Annual CO₂ fluxes from a cultivated fen with perennial grasses during two initial years of rewetting

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SUMMARY

Rewetting combined with biomass crop cultivation (paludiculture) has been proposed as a method for reducing carbon dioxide (CO₂) emissions from drained peatlands. This field experiment compared CO₂ fluxes from drained (control) and rewetted experimental plots in a temperate fen under reed canary grass cultivation over two successive years. The annual weighted mean water table depth from soil surface (WTD) during the study period was 9, 3 and 1 cm in control, semi-flooded and flooded plots, respectively. There were no significant effects of WTD treatment on biomass yields. The choice of response model for CO₂ fluxes influenced annual estimates of ecosystem respiration (ER) and gross primary production (GPP), but all models showed that ER and GPP decreased in response to rewetting. The resulting net ecosystem exchange (NEE) of CO₂, derived by combining eight ER and eight GPP models, varied widely. For example, NEE (expressed as CO₂-C) ranged from -935 to -208 g m⁻² yr⁻¹ for the flooded plots. One set of ER and GPP models was selected on the basis of statistical criteria and showed insignificant differences in NEE between the three water table treatments (-537 to -341 g CO₂-C m⁻² yr⁻¹). Treatment effects on CO₂ emission factors, calculated as the sum of NEE and C export in harvested biomass (58–242 g CO₂-C m⁻² yr⁻¹), were similarly insignificant. Thus, the results indicated that varying WTD within this narrow range could influence both ER and GPP without altering the net emissions of CO₂.

KEY WORDS: ecosystem respiration, gross primary production, paludiculture, reed canary grass

INTRODUCTION

Peatlands are important in the global carbon cycle because they store approximately 600 Pg of carbon (C) (Gorham 1991, Yu et al. 2011). However, drainage and subsequent use for agriculture and forestry have drastically altered the C storage functions of many peatlands during the last century (Wichtmann et al. 2016). In drained peat soils that are used for agriculture, peat oxidation and mineralisation processes contribute to large emissions of carbon dioxide (CO₂) resulting in peat subsidence rates of a few to 50 mm per year, depending on drainage intensity and climatic conditions, with the highest subsidence rates occurring in the tropics (Leifeld et al. 2011, Hooijer et al. 2012). Globally, the annual emissions of CO₂ from drained peatlands are estimated at 0.78 Pg, which is equivalent to 25 % of the net CO₂ emissions from the agriculture, forestry and land use sector (Tubiello et al. 2016). However, many peatlands which have been drained for agriculture (at least in northern Europe) are currently being abandoned due to peat degradation, declining productivity and the high cost of drain maintenance (Biancalani & Avagyan 2014, Kløve et al. 2017). To further reduce peat degradation and CO₂ emissions, novel yet socioeconomically viable approaches to the management of agricultural peatlands are needed (Joosten et al. 2015).

Paludiculture is an innovative land use concept for poorly drained and rewetted peatlands which involves harvesting natural or cultivated biomass for energy or industrial uses (Joosten et al. 2015, Wichtmann et al. 2016). While such management allows productive use of the land to continue, the shallower water table may restrict exposure of the peat to oxygen (O₂) - which diffuses more slowly in water-filled pores than in air-filled pores (Moldrup et al. 2000, Dinsmore et al. 2009, Karki et al. 2015b) - and thus result in reduced peat degradation and CO₂ emissions. Paludiculture may also improve ecosystem services such as nutrient and water retention and biodiversity (Wichtmann et al. 2016). Although it has been recommended as a promising management option for drained peatlands in recent reports of the Food and Agriculture Organization of the United Nations (Biancalani & Avagyan 2014) and the Intergovernmental Panel on Climate Change (IPCC
2014), there is still limited quantitative information on the effectiveness and optimisation of paludiculture as a tool for mitigating CO₂ emissions (IPCC 2014, Günther et al. 2015, Karki et al. 2016). So far, most studies of CO₂ fluxes from paludicultures have focused on rewetted peatlands with natural vegetation and low-input management such as no fertiliser and a single annual harvest (Beetz et al. 2013, Günther et al. 2015). For paludiculture to become socioeconomically viable, it is likely that more intensive management and dedicated biomass crops will be needed in the future (Günther et al. 2015). Karki et al. (2016) recently simulated intensive paludiculture with multiple harvests (cuts) and fertiliser applications each year, in a mesocosm study with newly established reed canary grass (RCG; Phalaris arundinacea L.). This study reported higher net uptake of CO₂ for completely rewetted peat soils than for drained and partially rewetted soils with constant water table depth below ground level (WTD). To substantiate these results, more comprehensive studies are needed to quantify the CO₂ emissions from rewetted sites where, for example, lateral water flow, fluctuating water table and in situ biomass development occur.

In the present study we measured CO₂ fluxes on a fen peatland that had been rewetted to various degrees and cultivated with RCG in a fertilised two-cut management system during two consecutive years after rewetting. The objectives of the study were to:

(i) quantify and compare the effects of different water table levels (treatments) on annual CO₂ balances and biomass yields under perennial grass cultivation; and

(ii) address the consistency of net annual CO₂ balances resulting from different modelling approaches.

**METHODS**

**Study site and cropping history**

The study site was a drained and cultivated fen peatland located in the Norræ river valley in central Jutland, Denmark (56° 27’ 32” N, 9° 40’ 40” E; 3 m a.s.l.), with temperate Atlantic climate. Average long-term (1985–2015) annual air temperature was 7.9 °C, total annual precipitation 650 mm and total annual global radiation 3540 MJ m⁻², equivalent to 1868 mmol m⁻² of photosynthetically active radiation (PAR). Global radiation was converted to PAR using a conversion factor of 1.9 µmol J⁻¹ (Al-Shooshan 1997). The fen was a minerotrophic wetland that received nutrients from the surrounding moraine landscape through drainage and surface runoff (Knadel et al. 2011, Walpersdorf et al. 2013).

The fen was drained for agricultural use by establishing open ditches in the early 20th century. Tile drain pipes at 60–80 cm depth were added in 1967. Continued agricultural use resulted in peat subsidence, and the drainage was reinforced with PVC drain pipes at 60–80 cm depth in 1985. In recent decades, the site was used for spring barley (Hordeum vulgare L.) cropping, either continuously or in rotation with grass-clover. In 2011, the soil was ploughed and sown with RCG (cultivar Bamse) for experimental purposes.

Details of soil properties at the study site were presented by Kandel et al. (2013b). Briefly, peat depth was >1 m and the topsoil (0–20 cm) was characterised by bulk density 0.29 g cm⁻³, organic C content 36.3 %, total nitrogen (N) content 3.0 % and pH(H₂O) in the range 6.1–7.1. Bulk density decreased with depth because the peat in deeper layers was less decomposed than the topsoil.

**Study design and crop management**

The study was conducted from March 2015 to February 2017. Hereafter, the period between March 2015 and February 2016 is referred to as Year 1 and the period between March 2016 and February 2017 is referred to as Year 2. The study was planned as a split block design with four blocks (14 × 18 m) and two plots with different water table treatments, representing control and continuous rewetting (water table close to the soil surface), in each block (Figure 1). A confinement was made around the ‘rewetted’ plot in each block using inert plastic strip (0.3 cm thick, 30 cm wide; Danbox Denmark ApS, Langå, Denmark). The plastic strip was inserted vertically to 25 cm depth leaving 5 cm above ground level to control surface runoff. Rewetting was accomplished by pumping water from a drainage ditch into elevated tanks, whence it could flow continuously (by gravity) through 4 cm diameter PVC tubing to the plots (Figure 1). The resulting WTD in each block and plot was influenced by the topography of the study area and the distance of the block from the drainage ditch. The four confined plots were always intentionally flooded, and the two unconfined (control) plots close to the drainage ditch (Figure 1) also had a high degree of rewetting after mid-June in Year 1 due to subsurface intrusion of water from the flooded plots. Therefore, the resulting water table treatments were designated as ‘flooded’ for the confined plots (n=4), ‘semi-flooded’ (n=2) for two of the unconfined plots, and ‘control’ (n=2) for the other two unconfined plots (farthest from the drainage ditch). Thus, the study followed an unbalanced split block design with three water table...
treatments. Two ‘GHG collars’ (details given later) were installed in each plot.

