

Modelling seasonal water table effects on tropical peatland CO₂ exchange

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Modelling effects of seasonal variation in water table depth on net ecosystem CO₂ exchange of a tropical peatland

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Abstract

Seasonal variation in water table depth (WTD) determines the balance between aggradation and degradation of tropical peatlands. Longer dry seasons together with human interventions (e.g. drainage) can cause WTD drawdowns making tropical peatland C storage highly vulnerable. Better predictive capacity for effects of WTD on net CO₂ exchange is thus essential to guide conservation of tropical peat deposits. Mathematical modelling of basic eco-hydrological processes under site-specific conditions can provide such predictive capacity. We hereby deploy a mathematical model *ecosys* to study effects of seasonal variation in WTD on net ecosystem productivity (NEP) of an Indonesian peatland. We simulated lower NEPs ($\sim -2 \text{ gC m}^{-2} \text{ d}^{-1}$) during rainy seasons with shallow WTD, higher NEPs ($\sim +1 \text{ gC m}^{-2} \text{ d}^{-1}$) during early dry seasons with intermediate WTD and again lower NEPs ($\sim -4 \text{ gC m}^{-2} \text{ d}^{-1}$) during late dry seasons with deep WTD during 2002–2005. These values were corroborated by regressions ($P < 0.0001$) of hourly modelled vs. eddy covariance (EC) measured net ecosystem CO₂ fluxes which yielded $R^2 > 0.8$, intercepts approaching 0 and slopes approaching 1. We also simulated a gradual increase in annual NEPs from 2002 (-609 gC m^{-2}) to 2005 (-373 gC m^{-2}) with decreasing WTD which was corroborated by EC-gap filled annual NEP estimates. These WTD effects on NEP were modelled from basic eco-hydrological processes including microbial and root oxidation-reduction reactions driven by soil and root O₂ transport and uptake which in turn drove soil and plant C, N and P transformations within a soil-plant-atmosphere water transfer scheme driven by water potential gradients. This modelling should therefore provide a predictive capacity for WTD management programs to reduce tropical peat degradation.

1 Introduction

Seasonal and interannual fluctuations in WTD can affect peatland net CO₂ exchange through complex effects on soil oxidation-reduction reactions and hence on nutrient

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transformations. Shallow WTD during rainy seasons slows convective-dispersive transport of O_2 through wet soils. Consequent reduction in soil O_2 concentrations slows O_2 uptake used to drive aerobic oxidation-reduction reactions by soil microbes and roots and hence reduces heterotrophic and root respiration. Microbial energy yield from oxidation coupled to reduction of O_2 under aerobic conditions exceeds that from oxidation coupled to reduction of alternative electron acceptors e.g. NO_3^- , SO_4^{2-} etc. (Brock and Madigan, 1991) under anaerobic conditions. Lower anaerobic energy yields slow microbial growth and therefore reduce heterotrophic respiration. Root oxidation-reduction reactions driving root growth and nutrient uptake also require O_2 which is scarce under shallow WTD condition. Reduced heterotrophic and root respiration thus result in reduced ecosystem respiration (R_e) with shallow WTD during rainy seasons, as reported in many field studies (Limpens et al., 2008; Couwenberg et al., 2009; Sulman et al., 2010; Flanagan and Syed, 2011). Slower microbial growth also reduces decomposition and nutrient mineralization, as well as root growth and nutrient uptake and hence gross primary productivity (GPP) (Cai et al., 2010; Murphy and Moore, 2010; Flanagan and Syed, 2011; Sulman et al., 2012).

More rapid O_2 transport with WTD drawdown during early dry seasons may increase root and heterotrophic respiration and hence R_e (Cai et al., 2010; Sulman et al., 2010). Consequent increases in mineralization and root growth, and thereby nutrient availability and uptake can also raise GPP during this hydroperiod (Cai et al., 2010; Flanagan and Syed, 2011; Jauhiainen et al., 2012a; Sulman et al., 2012). Increased GPP in this hydroperiod may further hasten R_e through increased production of fresh labile C in the forms of litter fall and root exudates (Limpens et al., 2008).

These increases, however, may not be sustained with further WTD drawdown in the later part of a prolonged dry season. When WTD falls below a certain level during the late dry season, desiccation of near surface peat layers may occur. Such desiccation might reduce near surface peat decomposition by reducing microbial access to substrate e.g. dissolved organic C (DOC) in desiccated near-surface soil (Dimitrov et al., 2010), thereby slowing oxidation-reduction reactions and hence microbial growth. The

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reduction in decomposition of desiccated near surface peat can be partially or fully offset by increases in decomposition of better aerated deeper peat, thereby causing no net changes in R_e during this hydroperiod (Lafleur et al., 2005; Strack and Waddington, 2007; Dimitrov et al., 2010). However, plant water stress from near surface peat desiccation might also cause a decline in GPP during deep WTD hydroperiods (Sulman et al., 2010; Dimitrov et al., 2011), thereby lowering NEP. Therefore, responses of peatland ecosystem net CO₂ exchange to WTD fluctuations are governed by basic soil hydrological and biological processes and their interactions with plant physiology.

