing season 2010 when compared to prior-flooding EVI. On the one hand, most of the dominant species at our study site have been shown to be resistant to flooding [e.g., Clevering and Hundscheid, 1998; Vretare *et al.*, 2001]. On the other hand, all of our dominant species are perennials that might suffer from flooding if they had spent the beginning of their life cycle under drier conditions [Zákravský and Hroudová, 1994; Clevering *et al.*, 1995; Coops *et al.*, 2003]. The variability of a phenotype in response to environmental factors is known as phenotypic plasticity [Sultan, 2000]. To nonadapted individuals, submergence triggers a variety of stress factors like oxygen deprivation up to anoxia, which is reflected in stomata closure and decreased metabolic activity, and might thus lead to decreased rates of CP and Reco.

[32] Further, low diffusion rates of CO₂ and O₂ in water and submergence of plant tissue might have acted as physical constraints for CO₂ exchange [Clevering *et al.*, 1995]. Plant tissue that has not yet grown out of the water surface might not be included in the EVI [Sakamoto *et al.*, 2007]. The slow increase in EVI during the first half of growing season 2010 suggests evidence for the submergence of plant tissue that “gets visible” and can effectively contribute to metabolism first after it has overgrown the water surface.

[33] Although CP and Reco rates at the beginning of growing season 2011 were still below those of 2009, cumulated fluxes of both Reco and CP doubled in comparison to the first year of inundation. This is consistent with a recent study of Schedlbauer *et al.* [2012], where CP fluxes of a seasonally flooded marsh were half of the CP fluxes from a year-round flooded marsh. Both sites shared the same dominant species, but only the plant community at the year-round flooded marsh had acclimatized to flooding. Again, phenotypic plasticity of the plants seems to cause this pattern. For perennials, it may take several months to 1 year to establish a flooding-resistant phenotype [Keeley, 1979]. The aboveground plant parts of most of the dominant species in our study site die back for winter. The amount of reserve carbohydrates in the rhizomes is then decisive for the maximum water depth that shoots can overgrow at the beginning of the next growing season [Blom, 1999]. Tubers of the Grey Club-rush (synonymous *Scirpus lacustris* L. ssp. *tabernaemontani* C. C. Gmel.) can survive 3 months of anoxia [Crawford, 1982]. Sea Club-rush (synonymous *Scirpus maritimus* L. Palla) and Common reed both have developed interesting response strategies to flooding, comprising the production of fewer, but taller culms associated with the accumulation of stem dry matter [Clevering and Hundscheid, 1998; Vretare *et al.*, 2001]. The buildup of aerenchyma for

enhanced oxygen transport into the rhizosphere represents a common plant response to flooding [Blom, 1999].

[34] When the water level reached values up to 120 cm due to extraordinary strong rainfalls in July 2011, daily fluxes of Reco and CP decreased by 55% and 32%, on average, respectively. Although net CO₂ storage rates were considerably lower, the site remained a net CO₂ sink. We assume that the plants that had adapted to the flooding with water levels around 30–45 cm above surface were again exposed to increased flooding stress, causing the metabolic activity to decrease. This corresponds well with the response of EVI, which levelled off in July 2011, thereby confirming the effect of additional plant tissue submergence and decreased plant vitality after the water level rise.

[35] The budgets of Reco and CP integrated over the growing season were similar to those of 2010, resulting in a net CO₂ storage that was slightly higher than those of the previous growing seasons. However, the period from 1 May to 12 July (i.e., during 72 of 183 total measurement days) that was characterized by stable, shallow flooding contributed more than half of the total growing season budgets (59% for CP and 50% for Reco).

5.3. Implications for Net CO₂ Exchange of a Temperate Fen During the Transition Phase From Moderately Rewetting to Flooding

[36] Despite different water regimes, the fen acted as a net CO₂ sink throughout all growing seasons. Indeed, low, but persistent Reco during winter might potentially offset the net CO₂ sink [Alm *et al.*, 1999] and cause more distinct differences between NEE budgets on a yearly basis. Nevertheless, this study spans the period of the year which coincides with the highest ecosystem activity and is therefore best suited to present ecosystem response to flooding. Indeed, rates of net CO₂ sequestration were similar during all growing seasons, but the values of CP and Reco differed considerably. Prior to flooding, the established macrophyte community was highly productive, and therefore, high CP rates were offsetting high Reco fluxes that were caused by low summer water levels. However, both NEE component fluxes decreased exponentially with rising water levels (Figure 4, $p < 0.001$). The drop of heterotrophic Reco under anaerobic conditions is a well-known effect [Komulainen *et al.*, 1999; Waddington *et al.*, 2010; Hatala *et al.*, 2012]. Here we show that CP can also decrease considerably after flooding. Although we cannot distinguish between autotrophic and heterotrophic Reco, the drop in CP suggests that the decrease in Reco is—at least in part—caused by a decrease in autotrophic Reco. Our results refer to a period immediately after flooding, which is characterized by plant stress response and the development of initial acclimatization strategies. Such transition phases are associated with changes in plant metabolic activity that might not be transferable to periods when plants have already acclimatized. As a consequence, ecosystem models that presume a certain response under rather stable conditions might not work properly under such transient conditions, i.e., the application of a functional NEE partitioning approach [Lasslop *et al.*, 2010] worked well prior to flooding, but the model performance decreased considerably in the first year of flooding (data not shown). Increasing CP and Reco fluxes in the beginning of growing season 2011 suggest that plants will acclimatize to flooding conditions in the long term.

6. Conclusions

[37] The fast rise of the water level posed an extraordinary disturbance to the vegetation that had been adapted to drier conditions after the drainage of the site. The term “disturbance” has been mainly considered for anthropogenic impacts on pristine ecosystems. However, since secondary ecosystems shift toward a new state of organization, the reestablishment of former conditions within the scope of revitalization operations also acts as a disturbance to the current biocenosis. Our results suggest that even plant individuals that belong to species that generally are well adapted to water-logged conditions might suffer when water levels increase rapidly since the tolerance spectrum of individuals is usually narrower than on the species level. As a consequence, revitalization measures that tempt to mitigate CO₂ emissions from drained peatlands have to consider a transition phase that is associated with the impairment of the CO₂ sequestration potential due to decreased CP. This is also valid when the plant community does not change abundance in reaction to flooding. At our site, the plants showed plastic response after 1 year of stable flooding, which was reflected in the increasing rates of CP and Reco. This relatively fast adaptation was not sufficient to get along with a further increase of the water level. Further research is needed to address the response capabilities of plants and plant species to long-term inundation and its implications for the net CO₂ balance of flooded peatlands.

[38] **Acknowledgments.** We thank the Editor, Dennis Baldocchi, and two anonymous reviewers for their constructive valuable comments on the manuscript. We think that the manuscript did profit considerably from the resulting edits. Further, we are grateful to the Scientific Writing Crew of the Department of Landscape Ecology for various useful comments on the manuscript. F.K. was supported by a scholarship of the Federal State of Mecklenburg-Western Pomerania and by the German Research Foundation (DFG). The German Academic Exchange Service (DAAD) funded the collaboration with I.F.

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