Fertilisation and harvest events in the years before and during the study period are presented in Figure 2. Crop management during the study period (2015–2017) was optimised to enhance the quality and quantity of biomass for biogas production, which required multiple harvests of green (above-ground) biomass and repeated fertiliser applications (Kandel et al. 2013a, 2013c). Standard mineral fertiliser (N-P-K at 80-13-62 kg ha⁻¹) was applied to all plots on 23 March 2015, five days prior to the start of flooding. The biomass inside the GHG collars was harvested manually on 15 June and fertilised again on 24 June. The regrowth was then harvested on 01 October to represent a two-cut management regime. In 2016, all plots were fertilised on 31 March during spring growth and biomass was harvested on

Figure 1. Layout of the field experiment. Four blocks (14 × 18 m) were divided into two plots (14 × 9 m) to impose flooding treatments. The water table treatments were flooded (F), semi-flooded (S-F), and control (C). Water was pumped from the drainage ditch (large dotted arrow) to the tank. The grey arrows indicate pipelines connecting water tanks to the flooded plots confined by plastic borders. Black squares at the southern end of each plot indicate the collars (0.55 × 0.55 m) installed for gas flux measurements.

Figure 2. Timeline of harvest (arrowheads) and fertilisation (upward arrows) before (May 2011 – February 2015; hatched area) and during the study period (March 2015 – March 2017). The study site was ploughed and sown with reed canary grass in May 2011. The experimental rewetting of the flooded plots started on 28 March 2015. Plots were fertilised with standard mineral fertilisers (80-13-62 kg N-P-K ha⁻¹).
13 June. After subsequent fertilisation on 21 June, a final harvest was taken on 31 October. Dry matter (DM) content of the biomass from each harvest was determined by oven drying all biomass inside the collars to constant weight at 60 °C. Biomass yields from a collar at the two harvest dates in each year were summed to obtain total annual yield.

**CO₂ flux measurements**

Three weeks prior to the first CO₂ flux measurements, two white PVC collars (55 × 55 × 11 cm) were inserted into the soil to a depth of 10 cm with a distance of 1 m between them. At collar installation (09 February 2015), the growing season had not yet started but the plots were covered with short green grass. Each collar had a 4 cm wide outer flange that was kept parallel to the soil surface and served to support the chamber top during flux measurements (Elsgaard et al. 2012). The collars remained in place for the entire study period. A PVC boardwalk was placed alongside the collars to reduce disturbance of soil gas profiles during measurements.

Fluxes of CO₂ were measured using a transparent chamber top (60 × 60 × 41 cm) made from Plexiglas and equipped with a temperature control unit, cooling and mixing fans, and a PAR sensor (190-SA; Li-Cor Inc., Lincoln, NE, USA). Details of the chamber design and data acquisition are described by Elsgaard et al. (2012). Briefly, the chamber was connected by 4 mm inlet and outlet tubing to a portable analysing unit where CO₂ and H₂O concentrations were measured at one-second intervals using an infrared gas analyser (Li-840A; Li-Cor Inc.). A chamber extension with the same dimensions as the chamber top was used later in the growing season, when plant height exceeded the height of the chamber. Fluxes were generally measured at two-week intervals from 05 March 2015 to 03 March 2017, but more frequently during periods of rapid growth.

During each measurement campaign, CO₂ fluxes at the 16 collars were measured at four levels of PAR, imposed by shrouding as described by Kandel et al. (2017). First, the CO₂ flux was measured for one minute under fully transparent conditions; this flux represented net ecosystem exchange (NEE) at the prevailing PAR. Then the chamber was covered with black netting to block ~50 % PAR and the vegetation was allowed to adapt to the new PAR level for one minute before a one-minute flux measurement. During the adaptation period, the side of the chamber facing the wind was lifted 15–20 cm from the collar to bring the CO₂ concentration back to atmospheric level. On rare occasions when there was no wind, a stream of air was created by waving a sheet of cardboard outside the chamber opening. A second layer of black netting was then added to block a total of ~75 % PAR, and the procedure was repeated. Finally, the chamber was covered with a white opaque cover to block 100 % PAR and the CO₂ flux (i.e., ecosystem respiration, ER) was measured after one minute of dark adaptation.

Fluxes were measured between 10:00 and 13:00 hrs. Measurement dates were normally fixed in advance and campaigns were carried out under the prevailing cloud conditions (sunny, partially cloudy or overcast days) but not on rainy days. On partially cloudy days, conditions of (nearly) constant PAR were achieved for individual measurements by timing chamber deployments with consideration of the movement of clouds across the sun.

Fluxes were calculated using the MATLAB® (MathWorks, Inc., Natick, MA, USA) protocol by Kutzbach et al. (2007), applying a water vapour correction. Data from the first ten seconds after chamber deployment were discarded as a dead-band. Linear (rather than non-linear) regression was used for flux calculation as it generally gives more stable results for short enclosure periods (Kandel et al. 2016).

**Ratio vegetation index**

Aboveground biomass development in each collar was monitored during the study period by measuring canopy light reflectance using a SpectroSense 2+ fitted with SKR1850 sensors (Skye Instruments, Powys, UK) as described by Kandel et al. (2017). The sensors were held at nadir angle at a height of 1 m above the ground, to cover a 0.15 m² area inside the collars. The sensors measured incident and reflected red (R) light at 640±10 nm and near-infrared (NIR) light at 778±16 nm ( Görres et al. 2014). The ratio vegetation index (RVI) was then calculated as (NIR/NIR)/(R/R), where the subscripts i and r denote the incident and reflected radiation, respectively. On all measurement days, reflectance was measured just before chamber deployment to record the reflectance from undisturbed biomass. Vegetation indices measured as canopy reflectance (such as RVI in the current study) combine information about the amount of vegetation and its photosynthetic activity and have been considered as proxies for photosynthetically active biomass (Wiegand & Richardson, 1984).

**Environmental variables**

Air temperature and PAR during chamber deployment were recorded by sensors inside the chamber (Elsgaard et al. 2012). Continuous hourly measurements of air temperature and PAR were obtained from the climate station of Aarhus University (Foulum, Denmark) 7 km from the study.
site. Soil temperature at 5 cm depth was recorded at hourly intervals using HOBO temperature data loggers (Model UA-001-64; Onset Computer Corporation, Bourne, MA, USA) installed in one plot for each treatment.

Volumetric water content (VWC) at 0–20 cm soil depth inside each collar was measured manually on flux measurement days when the soil was not frozen using permanently installed time domain reflectometer (TDR) probes (Plauborg et al. 2005). Relative VWC (i.e., proportion of maximum value measured under flooded conditions) for each collar was used to represent the water-filled pore space (Shrestha et al. 2014). Natural fluctuation of water table depth in the study area was monitored at hourly intervals from May 2015 in a PVC tube (5 cm diameter, 150 cm long; perforated all the way down from 5 cm below soil surface) installed about 50 m from the nearest plot, using a PTX 1730 pressure transducer sensor (GE Druck, Leicester, UK). Water table depth was also measured manually during each flux measurement campaign, in similar tubes installed within one metre of each collar.

Flux modelling and annual CO₂ fluxes
The CO₂ fluxes were partitioned into light-dependent GPP and light-independent ER. GPP was estimated as (NEE - ER), where ER is always positive (≥0) and GPP is always negative (≤0); hence the sign of NEE is positive when there is a net flux of CO₂ to the atmosphere (Kandel et al. 2017). GPP was calculated for each of the three NEE fluxes in a measurement cycle (at different PAR levels) by subtracting the corresponding ER measurement. Cumulative annual fluxes were derived from separate modelling of GPP and ER. Annual NEE was then calculated as (GPP + ER). CO₂ emission factors were then calculated by summing NEE and the C exported in harvested biomass (Renou-Wilson et al. 2014, Renou-Wilson et al. 2016, Tiemeyer et al. 2016).

GPP and ER were modelled with eight deductive response models each. Several deductive response models were compared using the same flux data, as model selection can markedly influence annual estimates of ER and GPP (Görres et al. 2014, Huth et al. 2017, Kandel et al. 2017). The models were selected from previous studies and included PAR (for GPP models only), temperature and RVI as driving variables (Tables 1 and 2). All models (except GPP Model 1) were fitted for each treatment by pooling the entire dataset. For GPP Model 1, fitting was done for each treatment and measurement date (Elsgaard et al. 2012). A few winter measurement dates were merged to achieve convergence of the Model 1

Table 1. Ecosystem respiration (ER) models adapted or modified from previous studies and used with the present dataset.