Process based ecosystem models can provide us with means of understanding basic mechanisms behind WTD effects on peatland net ecosystem CO₂ exchange. To accomplish this, a model should explicitly represent oxidation-reduction reactions, coupled with aqueous and gaseous transfers of their reactants and products. These processes require modelling WTD dynamics, soil moisture retention characteristics, gas transport through soil, differential substrate quality for microbial degradation and hydrolysis e.g. labile vs. recalcitrant, nutrient transformations driven by these reactions, and microbial and plant nutrient uptake. However, in a recent review of 7 widely used ecosystem models, Sulman et al. (2012) found only *ecosys* (Grant, 2001) included processes to limit both CO₂ fixation and respiration under shallow WTD. The predictive capacity of the other models were limited by (1) not explicitly simulating WTD dynamics and consequently not modelling aerobic vs. anaerobic zones from water influxes (e.g. precipitation, lateral recharge) vs. effluxes (e.g. evapotranspiration, lateral discharge) (e.g. van Huissteden et al., 2006; Kurbatova et al., 2009; St-Hilaire et al., 2010), (2) parameterizing models with empirical rate constants and/or scalar functions for aerobic vs. anaerobic decomposition (e.g. Frohling et al., 2002; Bond-Lamberty et al., 2007; St-Hilaire et al., 2010) instead of simulating biogeochemical oxidation-reduction reactions affected by soil aerobicity, and (3) using scalar functions that reduce productivity in wet soils through a driver variable such as stomatal conductance (g_s) (e.g. Frohling et al., 2002; Bond-Lamberty et al., 2007) instead of simulating nutrient limitations to CO₂ fixation imposed by reduced nutrient availability and root nutrient uptake caused

by slower O₂ transport processes through soils and roots. The general purpose terrestrial ecosystem model *ecosys* includes site-independent algorithms representing all the processes affected by aerobicity mentioned above, thereby excluding the need for arbitrary model parameterization. The model could therefore successfully simulate WTD effects on R_e and GPP of different peatlands without site-specific parameterization (e.g. Dimitrov et al., 2010, 2011; Grant et al., 2012a).

All of the previous peatland modelling studies mentioned above had been tested only against measurements from northern temperate and boreal peatlands. Modelling the fate of vulnerable C storage in tropical peatlands under WTD fluctuations is still largely under-investigated. For instance, modelling WTD effects on tropical peat soil respiration has to date predominantly included regressions of soil CO₂ fluxes against WTD (e.g. Melling et al., 2005; Jauhiainen et al., 2008, 2012b; Couwenberg et al., 2009; Hirano et al., 2009; Hooijer et al., 2010) without taking other confounding factors like land use, nutrient availability, nature of the peat, ecosystem productivity etc. into consideration (Murdiyarso et al., 2010). Modelling eco-physiological response to hydrology in a tropical peatland is particularly important since tropical peatlands are very different in their climates than those in northern temperate and boreal zones. Tropical peatlands are formed under high temperature and precipitation, an important consequence of which is that a small WTD drawdown might cause a large increase in peat decomposition (Page et al., 2009). Distinct dry seasons almost every year together with human intervention such as drainage have been reported to deepen WTD, thereby causing rapid decomposition of very old and thick (up to > 26 000 yr old and 9 m thick (Page et al., 2004)) tropical peat deposits (Jauhiainen et al., 2008; Couwenberg et al., 2009; Hirano et al., 2009, 2012). Moreover, tropical peatlands are generally formed by roots and remains of trees and devoid of bryophytes (e.g. mosses) as opposed to the northern peatlands that are mainly formed by mosses or co-existed by mosses and vascular plants. Differences in dominant vegetation can exhibit very different WTD effects on productivity of tropical peatland than of northern boreal and temperate peatlands due to different rooting and stomatal behaviour (e.g. mosses with shallow rhizoids and no

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stomatal regulation vs. trees with well developed root systems and stomatal regula-
tions) and consequent plant water and nutrient uptake. Besides, tropical peat deposits
formed by tree remains can have very different substrate quality for microbial decom-
position than boreal and temperate moss peatlands and hence may have a different
5 WTD – peat respiration interactions. Variations in climate and peat forming vegetation
thus necessitate rigorous testing of a process model against measurements across
peatlands developed under very different climate (e.g. boreal vs. tropical) and vegeta-
tion (e.g. moss vs. tree) to improve predictive capacity on eco-hydrological controls of
peatland C balance.

10 The hourly time step model *ecosys* previously simulated the effects of WTD fluctua-
tions on net CO₂ exchange of northern boreal peatlands (Dimitrov et al., 2011; Grant
et al., 2012a). Testing the same model against site measurements of a tropical peat-
land would thus be an important test of the versatility of its algorithms representing the
processes described above. Such a test will allow us to determine whether our cur-
rent understanding of peatland water, nutrient and C interactions is sufficiently robust
15 to capture complex WTD effects on peatland R_e and GPP over a wide range of cli-
mates (boreal to tropical). Our study hereby uses the process-based ecosystem model
ecosys to simulate WTD effects on net CO₂ exchange of a tropical peat swamp forest
at Palangkaraya, Central Kalimantan, Indonesia (Hirano et al., 2007). These effects are
20 summarized in modelling hypotheses during three seasonal hydroperiods as follows:

1. Shallow WTD in the rainy season (November–April) causes lower net ecosystem productivity (NEP) mainly through less CO₂ fixation due to reduced nutrient availability and uptake caused by slower nutrient transformation and root growth and uptake resulting from slower O₂ diffusion through wet soils.
2. When WTD increases during the early dry season (May–July), more rapid O₂ transport into larger unsaturated soil zones enables faster root growth and microbial nutrient transformations that in turns results in more rapid root nutrient uptake and CO₂ fixation which contributes to a higher NEP. Increased O₂ availability

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in this hydroperiod may, however, result in more rapid aerobic decomposition in deeper peat layers. Drying of surface residues and near surface peat layers at the same time can reduce surface and near surface soil respiration thereby offsetting the increase in deeper peat respiration, resulting in no net increase of R_e .

3. Deeper WTD during the late dry season (August–October), causes greater desiccation of near surface peat which forces declines in root and canopy water potentials, and consequently in canopy conductance and CO₂ fixation, thereby reducing NEP. Further deepening of the aerobic peat zone during this hydroperiod may lead to an increase in deeper peat respiration which exceeds reduction in near surface peat respiration through desiccation, raising R_e and further lowering NEP.

2 Methods

2.1 Model development

2.1.1 General

Ecosys is a general purpose terrestrial ecosystem model that simulates 3-D soil-microbes-plant-atmosphere water, energy, C and nutrient (N, P) transfer schemes (Grant, 2001). Details of the key algorithms in *ecosys* are given in the supplementary materials from Appendices A to H with definitions of the terms and references. Algorithms governing WTD effects on net ecosystem CO₂ exchange that are related to our modelling hypotheses are described in the following sections. For simplicity and clarity we have not put the equations within the text. Instead we have cited the equations within square brackets with the letter representing a particular appendix in the Supplement.

2.1.2 Heterotrophic respiration

Organic transformations in *ecosys* occur in five organic matter-microbe complexes (coarse woody litter, fine non-woody litter, animal manure, particulate organic C (POC), and humus), each of which consists of five organic states (three decomposition substrates: solid organic C, sorbed organic C and microbial residue C, as well as the decomposition product: DOC, and the decomposition agent: microbial biomass) in a surface residue layer and in each soil layer. The decomposition rates of each of the three substrates and resulting production of DOC in each complex is a first-order function of the active biomasses (M) of diverse heterotrophic microbial functional types, including obligate aerobes (bacteria and fungi), facultative anaerobes (denitrifiers), obligate anaerobes (fermenters), heterotrophic (acetotrophic) and autotrophic (hydrogenotrophic) methanogens, and aerobic and anaerobic heterotrophic diazotrophs (non-symbiotic N_2 fixers) [A1, A2]. Decomposition rates are calculated from the fraction of substrate mass colonized by M [A4]. Growth of M by each microbial functional type [A25] is calculated from its uptake of DOC [A21], driven by energy yields from growth respiration (R_g) [A20] remaining after subtracting maintenance respiration (R_m) [A18] from heterotrophic respiration (R_h) [A11] driven by DOC oxidation [A13]. This oxidation may be limited by microbial O_2 reduction [A14] driven from microbial O_2 demand [A16] and constrained by O_2 diffusion calculated from aqueous O_2 concentrations in soil ($[O_{2s}]$) [A17]. Values of $[O_{2s}]$ are maintained by convective-dispersive transport of O_2 from the atmosphere to gaseous and aqueous phases of the soil surface layer [D15], by convective-dispersive transport of O_2 through gaseous and aqueous phases in adjacent soil layers [D16, D19], and by dissolution of O_2 from gaseous to aqueous phases within each soil layer [D14a].

With shallower WTD during the rainy season, air-filled porosity (θ_g) above the water table may decline to values at which low O_2 diffusivity in the gaseous phase (D_g) [D17] may reduce gaseous O_2 transport [D16], while θ_g below the water table is zero and so prevents gaseous O_2 transport. During this hydroperiod, $[O_{2s}]$ relies more on O_2 trans-

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port through the slower aqueous phase [D19]. A consequent decline in $[O_{2s}]$ slows O_2 uptake [A17] and hence R_h [A14], R_g [A20] and growth of M [A25]. Lower M in turn slows decomposition of organic C [A1, A2] and production of DOC which further slows R_h [A13], R_g and growth of M . Although some microbial functional types can sustain DOC oxidation by reducing alternative electron acceptors (e.g. methanogens reducing acetate or CO_2 to CH_4 , and denitrifiers reducing NO_x to N_2O or N_2), lower energy yields from these reactions reduce R_g , and hence M growth, organic C decomposition and subsequent DOC production. Slower decomposition of organic C under low $[O_{2s}]$ also causes slower decomposition of organic N and P [A7] and production of dissolved organic nitrogen (DON) and phosphorus (DOP), which causes slower uptake of microbial nitrogen (N) and phosphorus (P) [A22] and hence M growth [A29]. This slower growth causes slower mineralization of NH_4^+ , NO_3^- and $H_2PO_4^-$ [A26], and hence lower aqueous concentrations of those ions.