<table>
<thead>
<tr>
<th>Model</th>
<th>Model structure for ER</th>
<th>References and comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( R_{10} \times e^{\left(1 + \frac{1}{\alpha(T_T - T_T^{0})}\right)} )</td>
<td>Lloyd &amp; Taylor 1994, Elsgaard et al. 2012, Beetz et al. 2013, Günther et al. 2015, Minke et al. 2016, Poyda et al. 2016.</td>
</tr>
<tr>
<td>2</td>
<td>( R_{10} \times e^{\alpha T} )</td>
<td>Soini et al. 2010, Vanselow-Algan et al. 2015, Järveoja et al. 2016.</td>
</tr>
<tr>
<td>3</td>
<td>( (R_{10} + (\alpha \times RVI)) \times e^{\alpha T} )</td>
<td>Kandel et al. 2013b.</td>
</tr>
<tr>
<td>4</td>
<td>( (R_{10} + (\alpha \times RVI)) \times e^{\left(1 + \frac{1}{\alpha(T_T - T_T^{0})}\right)} )</td>
<td>Modified version of Model 1 with RVI to model the influence of biomass on ER as in Model 3.</td>
</tr>
<tr>
<td>5</td>
<td>( R_{10} \times e^{\left(1 + \frac{1}{\alpha(T_T - T_T^{0})}\right)} + (\alpha \times RVI) )</td>
<td>Mäkiranta et al. 2010, Karki et al. 2016.</td>
</tr>
<tr>
<td>6</td>
<td>( (R_{10} + (\alpha \times RVI)) \times \left(\frac{47.9}{1 + e^{\frac{106}{T_T^{0} + 15}}}\right) )</td>
<td>Kandel et al. 2017, 2018, 2019.</td>
</tr>
<tr>
<td>7</td>
<td>( R_T + (b \times T) + (\alpha \times RVI) )</td>
<td>Wilson et al. 2007. RVI was used instead of vascular green area.</td>
</tr>
<tr>
<td>8</td>
<td>( e^{\beta T} + (\alpha \times RVI) )</td>
<td>Urbanová et al. 2013. RVI was used instead of vascular green area.</td>
</tr>
</tbody>
</table>

\( R_{10} \) is respiration at 10 °C, \( E_0 \) is the ecosystem sensitivity coefficient, \( T_{10} \) is a reference temperature at 10 °C, \( T \) is the air temperature (°C), \( T_0 \) is a theoretical zero respiration temperature, here fixed at -46 °C (Lloyd & Taylor 1994), \( R_0 \) is respiration at 0 °C, \( b \) is a temperature sensitivity parameter, RVI is the ratio vegetation index, \( \alpha \) is a scaling parameter of RVI. All model parameters obtained with the different models were significant (\( P < 0.05 \)).
algorithm. GPP and ER models were fitted using non-linear regression in SigmaPlot 11 (Systat Software Inc., San Jose, CA, USA).

Extrapolation of ER to annual fluxes was based on the estimated model parameters in combination with a continuous time series of air temperature and linearly interpolated (to hourly time steps) RVI. Extrapolation of GPP followed a similar approach based on hourly PAR and linearly interpolated RVI. For all models that included RVI (i.e., all models except GPP Model 1), extrapolation was carried out using one set of model parameters for each treatment. For GPP Model 1, a linear development of model parameters between measurement campaigns was assumed. The α and GPP_{\text{max}} values in GPP Model 1 (Table 1) were set to -0.0001 and -0.01 µg m^{-2} s^{-1}, respectively, after biomass harvests (Beetz et al. 2013).

The fit of individual models was evaluated on the basis of Nash-Sutcliffe modelling efficiencies (NSE), where NSE values closer to unity indicate higher accuracy (Nash & Sutcliffe 1970). Furthermore, accordance between modelled and measured fluxes was evaluated using different statistical indicators such as paired t-tests, correlation coefficient (r) and simultaneous F-test for unit slope and zero intercept (Haefner 2005, Piñero et al. 2008). The statistical performance of the model was rated from good to excellent, based on Hoffmann et al. (2015). Informed by these evaluations, we selected one ER and one GPP model as a basis for further comparisons of water table treatments with annual CO₂ fluxes. The selected models were used to estimate GPP and ER individually for each collar to provide insights about spatial variations in the annual CO₂ emissions.

### Statistical analyses

The effects of WTD treatments, year and time of harvest (first and second cut) on the biomass yield were analysed using the following linear mixed model:

\[
M_{yctbr} = \mu_{yct} + B_b + U_{btr} + E_{yctbr} \tag{1}
\]

where \(M_{yctbr}\) is the biomass yield of the \(r\)th \((r = 1, 2)\) repetition (collar) at the \(b\)th block \((b = 1, 2, 3, 4)\) of the \(c\)th time of cut \((c = 1, 2)\) in the \(y\)th year \((y = 1, 2)\) of an experimental unit subject to the \(t\)th WTD treatment \((t = \text{control, semi-flooded and flooded})\).

### Table 2. Gross primary production (GPP) models adapted or modified from previous studies and used with the present dataset.

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<tbody>
<tr>
<td>1</td>
<td>(\frac{GPP_{\text{max}} \times \alpha \times \text{PAR}}{GPP_{\text{max}} + \alpha \times \text{PAR}})</td>
<td>Thornley &amp; Johnson 1990, Elsgaard et al. 2012, Beetz et al. 2013, Günther et al. 2015, Vanselov-Algan et al. 2015, Minke et al. 2016, Poyda et al. 2016.</td>
</tr>
<tr>
<td>2</td>
<td>(\frac{GPP_{\text{max}} \times \text{RVI} \times \alpha \times \text{PAR}}{(GPP_{\text{max}} \times \text{RVI}) + (\alpha \times \text{PAR})})</td>
<td>Kandel et al. 2013a, Görres et al. 2014, Karki et al. 2016.</td>
</tr>
<tr>
<td>3</td>
<td>(\frac{GPP_{\text{max}} \times \text{RVI} \times \alpha \times \text{PAR}}{(GPP_{\text{max}} \times \text{RVI}) + (\alpha \times \text{PAR})} \times \text{FT})</td>
<td>Kandel et al. 2017.</td>
</tr>
<tr>
<td>4</td>
<td>(\frac{GPP_{\text{max}} \times \text{PAR}}{\kappa + \text{PAR}} \times \text{RVI})</td>
<td>Wilson et al. 2007, 2013, Soini et al. 2010, Urbanová et al. 2013. RVI was used instead of vascular green area or green area index.</td>
</tr>
<tr>
<td>5</td>
<td>(\frac{GPP_{\text{max}} \times \text{PAR}}{\kappa + \text{PAR}} \times \left(\frac{\text{RVI}}{\text{RVI} + \alpha}\right))</td>
<td>Wilson et al. 2013, Renou-Wilson et al. 2014, 2016. RVI was used instead of leaf area index, vascular green area, or green area index.</td>
</tr>
<tr>
<td>6</td>
<td>(\frac{GPP_{\text{max}} \times \text{PAR}}{\kappa + \text{PAR}} \times (1 - e^{(-\alpha \times \text{RVI})}))</td>
<td>Urbanová et al. 2013. RVI was used instead of vascular green area.</td>
</tr>
<tr>
<td>7</td>
<td>(\frac{GPP_{\text{max}} \times \text{PAR}}{\kappa + \text{PAR}} \times \left(\frac{\text{RVI}}{\text{RVI} + \alpha}\right) \times \text{FT})</td>
<td>Modified version of Model 5 where a temperature dependence function (FT) was included as in Model 3.</td>
</tr>
<tr>
<td>8</td>
<td>(\frac{GPP_{\text{max}} \times \text{PAR}}{\kappa + \text{PAR}} \times (a + \text{RVI}))</td>
<td>Soini et al. 2010. RVI was used instead of vascular green area.</td>
</tr>
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</table>

GPP_{\text{max}} is the asymptotic maximum rate of GPP at increasing photosynthetically active radiation (PAR), \(\alpha\) is the initial light response efficiency in the original Model 1, RVI is the ratio vegetation index, FT is a temperature dependent function of photosynthesis set to 0 below -2 °C and 1 above 10 °C and with an exponential increase between -2 and 10 °C, \(\kappa\) is the PAR value at which GPP reaches half of its maximum (half saturation constant), and \(a\) is model-specific parameter.
\( \mu_{yc} \) is a fixed effect representing the mean biomass yield of the \( c^{th} \) time of cut at \( r^{th} \) WTD treatment in the \( y^{th} \) year. \( B_p, U_{btr} \) and \( E_{ycbtr} \) are independent random components representing block, experimental unit as the \( r^{th} \) repetition of the \( p^{th} \) plot (\( p=1,2 \)) and the residual variation, respectively. The experimental design adopted (see Figure 1) is such that the plots are identified in the model by the \( r^{th} \) management of the \( b^{th} \) block. A similar model without time of harvest was used to analyse the effects of WTD treatments and year on annual cumulative CO\(_2\) fluxes, i.e., ER, GPP, NEE and the CO\(_2\) emission factor. The statistical inference of the linear mixed models was performed using the ‘lme4’ package in R (R Core Team 2016). The basic assumptions of normality and variance homogeneity were verified using the Shapiro-Wilks test and the Bartlett test, respectively, applied to the raw residuals; no significant departures from these assumptions were found. Post-hoc analyses grouping the treatments for each year and comparing the two years for each treatment were performed using the package ‘pairwiseComparisons’ in R (Labouriau 2018); all post-hoc tests were corrected for multiple testing using the false discovery rate method (Benjamini & Hochberg 1995, Benjamini & Yekutieli 2001).

RESULTS

Climate conditions
In both study years, mean annual temperature (8.3 °C in Year 1, 8.7 °C in Year 2) and total annual precipitation (821 mm in Year 1, 755 mm in Year 2) exceeded the long-term (1985–2015) average values for the area (7.9 °C, 650 mm). The study years differed mainly in terms of mean temperature during the growing season (March–September), which was 10.9 °C in Year 1 and 12.1 °C in Year 2 (Figure 3a). Although total precipitation during the growing season was similar in the two years (Figure 4a), Year 2 had more precipitation in April and July and markedly less in September (Figure 3b). Global radiation was close to the long-term average in both Year 1 (3580 MJ m\(^{-2}\), equivalent to 1889 mmol m\(^{-2}\) PAR) and Year 2 (3440 MJ m\(^{-2}\), equivalent to 1816 mmol m\(^{-2}\) PAR) (Figure 3c).

The average soil temperatures at 5 cm soil depth for the flooded, semi-flooded and control plots were 8.6, 9.0, and 8.8 °C, respectively, in Year 1; and 9.0, 9.3, and 9.1 °C, respectively, in Year 2 (data not shown). The highest soil temperatures were observed in the semi-flooded plots and the lowest in the flooded plots, but they differed by less than 0.4 °C in both years.

Water table and soil moisture content
The mean position of the water table in the study area (~ 50 m from the nearest plot) was about 15 cm below the soil surface in both years. During growing periods, the water table generally fluctuated between 5 cm and 40 cm (mean 18 cm) below the soil surface in Year 1, and between 8 cm above and 55 cm below the soil surface (mean 20 cm below) in Year 2 (Figure 4b).

The mean annual WTD in the experimental plots (treatments) differed slightly and corresponded to two-year weighted averages of 1, 3 and 9 cm below the soil surface for the flooded, semi-flooded and control plots, respectively (Figure 4c). The water table was always at the soil surface in the flooded plots, except for few days in March and September in

![Figure 3. Mean monthly (a) air temperature, (b) precipitation and (c) global radiation in the study area during Year 1 (March 2015 – February 2016), Year 2 (March 2016 – February 2017), and during the long-term period 1985–2015.](image-url)
Year 2 when it dropped to 10 cm below the soil surface due to failure of the pumping system. The WTD treatment difference between the plots was more evident during the growing periods than during the non-growing periods (October–February). Thus, the mean WTD among the treatments in the growing periods was 1, 5 and 14 cm for the flooded, semi-flooded and control plots, respectively (Figure 4c). During winter, the rewetting system failed periodically due to frozen water in the tanks and tubing. However, the water table was mostly at the soil surface in the whole study area during these periods.

Relative VWC in control plots ranged from around 0.76 to 0.96 with a mean of 0.87 for both years (Figure 4d). Overall, the treatment effects were moderate but, as also seen for WTD dynamics, VWC differences among the treatments were observed during the growing periods; VWC was always higher in the flooded plots than in the control plots.

**Biomass development and yield**

Dynamics of RVI were similar for all treatments until the first harvest in both years (Figure 5c). After the first harvest, RVI in the flooded plots was lower than
Figure 5. (a) Mean air temperature during flux measurements, (b) photosynthetically active radiation (PAR) inside fully transparent chamber at prevailing light conditions during flux measurements, (c) ratio vegetation index (RVI) as a proxy of green biomass, (d) mid-day net ecosystem exchange (NEE) at prevailing PAR, (e) mid-day ecosystem respiration (ER), and (f) gross primary production (GPP) calculated as GPP = NEE - ER. Data are shown for flooded (F), semi-flooded (S-F) and control (C) plots. Error bars represent the spatial variation (standard error, $n = 4$ for F plots and $n = 2$ for S-F and C plots). Arrows indicate harvest events. The dotted vertical line demarks the two study years.
in the semi-flooded and control plots at the beginning of the regrowth period, as grasses were more impaired (and partly killed) in the flooded plots. When new biomass eventually emerged in the flooded plots, this regrowth subsequently reached similar RVI peaks as seen for semi-flooded and control plots. Yet, as regrowth of grasses in the flooded plots started later, they also reached senescence later. After the final harvest in autumn, regrowth of grasses other than RCG was observed (albeit weak) and the plots stayed green during winter. When comparing biomass growth between the two study years, the most notable difference was observed after the first harvest where RVI was lower in Year 2, especially in the flooded plots.

There was no significant effect of WTD treatments on biomass yield ($P = 0.175$), but the yields in the two years were significantly different ($P < 0.001$), i.e., on average $19\%$ lower in Year 2 than in Year 1 (Figure 6). This was mainly caused by yield reduction of the biomass in the second cut in Year 2. There was no significant effect ($P = 0.163$) of different cuts (i.e., first and second cut) on biomass yield in Year 1, but the biomass yield in the second cut in Year 2 was significantly lower than in the first cut ($P < 0.001$) and also significantly lower than in the second cut in Year 1 ($P < 0.001$).

**Dynamics of mid-day CO$_2$ fluxes**

The mid-day NEE followed a seasonal pattern with large net CO$_2$ uptake during growing periods, which decreased and remained close to zero during the non-growing periods (Figure 5d). NEE was similar in all treatments during the first cut periods in both years. However, as the regrowth of biomass was delayed in the flooded plots after the first harvest, particularly in Year 2, the net uptake of CO$_2$ was weaker during that period. The NEE fluxes in non-growing periods were small but mostly negative, as the plots contained green biomass after the final harvest in autumn and soil respiration was restricted due to flooded field conditions.

The mid-day ER followed a strong seasonal trend (Figure 5e) and correlated well with air temperature (mean $r = 0.82$; range 0.79–0.86 for individual collars), RVI (mean $r = 0.84$; range 0.81–0.86) and WTD (mean $r = 0.49$; range 0.23–0.67 for individual collars in semi-flooded and control plots). This indicated that temperature, green biomass (Figure 5a,c) and water table (Figure 4c) were the major driving factors for seasonal variations in ER. During the growing periods, ER in the flooded plots was consistently lower than in the semi-flooded and control plots. However, ER was similar in all treatments during the non-growing periods in accordance with similar WTD and RVI.

Mid-day GPP showed a clear correlation to PAR (mean $r = 0.82$; range 0.76–0.87 for individual collars) and RVI (mean $r = 0.58$; range 0.52–0.61), thus following a seasonal trend and responding to harvest events (Figure 5). Dynamics of GPP at all WTD treatments were generally similar but absolute GPP was lower in the flooded plots after the first harvest, particularly in Year 2 (Figure 5f).