Increase in θ_g with WTD drawdown during the dry season results in greater D_g [D17] and hence more rapid gaseous O_2 transport. A consequent rise in $[O_{2s}]$ increases O_2 uptake [A17] and hence R_h [A14], R_g [A20] and growth of M [A25]. Larger M in turn hastens decomposition of organic C [A1, A2] and production of DOC which further accelerates R_h [A13], R_g and growth of M . More rapid decomposition of organic C under adequate $[O_{2s}]$ in this hydroperiod also causes more rapid decomposition of organic N and P [A7] and production of DON and DOP, which increases uptake of microbial N and P [A22] and hence M growth [A29]. This rapid growth causes rapid mineralization of NH_4^+ , NO_3^- and $H_2PO_4^-$ [A26], and hence greater aqueous concentrations of those ions.

However, soil surface and near surface desiccation resulting from deepening WTD decreases soil water content and soil water potentials (ψ_s) which causes an increase in aqueous microbial concentrations $[M]$ [A15] in desiccated soil layers. This reduces microbial access to the substrate for decomposition through an algorithm for competitive inhibition of microbial exo-enzymes [A4] from Lizama and Suzuki (1990), thereby reducing R_h [A13].

2.1.3 Autotrophic respiration and growth

Growth of root and shoot phytomass in each plant population is calculated from its assimilation of the non-structural C product of CO₂ fixation (σ_C) [C20]. Assimilation is driven by R_g [C17] remaining after subtracting R_m [C16] from autotrophic respiration (R_a) [C13] driven by oxidation of σ_C [C14]. This oxidation in roots may be limited by root O₂ reduction [C14b] which is driven by root O₂ demand to sustain C oxidation and nutrient uptake [C14e], and constrained by O₂ uptake controlled by concentrations of aqueous O₂ in the soil ([O_{2s}]) and roots ([O_{2r}]) [C14d]. Values of [O_{2s}] are maintained by convective-dispersive transport of O₂ through soil gaseous and aqueous phases and by dissolution of O₂ from soil gaseous to aqueous phases. Values of [O_{2r}] are maintained by convective-dispersive transport of O₂ through the root gaseous phase [D16d] and by dissolution of O₂ from root gaseous to aqueous phases [D14b] through processes analogous to those described under Sect. 2.1.2 above. This transport depends on species-specific values used for root air-filled porosity (θ_{pr}) [D17b].

Low θ_g with shallow WTD during the rainy season reduces soil O₂ transport, forces root O₂ uptake to rely more on [O_{2r}] and hence on root O₂ transport determined by θ_{pr} . If this transport is inadequate, decline in [O_{2r}] slows root O₂ uptake [C14c, d] and hence R_a [C14b], R_g [C17] and root growth [C20b]. Increased θ_g with WTD drawdown during the dry season, however, facilitates rapid D_g which allows root O₂ demand to be almost entirely met from [O_{2s}] [C14c, d].

2.1.4 Gross primary productivity

By reducing root O₂ uptake, shallow WTD slows root growth [C20b] and root N and P uptake [C23b, d, f]. Root N and P uptake in this hydroperiod is further slowed by reductions in aqueous concentrations of NH₄⁺, NO₃⁻ and H₂PO₄⁻ [C23a, c, e] from slower mineralization of organic N and P as described in Sect. 2.1.2 above. Slower root N and P uptake in turn reduces concentrations of non-structural N and P products of root

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uptake (σ_N and σ_P) with respect to that of σ_C in leaves [C11], thereby slowing CO_2 fixation [C6] and hence GPP.

Increased availability of $[\text{O}_{2s}]$ with WTD drawdown during the dry season hastens root O_2 uptake and so enables rapid root growth and N and P uptake as discussed in Sect. 2.1.3 above. Increased root growth and N and P uptake is further stimulated by increased aqueous concentrations of NH_4^+ , NO_3^- and H_2PO_4^- [C23a, c, e] from rapid mineralization of organic N and P during this hydroperiod as described in Sect. 2.1.2 above. Greater root N and P uptake in turn increases concentrations of σ_N and σ_P with respect to σ_C in leaves [C11], thereby facilitating rapid CO_2 fixation [C6] and hence GPP.

With deeper WTD during the late dry season, GPP is not limited by root and microbial growth and nutrient uptake as discussed above. However, GPP in this hydroperiod can be adversely affected by water stress. When WTD deepens past a certain point, inadequate capillary rise [D9a] causes near-surface peat desiccation, reducing soil water potential (ψ_s) and increasing soil hydraulic resistance (Ω_s) [B9], forcing lower root, canopy and turgor (ψ_r , ψ_c and ψ_l) potentials [B4] and hence lower g_s [B2b] to be calculated when equilibrating plant water uptake with transpiration (T) [B14]. Lower g_s in turn reduces CO_2 diffusion into the leaves thereby reducing CO_2 fixation [C6] and hence GPP during this hydroperiod.

Thus WTD effects on R_h , R_a and GPP in *ecosys* are not parameterized from ecosystem level observations, but instead are governed by basic processes of O_2 transport and uptake; root and microbial energy yields, growth and nutrient uptake; and stomatal regulation controlled by root water uptake parameterized from independent research.