**Comparative CO$_2$ flux modelling**

**Model performance and model selection**

Among the models for ER, the NSE across the treatments was 0.63–0.75 for models with temperature as the only predictor (Models 1 and 2), indicating good statistical performance (Tables A1–A3 in the Appendix). Yet NSE was higher (0.77–0.88) for models with both temperature and RVI as predictors (Models 3–8), indicating very good statistical performance. Also, the consistency of NSE across WTD treatments was higher for Models 3–8 than for Models 1 and 2.

Among the GPP models that included PAR and RVI (Models 2–8), the NSE across the treatments was 0.82–0.92 (Tables A4–A6), i.e., indicating very good to excellent statistical performance. For GPP Model 1 (without RVI), NSE at individual campaigns mostly ranged from 0.44 to 0.99, except on a few occasions (< 5%) where the modelled light response curves had lower NSE, i.e., after harvest and in winter. The average NSE for GPP Model 1 was 0.80.
Although comparative flux modelling highlighted RVI as a useful variable in the ER and GPP model structures, it did not allow rigorous selection among the relevant models due to rather similar NSE values. Further model evaluation based on Akaike Information Criterion (AIC) and adjusted $R^2$ resulted in similar conclusions (data not shown). However, model validation using simultaneous $F$-test for unit slope and zero intercept indicated a bias ($P < 0.05$) for ER Models 3 and 6 for flooded treatments (Tables A1–A3) and also for GPP Models 2, 4 and 6 for all treatments (Tables A4–A6). The combination of higher NSE and non-significant $P$-value for the $F$-test indicated that ER Model 4 was the most suitable model for flooded treatments and ER Models 4, 5 and 6 were equally suitable models for semi-flooded and control treatments. As Model 4 was generally better for all treatments, this model was selected for further collar-scale assessment of WTD treatment effects on annual ER. For GPP, Models 3, 5 and 7 performed the best and equally well for all treatments. However, Model 5 without temperature scaling (FT) was not used as it did not account for the effect of low temperature on photosynthesis. Model 7 with marginally higher NSE than Model 3 across all treatments was selected for further assessment of WTD treatment effects on annual GPP for each collar.

**Annual estimates and CO₂ emission factors in relation to modelling uncertainty**

The mean and range of annual ER (expressed as CO₂-C; g m⁻² year⁻¹) estimated with the eight models for flooded, semi-flooded and control plots were 1128 ± 20 %, 1402 ± 21 % and 1496 ± 22 %, respectively, in Year 1 and 1079 ± 19 %, 1418 ± 15 % and 1490 ± 14 %, respectively, in Year 2 (Figure 7a,b). The lowest annual ER estimates were generally derived from Models 1 and 2 (without RVI) and 6, whereas

![Figure 7](image-url)

**Figure 7.** (a, b) Annual ecosystem respiration (ER) and (c, d) annual gross primary production (GPP) estimates with different ER and GPP models (see Tables 1 and 2) at the different WTD treatments, i.e., flooded (F), semi-flooded (S-F) and control (C). Data are shown for each study year.
the highest estimates were derived from Model 8. Despite the differences in absolute ER values, all models showed a consistent pattern of WTD treatment effects where ER increased from flooded to semi-flooded to control treatments (Figure 7a,b).

Annual GPP (g CO₂-C m⁻² year⁻¹; numerical values) estimated with the eight models for flooded, semi-flooded and control plots were 1704 ± 12 %, 1869 ± 11 % and 1973 ± 10 %, respectively, in Year 1 and 1594 ± 14 %, 1859 ± 11 % and 1862 ± 15 %, respectively, in Year 2 (Figure 7c,d). For all individual GPP models (and years) it was found that CO₂ uptake generally increased from flooded to semi-flooded to control management (Figure 7c,d).

Although treatment effects on ER and GPP were robust among the different models, the resulting outcome for annual NEE was highly uncertain due to NEE being the (small) difference between two large component fluxes (Figure 8). Thus, the 64 possible NEE combinations (from the eight ER and eight GPP estimates) led to different but negative NEE depending on model selection, yet with two combinations indicating control treatments as weak sources of CO₂. CO₂ emission factors varied between

![Bubble plot of resulting net ecosystem exchange (NEE) of CO₂ derived by combining the eight times eight ecosystem respiration (ER) and gross primary production (GPP) models (as depicted in Tables 1 and 2) for individual treatments and study years. Maximum symbol size corresponds to a NEE sink strength of -935 g CO₂-C m⁻² year⁻¹. Red symbols show the resulting NEE from the two selected models, ER Model 4 and GPP Model 7. Crosses show incidences of small positive NEE fluxes.](image-url)
strong sink and source of CO₂, depending on model selection (Figure 9). However, more frequent indication of sinks of CO₂ (negative emission factor) was observed for flooded treatments.

**Annual CO₂ emissions in relation to WTD treatments**

The two selected models, ER Model 4 and GPP Model 7, were individually run for each collar and showed a significant effect of WTD treatment on both ER ($P < 0.001$) and GPP ($P = 0.003$) (Figure 10).

Annual ER increased significantly in Year 2 except for the flooded treatment ($P = 0.003$), whereas annual GPP decreased significantly in Year 2 ($P < 0.001$) in all treatments. There was no significant effect of WTD treatment on annual NEE ($P = 0.069$). However, annual NEE was significantly lower in Year 2 as compared to Year 1 ($P < 0.001$). There were no significant effects of year ($P = 0.094$) and WTD treatment ($P = 0.105$) on the annual CO₂ emission factors.

Figure 9. Bubble plot of resulting emission factors of CO₂ derived from net ecosystem exchange (NEE) of CO₂ and biomass yield C export for individual treatments and study years. NEE of CO₂ was derived by combining the eight times eight ecosystem respiration (ER) and gross primary production (GPP) models (as depicted in Tables 1 and 2). Maximum symbol size corresponds to numerical emission factors of $709 \text{ g CO}_2 \cdot \text{C m}^{-2} \cdot \text{year}^{-1}$. Grey symbols indicate negative emissions (sink of CO₂); maroon symbols show positive emissions (source of CO₂). Maroon symbols with cross show the resulting CO₂ emission factor from the two selected models, ER Model 4 and GPP Model 7.
After the summer harvests, the stubble remaining below the water surface for extended periods in the flooded and semi-flooded plots, which delayed regrowth of the plants. As observed in this study, Fraser & Karnezis (2005) also reported dieback of flood-tolerant grasses including RCG when the plants were submerged. This indicates that the perennial grasses under paludiculture should be harvested to ensure that stubble height is above the flooding level.

**DISCUSSION**

The two-year field study was designed to compare CO₂ fluxes from side-by-side rewetted and drained (control) plots cultivated with perennial grasses. However, as both study years were wetter than the long-term average, differences in WTD among the treatments were less than expected, and hence CO₂ fluxes were studied at scenarios of rather shallow water table corresponding to (two-year) weighted mean WTDs of 1, 3 and 9 cm below the soil surface for flooded, semi-flooded and control plots, respectively. Therefore, the annual average WTD in the control plots (9 cm) was much shallower than observed previously in the same site (40 cm; Karki et al. 2015a). This may, to some extent, also be related to the gradually deteriorating maintenance of the drainage system at the study site.

**Biomass yield**

Total annual biomass yields (11–16 Mg DM ha⁻¹) obtained in this study were within the range observed under similar intensive management of perennial grasses in field and mesocosm studies (Kandel et al. 2013a, Karki et al. 2016). In Year 2, plant growth was restricted due to higher water table after the first cut, which contributed to significantly lower biomass yield. Compared to Year 1, the site received 90 mm more precipitation during the month following first harvest in Year 2, which caused flooding at most of the plots. After the summer harvests, the stubble remained below the water surface for extended periods in the flooded and semi-flooded plots, which delayed regrowth of the plants. As observed in this study, Fraser & Karnezis (2005) also reported dieback of flood-tolerant grasses including RCG when the plants were submerged. This indicates that the perennial grasses under paludiculture should be harvested to ensure that stubble height is above the flooding level.

**Model selection**

Model validation is important for model selection but can be done with several approaches each with specific justifications (Haefner 2005). Validation and selection based on NSE indicated that several of the tested models could qualify for extrapolation of the CO₂ fluxes to annual estimates. However, analysis of modelled versus measured CO₂ fluxes by simultaneous F-test for unit slope and zero intercept indicated potential bias for some models even with high NSE. Also, ER Model 7 had a higher NSE, but predicted negative ER when the temperature was below zero, which is biologically incorrect.

In the present study, temperature and RVI were included as driving factors for ER. However, ER is also affected by WTD, and it is common to include WTD in the model structure to achieve a better prediction of ER (Rowson et al. 2013, Karki et al. 2014, Kandel et al. 2018). In the present study, the effect of including WTD was tentatively tested for the selected ER model (Model 4) as suggested by Karki et al. (2014), using hourly values of WTD as reconstructed from linear interpolation between measurement days (data not shown). However, the inclusion of WTD for analyses of ER did not lead to an improvement for the flooded plots (where WTD was rather constant during the entire measurement period) and including WTD only improved model performance slightly for the semi-flooded and control plots with an increase in NSE from 0.88 to 0.92 and from 0.82 to 0.85, respectively. Furthermore, there were only minor differences in annual ER estimates (< 5 %) derived from models with and without WTD (data not shown).

Model 1 for GPP is the most commonly used model for annual estimations of GPP (Elsgaard et al. 2012, Beetz et al. 2013, Minke et al. 2016). However, this approach requires that models are run for each measurement campaign, and it poorly captures temporal variability especially under field conditions with management interventions such as harvest
(Görres et al. 2014). The use of GPP models that include RVI (or other vegetation indices) can provide more robust methods for capturing such temporal variations (Wohlfahrt et al. 2010, Kandel et al. 2013b; Kandel et al. 2017). In addition, such models can be analysed in one single run integrating information obtained from the entire study period. A temperature modifier function (FT) was included in several models to adjust for low temperature constraints on photosynthesis (Kandel et al. 2017). The importance of including FT was seen, for example, with GPP Model 3 where it corrected the bias observed without the FT function (Model 2).

Uncertainties in CO$_2$ fluxes from rewetted peatlands, recognised in IPCC Tier 1 emission factors, are already considerable due to variations in variables such as peat type (fen or bog), nutrient status, vegetation, hydrology, number of years after rewetting, previous land use and climate (Wilson et al. 2016a). In addition, the use of different measurement and gap filling strategies leads to further uncertainty in annual fluxes (Huth et al. 2017). Our results indicate that the selection of response models for ER and GPP strongly contributes to uncertainties and substantiates the importance of working towards unified and comparable approaches for modelling CO$_2$ fluxes from chamber measurements (Huth et al. 2017). Although we found that individual ER and GPP models provided a consistent pattern in relation to WTD treatment effects, arbitrary combinations of the two component fluxes into NEE resulted in a wide range of outcomes.

**Annual CO$_2$ budgets**
The annual ER in the control plots in Year 1 obtained with Model 6 (1356 g CO$_2$·C m$^{-2}$) was similar to the annual ER in a concurrent study at the same site where fensulolium (fescue-ryegrass hybrid) and tall fescue were cultivated under a two-cut management system (1368 g CO$_2$·C m$^{-2}$) when analysed by the same model (Kandel et al. 2017). The annual ER was significantly lower from the flooded plots than the semi-flooded and control plots, despite the small difference in annual WTD. According to Chimner & Cooper (2003) and Riutta et al. (2007), most of the easily oxidised labile C is present near the soil surface (the upper 0–15 cm) and exposing this zone to anaerobic conditions can significantly reduce soil respiration. Moreover, plant respiration may also be lowered in flooded plots due to decreased GPP (Karki et al. 2015b, Järveoja et al. 2016). The strong correlation between all measured GPP at 100 % PAR and ER ($r = 0.85$, $P < 0.001$) underlined the importance of plant respiration for total ER.

An effect of WTD management on GPP in peatlands has been frequently observed, substantiated by changes in biomass yield and composition (Riutta et al. 2007, Waddington et al. 2010, Järveoja et al. 2016, Laine et al. 2016). In the present study, neither the biomass yield nor the biomass composition was significantly different among the WTD treatments. The biomass was mainly composed of RCG and Poa spp. in all plots. In this study, reduced GPP in the flooded plots was mostly due to restriction of plant growth for the extended period after the first cut because of higher water table.

In a meta-analysis, Wilson et al. (2016a) reported that net uptake of CO$_2$ increased linearly with decreasing WTD for a gradient from 30 cm below to 20 cm above the soil surface. In this study, where the annual WTD varied within a narrow range between treatments, no significant effect of WTD on annual NEE could be registered. In the current study, smaller WTD reduced both ER and GPP thus counterbalancing the effect on NEE as reported by Järveoja et al. (2016). Inter-annual variability in NEE from peatlands is often seen due to high sensitivity to prevailing weather conditions (Herbst et al. 2013, Helfter et al. 2015, Wilson et al. 2016b). Indeed, both study years were wetter than long-term average, so potential interactions between WTD treatments and more dry weather conditions could not be assessed. The range of annual NEE values obtained in this study was generally at the lower range (higher net CO$_2$ uptake) of NEE previously reported from diverse rewetted fen peatlands (IPCC 2014, Minke et al. 2016, Wilson et al. 2016a). However, relatively similar low NEE has been observed in rewetted peatlands with productive species like RCG and Typha latifolia (Wilson et al. 2007), Phragmites australis (Minke et al. 2016) and Eriophorum angustifolium (Wilson et al. 2013). Yet, direct comparison of annual fluxes with other studies is difficult as it partly depends on the methods used to estimate annual emissions.

**CO$_2$ emission factors**
CO$_2$ emission factors ranged from 0.6 to 2.4 Mg CO$_2$·C ha$^{-1}$ yr$^{-1}$ which fall within or slightly above the 95 % confidence interval (-0.71 to 1.71 Mg CO$_2$·C ha$^{-1}$ yr$^{-1}$) of emission factors for rewetted nutrient rich temperate fens proposed by the IPCC (2014). Nevertheless, similar emission factors of up to 2.1 Mg CO$_2$·C ha$^{-1}$ yr$^{-1}$ have been reported from rewetted peatlands where biomass was removed by grazing (Renou-Wilson et al. 2016). The CO$_2$ emission factors obtained in this study were substantially lower than the emission factors (6–12 Mg CO$_2$·C ha$^{-1}$ yr$^{-1}$) reported for deeper
drained peatlands in Denmark (Elsgaard et al. 2012, Kandel et al. 2013b) supporting the conclusion that rewetting and biomass cultivation can amply reduce CO₂ losses from drained peatlands (Gunther et al. 2015, Karki et al. 2016). This is despite the fact that biomass yield was optimised by intensive management, such as multiple harvesting and fertilisation. Yet, in comparing CO₂ emission factors among rewetted and drained peatlands, the role of methane (CH₄) emissions for the C balance at rewetted sites should also be considered. Rewetting and subsequent colonisation by wetland plants may generally increase the CH₄ emissions (Gunther et al. 2015, Harpenslager et al. 2015, Vanselow-Algan et al. 2015, Karki et al. 2016).

In conclusion, this field study showed significant differences in both annual ER and GPP despite a small difference in WTD treatments with two-year annual means of 1, 3 and 9 cm below the soil surface. The choice of response models for annual estimations of flux measurements contributed to uncertainties in estimates of ER and GPP. However, the WTD treatment effects were generally robust among the different response models. There was no significant difference in NEE and CO₂ emission factors (the sum of NEE and carbon export in harvested biomass) among the shallow WTD treatments (annual means, < 10 cm below the soil surface). However, the effects of other factors such as changes in vegetation composition and inter-annual climate variability may need to be addressed on a longer time scale than achieved in the present study, which was restricted to the first two years following rewetting.

ACKNOWLEDGEMENTS

The study was financially supported by the Innovation Fund Denmark under the EU FACCE ERA-NET+ on Climate Smart Agriculture as a part of the CAOS project (www.caos-project.eu) and the PEATWISE project (http://eragas.eu/index.php/research-projects/peatwise) in the frame of the ERA-NET FACCE ERA-GAS. FACCE ERA-GAS has received funding from the European Union’s Horizon 2020 research and innovation program under Grant Agreement No. 696356. The authors would like to express their gratitude for assistance provided by Jens B. Kjeldsen and the team of technicians in crop management and harvesting at AU-Foulumgård. We also wish to acknowledge the skilled technical assistance of Ahammad Mostafa Kamal, Bodil Stensgaard, Ben McCarthy, Henrik Nørgaard, Michael Koppelgaard, Morten Skov and Suman Thapa. This article is based on a presentation at the international conference Renewable Resources from Wet and Rewetted Peatlands held on 26–28 September 2017 at the University of Greifswald, Germany. We thank the two anonymous referees and David Wilson for their comments which helped us to improve the manuscript.