2.2 Modelling experiment

2.2.1 Site conditions

The *ecosys* algorithms for simulating WTD effects on net ecosystem CO_2 exchange were tested against the measurements over Palangkaraya Peat Swamp Forest (PPSF),

Central Kalimantan, Indonesia ($2^{\circ}20'42''$ S and $114^{\circ}2'11''$ E). The site is a tropical bog peatland formed mainly by roots and remains of trees where the major source of water and nutrient inputs is through precipitation. Vegetation of these peatlands includes evergreen overstorey trees and dense understorey of dominant tree seedlings with no mosses. These peatlands were drained by excavating drainage canals approximately 4 yr before the measurements started in 2002 at a flux station established in PPSF. Peat depth around the flux tower site was about 4 m. Detailed description of the site as well as the procedures of eddy covariance (EC) CO_2 flux measurements and quality control and other supplementary measurements can be found in Hirano et al. (2007).

2.2.2 Model runs

For our modelling experiment, the PPSF landscape was represented by one hummock and one hollow grid cell each of which had a dimension of $1 \text{ m} \times 1 \text{ m}$. Both of the grid cells had identical soil properties except that the hollow grid cell had a fibric layer thinner by 0.15 m than the hummock cell to represent the average site micro-topography described by Jauhiainen et al. (2008) (Table 1). Physical and hydrological characteristics of the PPSF peatland and their representation in our modelling study were described in our concurrent paper on modelling seasonal variation in WTD and surface energy exchange over PPSF (Mezbahuddin et al., 2013). Very high C : N and N : P ratios with low pH are typical characteristics of tropical peatlands which were represented in our modelling experiment by inputs measured either at the same site or at similar surrounding sites (Table 1). Both hummock and hollow grid cells were seeded with evergreen tropical rainforest over- and under-storey vascular vegetation using the same plant functional types used in earlier studies (Grant et al., 2009), except that θ_{pr} [D17d] was raised to 0.2 to represent peatland plant adaptation (Visser et al., 2000). These peatlands under study are generally devoid of mosses and hence we did not simulate any moss species. The model was then run for 44 yr under repeating 4 yr sequences of hourly weather data (solar radiation, air temperature, wind speed, humidity and precipitation) recorded at the site from 2002 to 2005. This period allowed CO_2 exchange

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in the model to achieve stable values through successive weather sequences. Model results for the final 4 yr of the run were compared with measurements at PPSF from 2002–2005.

2.2.3 Model validation

Hourly CO₂ fluxes modelled over the hummock and the hollow were spatially averaged to represent a 50 : 50 hummock-hollow ratio as described by Jauhiainen et al. (2008), and then regressed on hourly measured EC CO₂ fluxes for each year from 2002–2005. Model performance was evaluated from regression intercepts ($a \rightarrow 0$), slopes ($b \rightarrow 1$) and coefficients of determination ($R^2 \rightarrow 1$) for each study year in order to test whether there was any systematic divergence between the modelled and gap-filled CO₂ fluxes. This test is very important since any small divergence between hourly modelled and gap-filled CO₂ fluxes can result in a large divergence between modelled and EC-gap filled annual estimates.

2.2.4 Model sensitivity to drained vs. undrained WTD

WTD in the modelled landscape in *ecosys* arises from water exchanges with the atmosphere in the forms of vertical water influxes (e.g. precipitation) and effluxes (e.g. evapotranspiration) through surface boundary and in the forms of recharge and discharge with an adjacent ecosystem through lateral boundary. The distance and hydraulic gradient between modelled WTD and a set external water table depth (WTD_x, representing mean water table depth of the adjacent watershed) generally governs the rate of lateral recharge and discharge. All modelled WTDs were spatially averaged for the hummock and the hollow grid cell. Since the field measured WTDs were with reference to the hollow surface, all the WTDs and WTD_xs in this study are henceforth referenced from the hollow surface. The WTD_x for the simulation in this study was set at 0.45 m below the hollow surface (i.e. 0.60 m below the hummock surface) so as to represent the average watershed WTD for our drained site (Mezbahuddin, et al., 2013). Since drainage

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is a key disturbance reported to alter WTD and hence C balance of Southeast Asian peatlands (Couwenberg et al., 2009; Hooijer et al., 2010), we performed a parallel simulation with WTD_x raised from 0.45 m below the hollow surface to 0.15 m above the hollow surface (i.e. level with the hummock surface) with everything else unchanged to represent the undrained condition. The difference between the two WTD_x s was based on the maximum observed difference between mean annual WTDs over our drained site and a nearby similar undrained site as reported by Hirano et al. (2012). The purpose of this undrained simulation was to test the sensitivity of the modelled NEPs to the difference in drained vs. undrained WTD.

3 Results

3.1 Modelled vs. measured ecosystem net CO₂ fluxes

Regressions of hourly modelled vs. measured net ecosystem CO₂ fluxes gave intercepts within $1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ of zero, and slopes within 0.1 of one, indicating minimal bias in modelled values for all years of the study except 2005 when modelled fluxes gave a positive bias slightly greater than $1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 2). Values for coefficients of determination (R^2) and RMSD were ~ 0.8 ($P < 0.0001$) and $\sim 5.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 2). Much of the unexplained variance in EC-measured CO₂ fluxes could be attributed to a random error of ca. 20 % in EC methodology (Wesely and Hart, 1985). This attribution was corroborated by root mean squares for error (RMSE) in EC measurements, calculated for forests with similar CO₂ fluxes from Richardson et al. (2006) that were similar to RMSD. These similar values indicated that further constraint in model testing could not be achieved without further precision in EC measurements. Regressions of modelled vs. gap-filled CO₂ fluxes gave larger slopes than those of modelled vs. EC measured CO₂ fluxes despite higher R^2 and lower RMSDs indicating the diurnal variation of the gap-filled fluxes was systematically smaller than that of the modelled CO₂ fluxes (Table 2).