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Submitted 19 Dec 2017, revision 26 Apr 2018
Editor: David Wilson

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Appendix

Table A1. Model performance statistics for ecosystem respiration (ER) models fitted to data from flooded (F) treatments.

<table>
<thead>
<tr>
<th>Model</th>
<th>Data (n)</th>
<th>Mean rate simulated</th>
<th>Mean rate observed</th>
<th>Paired t-test ((P)^a)</th>
<th>Correlation ((r))</th>
<th>Mean bias</th>
<th>Slope</th>
<th>Intercept ((P)^a)</th>
<th>(F)-test ((P)^a)</th>
<th>NSE(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ER 1</td>
<td>416</td>
<td>194</td>
<td>191</td>
<td>0.644(^{ns})</td>
<td>0.806</td>
<td>-2.3</td>
<td>1.03</td>
<td>-7.1</td>
<td>0.715(^{ns})</td>
<td>0.649</td>
</tr>
<tr>
<td>ER 2</td>
<td>416</td>
<td>200</td>
<td>191</td>
<td>0.075(^{ns})</td>
<td>0.797</td>
<td>-9.0</td>
<td>1.02</td>
<td>-12.4</td>
<td>0.186(^{ns})</td>
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</tr>
<tr>
<td>ER 3</td>
<td>416</td>
<td>207</td>
<td>191</td>
<td>0.000(^{***})</td>
<td>0.921</td>
<td>-15.6</td>
<td>0.93</td>
<td>-0.3</td>
<td>0.000(^{***})</td>
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<tr>
<td>ER 4</td>
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<td>191</td>
<td>0.914(^{ns})</td>
<td>0.923</td>
<td>-0.3</td>
<td>1.01</td>
<td>-1.6</td>
<td>0.948(^{ns})</td>
<td>0.852</td>
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<tr>
<td>ER 5</td>
<td>416</td>
<td>194</td>
<td>191</td>
<td>0.361(^{ns})</td>
<td>0.914</td>
<td>-3.1</td>
<td>1.03</td>
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<td>186</td>
<td>191</td>
<td>0.120(^{ns})</td>
<td>0.922</td>
<td>5.0</td>
<td>0.96</td>
<td>12.2</td>
<td>0.048(^{ns})</td>
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<tr>
<td>ER 7</td>
<td>416</td>
<td>191</td>
<td>191</td>
<td>0.965(^{ns})</td>
<td>0.897</td>
<td>0.2</td>
<td>1.00</td>
<td>0.1</td>
<td>0.999(^{ns})</td>
<td>0.805</td>
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<tr>
<td>ER 8</td>
<td>416</td>
<td>193</td>
<td>191</td>
<td>0.750(^{ns})</td>
<td>0.907</td>
<td>-1.1</td>
<td>1.00</td>
<td>-0.9</td>
<td>0.949(^{ns})</td>
<td>0.822</td>
</tr>
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</table>

\(^{a}\) ns, not significant \((P > 0.05)\); \(^*\), \(P < 0.05\); \(^{**}\), \(P < 0.01\); \(^{***}\), \(P < 0.001\); \(^{b}\) NSE, Nash-Sutcliffe modelling efficiency.

Table A2. Model performance statistics for ecosystem respiration (ER) models fitted to data from semi-flooded (S-F) treatments.

<table>
<thead>
<tr>
<th>Model</th>
<th>Data (n)</th>
<th>Mean rate simulated</th>
<th>Mean rate observed</th>
<th>Paired t-test ((P)^a)</th>
<th>Correlation ((r))</th>
<th>Mean bias</th>
<th>Slope</th>
<th>Intercept ((P)^a)</th>
<th>(F)-test ((P)^a)</th>
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<td>272</td>
<td>253</td>
<td>0.011(^*)</td>
<td>0.868</td>
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<td>1.00</td>
<td>-17.3</td>
<td>0.042(^*)</td>
<td>0.745</td>
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<td>253</td>
<td>0.828(^{ns})</td>
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<td>1.1</td>
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<td>-7.6</td>
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<td>253</td>
<td>0.488(^{ns})</td>
<td>0.940</td>
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<td>ER 6</td>
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<td>253</td>
<td>0.659(^{ns})</td>
<td>0.940</td>
<td>2.2</td>
<td>0.99</td>
<td>5.6</td>
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<td>253</td>
<td>0.984(^{ns})</td>
<td>0.926</td>
<td>-0.1</td>
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<td>0.999(^{ns})</td>
<td>0.858</td>
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<td>208</td>
<td>252</td>
<td>253</td>
<td>0.828(^{ns})</td>
<td>0.926</td>
<td>1.2</td>
<td>0.96</td>
<td>12.1</td>
<td>0.278(^{ns})</td>
<td>0.855</td>
</tr>
</tbody>
</table>

\(^{a}\) ns, not significant \((P > 0.05)\); \(^*\), \(P < 0.05\); \(^{**}\), \(P < 0.01\); \(^{***}\), \(P < 0.001\); \(^{b}\) NSE, Nash-Sutcliffe modelling efficiency.
Table A3. Model performance statistics for ecosystem respiration (ER) models fitted to data from control (C) treatments.

<table>
<thead>
<tr>
<th>Model</th>
<th>Data (n)</th>
<th>Mean rate simulated</th>
<th>Mean rate observed</th>
<th>Paired t-test (P)</th>
<th>Correlation (r)</th>
<th>Mean bias</th>
<th>Slope</th>
<th>Intercept</th>
<th>F-test (P)</th>
<th>NSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>ER 1</td>
<td>210</td>
<td>285</td>
<td>280</td>
<td>0.596**</td>
<td>0.843</td>
<td>-5.1</td>
<td>1.03</td>
<td>-14.1</td>
<td>0.682**</td>
<td>0.710</td>
</tr>
<tr>
<td>ER 2</td>
<td>210</td>
<td>271</td>
<td>280</td>
<td>0.361**</td>
<td>0.834</td>
<td>9.2</td>
<td>1.18</td>
<td>-39.0</td>
<td>0.003***</td>
<td>0.679</td>
</tr>
<tr>
<td>ER 3</td>
<td>210</td>
<td>294</td>
<td>280</td>
<td>0.072**</td>
<td>0.901</td>
<td>-14.0</td>
<td>0.99</td>
<td>-12.4</td>
<td>0.197**</td>
<td>0.808</td>
</tr>
<tr>
<td>ER 4</td>
<td>210</td>
<td>284</td>
<td>280</td>
<td>0.642**</td>
<td>0.903</td>
<td>-3.5</td>
<td>1.02</td>
<td>-8.4</td>
<td>0.788**</td>
<td>0.816</td>
</tr>
<tr>
<td>ER 5</td>
<td>210</td>
<td>283</td>
<td>280</td>
<td>0.668**</td>
<td>0.904</td>
<td>-3.3</td>
<td>1.02</td>
<td>-8.7</td>
<td>0.774**</td>
<td>0.816</td>
</tr>
<tr>
<td>ER 6</td>
<td>210</td>
<td>282</td>
<td>280</td>
<td>0.816**</td>
<td>0.904</td>
<td>-1.8</td>
<td>1.01</td>
<td>-5.1</td>
<td>0.914**</td>
<td>0.816</td>
</tr>
<tr>
<td>ER 7</td>
<td>210</td>
<td>281</td>
<td>280</td>
<td>0.956**</td>
<td>0.880</td>
<td>-0.5</td>
<td>1.00</td>
<td>-0.1</td>
<td>0.998**</td>
<td>0.774</td>
</tr>
<tr>
<td>ER 8</td>
<td>210</td>
<td>268</td>
<td>280</td>
<td>0.143**</td>
<td>0.880</td>
<td>12.4</td>
<td>0.97</td>
<td>21.3</td>
<td>0.225**</td>
<td>0.771</td>
</tr>
</tbody>
</table>

a ns, not significant (P > 0.05); *, P < 0.05; **, P < 0.01; ***, P < 0.001; b NSE, Nash-Sutcliffe modelling efficiency.