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3.2 Seasonal variation in WTD and daily net ecosystem CO₂ exchange

WTD in PPSF showed distinct seasonality in each year from 2002 to 2005 (Mezbahuddin et al., 2013). Observed WTDs were typically within 0.3 m of the hollow surface during the rainy season (November–April) increasing to 0.5–0.8 m below the hollow surface at the onset of the dry season (May–July) (Figs. 1c, 2c, 3c and 4c). During late dry seasons (August–October) observed WTD fell below 1.0 m from the hollow surface in all years and below 1.5 m in drier years. Increasing amounts and declining seasonality of precipitation caused the WTD to decline more and more gradually from the driest year 2002 to the wettest year 2005.

NEP modelled and measured over PPSF showed a distinct seasonality, with negative values over shallow WTD (within 0.3 m below the hollow surface) during the rainy season, near neutral or slightly positive values over intermediate WTD (0.5–0.8 m below the hollow surface) during the early dry season, and returning to negative values over deep WTD (> 1.0 m below the hollow surface) in the late dry season during each year from 2002 to 2005 (Figs. 1a, 2a, 3a and 4a). These values indicated that the ecosystem was a C source when the WTD was shallow, became a smaller source or C neutral when WTD receded to an intermediate position, and again became a large source of C when WTD further deepened (Figs. 1–4) (Table 3). The decline in late dry season NEP during 2002 (Fig. 1a) might have been made larger by a decline in GPP with reduced net radiation (R_n) (Fig. 1b) caused by smoke haze shading from regional forest fires as reported by Hirano et al. (2007).

In addition to the successful simulations of long term seasonal cycle of NEP, *ecosys* was adequately sensitive to the short-term variations in NEP caused by changes in weather. There were several short-term dips in EC-gap filled NEP e.g. DOY 160–170 in 2002 (Fig. 1), DOY 258–262 in 2003 (Fig. 2), DOY 143–146 in 2004 (Fig. 3), DOY 259–262 in 2005 (Fig. 4) etc. caused by smaller CO₂ influxes and larger CO₂ effluxes on cloudy and rainy days. These dips were modelled from less CO₂ fixation under

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data. During 2005, simulated night-time CO₂ effluxes showed a decrease with WTD drawdown from rainy to early dry season and an increase with further WTD recession from early to late dry season (Fig. 5) similar to the trends in other years. Again, considerable scatter in night-time EC CO₂ effluxes (5–12 μmol m⁻² s⁻¹ in Fig. 5) with little fluctuations in boundary conditions (e.g. air temperature and wind speed) during the shallow WTD hydroperiod in 2005 could not be modelled which resulted in a divergence of modelled vs. measured CO₂ effluxes during this hydroperiod. Our modelled effects of WTD on seasonal variations in diurnal CO₂ effluxes were further corroborated by little decrease or no change in hourly EC-gap filled CO₂ effluxes with WTD drawdown below 0.5–0.8 m in early dry seasons and an increase in effluxes with further WTD drawdown in late dry seasons as shown by Hirano et al. (2012) for our study site.

Significant ($P < 0.0001$) quadratic relationships between EC-derived (Hirano et al., 2007) and simulated monthly NEP, GPP and R_e vs. monthly averaged WTD during 2002–2004 (Fig. 6) further corroborate the effects of seasonal variations in WTD on seasonal variations in diurnal ecosystem CO₂ fluxes as discussed above. Lower monthly modelled and EC-gap filled NEP under shallow WTD condition was mainly caused by lower GPP (Fig. 6). With gradual drawdown of WTD, monthly modelled and simulated NEP became larger with a combination of higher GPP and little decrease or no change in R_e (Fig. 6). Further WTD drawdown caused monthly modelled and EC-gap filled NEP to drop again with a combination of a decrease in GPP and a concurrent rise in R_e (Fig. 6).

3.4 Interannual variation in WTD and net ecosystem CO₂ exchange

Interannual variation in NEP over PPSF from 2002 to 2005 was caused by interannual variation in WTD. A gradual rise in both modelled and EC gap-filled annual NEP was found from 2002 to 2005 with progressively shallower WTD (Table 4). However, modelled NEPs were considerably lower than the EC gap-filled estimates of NEP in 2003 and 2004 (Table 4). This can be explained by the presence of large number of gap-filled CO₂ fluxes (~ 65 % of CO₂ fluxes from 2002 to 2005) in EC-derived annual

NEP estimates. These gap-filled fluxes, mostly nighttime effluxes, were systematically smaller than the modelled fluxes as shown by slopes $> 1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ and negative intercepts in modelled vs. gap-filled flux regressions during those years (Table 2). The decreasing WTD from 2002 to 2005 (Figs. 1–4) resulting from the increase in annual precipitation (Table 4) suppressed the modelled annual GPP, R_a and R_h and hence RE (Table 4). Similar declines in modelled GPP and R_a with shallower WTD left modelled NPP almost unchanged throughout the study period (Table 4). However, suppression of annual R_h by shallow WTD caused annual NEP to become gradually less negative from 2002 to 2005 (Table 4). An increase in modelled CH_4 emissions with declining WTD was also found from 2003–2005 (Table 4).

4 Discussion

4.1 Hypothesis 1: WTD and NEP during rainy season

A shallower aerobic zone (Fig. 7) and resulting lower $[\text{O}_{2s}]$ modelled during shallow WTD (within 0.3 m of the hollow surface) hydroperiod reduced rates of C oxidation by microbial populations [A13-A14] which limited microbial growth [A25] and hindered nutrient mineralization [A26]. Moreover, low $[\text{O}_{2s}]$ caused by shallow WTD forced $[\text{O}_{2r}]$ to depend predominantly upon O_2 transport through root gaseous phase controlled by θ_{pr} as discussed in Sect. 2.1.3. Our input of 0.20 for θ_{pr} to represent peatland species adaptation (Visser et al., 2000), however, was not enough to maintain adequate $[\text{O}_{2r}]$ during this hydroperiod. Lower $[\text{O}_{2r}]$ suppressed rates of C oxidation by root and mycorrhizal populations [C14a, b], slowing root and mycorrhizal growth [C20b] and plant N and P uptake [C23b, d, f]. Root and mycorrhizal growth in this hydroperiod were largely confined to the shallow aerobic zone, thus limiting the soil volume from which N and P uptake could occur. Slow N and P uptake in turn reduced σ_N and σ_P with respect to σ_C in leaves [C11], thereby slowing CO_2 fixation [C6] and hence GPP

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in the model as discussed in Sect. 2.1.4. This slowing was also apparent in the lower CO_2 influxes measured with shallow WTD (Fig. 5).

These results from the model are consistent with those from Milner (2009) who measured lower tree growth with shallower WTD while studying soil fertility effects on vegetation diversity of tropical peat swamp forests nearby our site, which she attributed to less availability of N and P under wet soil conditions. Similar suppression of productivity by shallow WTD has also been reported in other experimental (Sulman et al., 2010; Flanagan and Syed, 2011) and modelling studies (Grant et al., 2012a; Sulman et al., 2012) across northern boreal peatlands. This suppression of productivity with shallow WTD was also apparent in higher modelled and measured Bowen ratios ($\beta = H/LE$) resulting from lower g_s required to conserve $c_c : c_a$ ratios with slower CO_2 diffusion (Mezbahuddin et al., 2013).

During shallow WTD in rainy seasons, $[\text{O}_{2s}]$ below the water table was almost zero (Fig. 7) and well below the Michaelis–Menten constant (K_m) used for microbial, root and mycorrhizal uptake in *ecosys* [A17a, C14c] so that DOC oxidation coupled with O_2 reduction was strongly limited by $[\text{O}_{2s}]$. In these layers, DOC oxidation was coupled with DOC reduction by anaerobic heterotrophic fermenters, which yielded much less energy than did O_2 reduction and so resulted in slower microbial growth [A25] and R_h [A13] as discussed in Sect. 2.1.2. This DOC reduction also generated CO_2 , H_2 and acetate that drove CH_4 production [G1, G7, G12] and enabled *ecosys* to model larger CH_4 emissions in the wetter years with shallower WTD (Table 4). However, $[\text{O}_{2s}]$ above the water table during shallow WTD hydroperiod was well above K_m (Fig. 7) used for simulated microbial, root and mycorrhizal O_2 uptake so that R_h in this zone was not limited by $[\text{O}_{2s}]$. Moreover, frequent precipitation throughout this hydroperiod kept the surface residue layer moist and maintained optimum heterotrophic microbial concentrations for decomposition [A3, A5] and growth [A15], driving surface CO_2 flushes.

Shallow WTD during the rainy season thus caused lower NEP (Figs. 1a, 2a, 3a and 4a) (Table 2) to be modelled over PPSF through reducing GPP and hence net CO_2 uptake (Figs. 5–6).

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4.2 Hypothesis 2: WTD and NEP during early dry seasons

Increased availability of $[O_{2s}]$ with an intermediate WTD (0.5–0.8 m below the hollow surface) during the early dry season almost entirely met root O_2 demand and hence facilitated rapid and deeper root growth [C20b] and N and P uptake [C23b, d, f]. Uptake was further stimulated by more rapid mineralization of organic N and P [C23a, c, e] driven by more rapid microbial O_2 uptake [A17], C oxidation [A1, A2], growth [A25] and R_h [A13, A20] as described in Sects. 2.1.2 and 2.1.3. Greater root N and P uptake in turn increased $\sigma_N : \sigma_C$ and $\sigma_P : \sigma_C$ in leaves [C11], thereby facilitating rapid CO_2 fixation [C6] and hence GPP as discussed in Sect. 2.1.4. Increased GPP with WTD drawdown was also measured by Sulman et al. (2009) and Flanagan and Syed (2011) for northern boreal peatlands. Improved plant nutrient status was also apparent in lower measured and modelled β resulting from greater g_s as described in our concurrent paper on modelling WTD effects on surface energy exchange over PPSF (Mezbahuddin et al., 2013).