Table A4. Model performance statistics for gross primary production (GPP) models fitted to data from flooded (F) treatments.

<table>
<thead>
<tr>
<th>Model</th>
<th>Data (n)</th>
<th>Mean rate simulated</th>
<th>Mean rate observed</th>
<th>Paired t-test (P)</th>
<th>Correlation (r)</th>
<th>Mean bias</th>
<th>Slope</th>
<th>Intercept</th>
<th>F-test (P)</th>
<th>NSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP 2</td>
<td>1613</td>
<td>-299</td>
<td>-287</td>
<td>0.000***</td>
<td>0.942</td>
<td>12.5</td>
<td>1.03</td>
<td>20.9</td>
<td>0.000***</td>
<td>0.885</td>
</tr>
<tr>
<td>GPP 3</td>
<td>1613</td>
<td>-286</td>
<td>-287</td>
<td>0.844**</td>
<td>0.945</td>
<td>-0.6</td>
<td>1.00</td>
<td>1.6</td>
<td>0.669**</td>
<td>0.892</td>
</tr>
<tr>
<td>GPP 4</td>
<td>1613</td>
<td>-261</td>
<td>-287</td>
<td>0.000***</td>
<td>0.923</td>
<td>-25.5</td>
<td>0.95</td>
<td>-34.0</td>
<td>0.000***</td>
<td>0.845</td>
</tr>
<tr>
<td>GPP 5</td>
<td>1613</td>
<td>-288</td>
<td>-287</td>
<td>0.657**</td>
<td>0.945</td>
<td>1.4</td>
<td>1.00</td>
<td>2.4</td>
<td>0.829**</td>
<td>0.894</td>
</tr>
<tr>
<td>GPP 6</td>
<td>1613</td>
<td>-304</td>
<td>-287</td>
<td>0.000***</td>
<td>0.946</td>
<td>16.8</td>
<td>0.96</td>
<td>5.5</td>
<td>0.000***</td>
<td>0.891</td>
</tr>
<tr>
<td>GPP 7</td>
<td>1613</td>
<td>-283</td>
<td>-287</td>
<td>0.195**</td>
<td>0.946</td>
<td>-4.1</td>
<td>1.00</td>
<td>-5.4</td>
<td>0.366**</td>
<td>0.895</td>
</tr>
<tr>
<td>GPP 8</td>
<td>1613</td>
<td>-288</td>
<td>-287</td>
<td>0.763**</td>
<td>0.934</td>
<td>1.0</td>
<td>1.00</td>
<td>0.7</td>
<td>0.950**</td>
<td>0.873</td>
</tr>
</tbody>
</table>

a ns, not significant (P > 0.05); *, P < 0.05; **, P < 0.01; ***, P < 0.001; b NSE, Nash-Sutcliffe modelling efficiency.
Table A5. Model performance statistics for gross primary production (GPP) models fitted to data from semi-flooded (S-F) treatments.

<table>
<thead>
<tr>
<th>Model</th>
<th>Data (n)</th>
<th>Mean rate simulated</th>
<th>Mean rate observed</th>
<th>Paired t-test (P)a</th>
<th>Correlation (r)</th>
<th>Mean bias</th>
<th>Slope</th>
<th>Intercept</th>
<th>F-test (P)a</th>
<th>NSEb</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP 2</td>
<td>805</td>
<td>-333</td>
<td>-323</td>
<td>0.025*</td>
<td>0.947</td>
<td>10.7</td>
<td>1.03</td>
<td>20.6</td>
<td>0.005**</td>
<td>0.895</td>
</tr>
<tr>
<td>GPP 3</td>
<td>805</td>
<td>-319</td>
<td>-323</td>
<td>0.407ns</td>
<td>0.949</td>
<td>-3.9</td>
<td>1.01</td>
<td>-0.7</td>
<td>0.503ns</td>
<td>0.900</td>
</tr>
<tr>
<td>GPP 4</td>
<td>805</td>
<td>-297</td>
<td>-323</td>
<td>0.000***</td>
<td>0.931</td>
<td>-25.5</td>
<td>0.95</td>
<td>-39.0</td>
<td>0.000***</td>
<td>0.862</td>
</tr>
<tr>
<td>GPP 5</td>
<td>805</td>
<td>-325</td>
<td>-323</td>
<td>0.531ns</td>
<td>0.951</td>
<td>2.9</td>
<td>1.00</td>
<td>2.9</td>
<td>0.822ns</td>
<td>0.905</td>
</tr>
<tr>
<td>GPP 6</td>
<td>805</td>
<td>-336</td>
<td>-323</td>
<td>0.003**</td>
<td>0.951</td>
<td>13.5</td>
<td>0.97</td>
<td>4.1</td>
<td>0.001***</td>
<td>0.903</td>
</tr>
<tr>
<td>GPP 7</td>
<td>805</td>
<td>-319</td>
<td>-323</td>
<td>0.442ns</td>
<td>0.951</td>
<td>-3.5</td>
<td>0.99</td>
<td>-6.7</td>
<td>0.504ns</td>
<td>0.904</td>
</tr>
<tr>
<td>GPP 8</td>
<td>805</td>
<td>-332</td>
<td>-323</td>
<td>0.047*</td>
<td>0.942</td>
<td>9.8</td>
<td>0.99</td>
<td>6.4</td>
<td>0.101ns</td>
<td>0.887</td>
</tr>
</tbody>
</table>

a ns, not significant (P > 0.05); *, P < 0.05; **, P < 0.01; *** P < 0.001; b NSE, Nash-Sutcliffe modelling efficiency.

Table A6. Model performance statistics for gross primary production (GPP) models fitted to data from control (C) treatments.

<table>
<thead>
<tr>
<th>Model</th>
<th>Data (n)</th>
<th>Mean rate simulated</th>
<th>Mean rate observed</th>
<th>Paired t-test (P)a</th>
<th>Correlation (r)</th>
<th>Mean bias</th>
<th>Slope</th>
<th>Intercept</th>
<th>F-test (P)a</th>
<th>NSEb</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP 2</td>
<td>793</td>
<td>-353</td>
<td>-337</td>
<td>0.001**</td>
<td>0.955</td>
<td>15.9</td>
<td>1.01</td>
<td>19.4</td>
<td>0.003**</td>
<td>0.911</td>
</tr>
<tr>
<td>GPP 3</td>
<td>793</td>
<td>-334</td>
<td>-337</td>
<td>0.514ns</td>
<td>0.957</td>
<td>-3.1</td>
<td>1.01</td>
<td>1.7</td>
<td>0.330ns</td>
<td>0.915</td>
</tr>
<tr>
<td>GPP 4</td>
<td>793</td>
<td>-300</td>
<td>-337</td>
<td>0.000***</td>
<td>0.930</td>
<td>-36.3</td>
<td>0.95</td>
<td>-52.5</td>
<td>0.000***</td>
<td>0.856</td>
</tr>
<tr>
<td>GPP 5</td>
<td>793</td>
<td>-336</td>
<td>-337</td>
<td>0.902ns</td>
<td>0.960</td>
<td>-0.6</td>
<td>1.00</td>
<td>0.9</td>
<td>0.907ns</td>
<td>0.921</td>
</tr>
<tr>
<td>GPP 6</td>
<td>793</td>
<td>-348</td>
<td>-337</td>
<td>0.013**</td>
<td>0.960</td>
<td>11.4</td>
<td>0.97</td>
<td>0.6</td>
<td>0.000***</td>
<td>0.921</td>
</tr>
<tr>
<td>GPP 7</td>
<td>793</td>
<td>-334</td>
<td>-337</td>
<td>0.586ns</td>
<td>0.960</td>
<td>-2.5</td>
<td>0.99</td>
<td>-5.2</td>
<td>0.622ns</td>
<td>0.922</td>
</tr>
<tr>
<td>GPP 8</td>
<td>793</td>
<td>-338</td>
<td>-337</td>
<td>0.880ns</td>
<td>0.948</td>
<td>0.8</td>
<td>1.00</td>
<td>2.4</td>
<td>0.912ns</td>
<td>0.898</td>
</tr>
</tbody>
</table>

a ns, not significant (P > 0.05); *, P < 0.05; **, P < 0.01; *** P < 0.001; b NSE, Nash-Sutcliffe modelling efficiency.