A deeper aerobic zone and resulting increase in $[O_{2s}]$ during the intermediate WTD hydroperiod in the early dry season (Fig. 7) stimulated R_h [A13, A20] as described above. However, this increase in deeper R_h was fully, and sometimes more than fully, offset by decreases in surface and near-surface R_h caused by near-surface peat desiccation which reduced microbial access to substrate for decomposition [A15] (Sect. 2.1.2). This enabled *ecosys* to simulate CO_2 effluxes measured by EC during intermediate WTD hydroperiods that were similar to or lower than those in shallow WTD hydroperiods. This modelling hypothesis in *ecosys* was further corroborated by soil CO_2 effluxes measured with surface chambers by Sundari et al. (2012) over our study site and by Jauhiainen et al. (2008) over a nearby similar site during intermediate WTD hydroperiods that were similar or lower than those in shallow WTD hydroperiods. Declines in R_h due to near surface peat desiccation were also modelled by Dimitrov et al. (2010) and Grant et al. (2012a) by using the same model *ecosys* over two contrasting northern boreal peatlands.

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Intermediate WTD during the early dry season thus caused higher NEP (Figs. 1a, 2a, 3a and 4a) (Table 2) over PPSF by a combination of increased GPP and unchanged or slightly decreased R_e (Figs. 5–6).

4.3 Hypothesis 3: WTD and NEP during late dry seasons

GPP during late dry season with deep WTD (> 1.0 m below the hollow surface) was limited not by plant nutrient status but by plant water stress. Inadequate recharge of near surface peat layers through a combination of less precipitation and slow capillary rise [D9a] during this hydroperiod reduced ψ_s and increased Ω_s [B9] in those layers where most of the plant roots were. These changes in turn forced higher Ω_r [B10], lower ψ_r , ψ_c , ψ_t [B4] and g_s [B2b] (Mezbahuddin et al., 2013) and hence slower CO_2 diffusion [C6] through stomata and consequently less GPP (Sect. 2.1.4). Similar reductions in GPP due to plant water stress were reported during the late dry season in Hirano et al. (2012) for a drained and burnt tropical peat swamp forest.

Deeper peat respiration during the deep WTD hydroperiod greatly increased due to abundant $[\text{O}_{2s}]$ in the deeper aerobic zone (Fig. 7) and resulting rapid microbial O_2 uptake [A17], C oxidation [A1, A2], growth [A25] and R_h [A13, A20] as discussed in Sect. 2.1.2. This increase in deeper R_h was greater than the reduction in surface and near-surface microbial respiration due to desiccation as discussed in Sect. 4.2, which led to a net increase in R_e during this hydroperiod. This modelling hypothesis was further corroborated by larger soil CO_2 effluxes measured by Sundari et al. (2012) over our study site during the deep WTD hydroperiod than during the rest of the year. Cai et al. (2010) also measured a stimulation of respiration over a northern boreal peatland with deepening of WTD.

Deep WTD during the late dry season thus caused lower NEP (Figs. 1a, 2a, 3a and 4a) (Table 2) by a combination of reduced GPP and increased R_e (Figs. 5–6).

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4.4 Modelling WTD effects on annual tropical peatland C balance

At an annual time scale, reductions in both GPP and R_e with a gradually shallower WTD from 2002 to 2005 in *ecosys* were not corroborated by changes in GPP and R_e partitioned from gap-filled EC fluxes by Hirano et al. (2007) (Table 4) although monthly partitioned GPP and R_e showed the similar seasonal trends as those modelled (Fig. 6). This discrepancy may have occurred because in *ecosys* basic processes representing dynamic WTD effects on root and microbial respiration, nutrient transformation and microbial and plant nutrient uptake above were explicitly simulated based on independent research as described in Sects. 4.1 and 4.2. On the other hand, gap-filling of EC fluxes to derive GPP and R_e was based on numerical relationships with environmental variables e.g. soil water content, soil temperature, vapor pressure deficit and radiation (Hirano et al., 2007) without considering complex WTD effects on soil physical and biological processes that govern ecosystem physiology. The gap-filled fluxes used in partitioning were consistently lower by $\sim 12\%$ than the modelled fluxes (Table 2). These lower values caused annual GPP and R_e derived from the partitioned fluxes to be lower by 21% on average from those modelled during 2002–2004 (Table 4). Grant et al. (2009) also modelled GPP and R_e higher than the partitioned fluxes by similar magnitudes while modelling NEP over an Amazonian rainforest by using *ecosys*.

The components of modelled annual C balance were also comparable with biometric measurements and estimations from other studies on similar ecosystems. Modelled net primary productivity (NPP) was comparable with values estimated for Amazonian rainforests and oil palm plantations in tropical peatlands (Table 4). Modelled R_h was comparable with R_h measured for a mature *Acacia* plantation on drained Indonesian peatlands (Table 4). Modelled annual CH_4 emissions were substantially higher than what was measured on the site ca. $1.1\text{--}1.3\text{ g CH}_4\text{ - C m}^{-2}\text{ yr}^{-1}$ (Hirano et al., 2009) (Table 4). However, those were very close to the range of mean annual CH_4 emissions reported from other Southeast Asian peatlands (Table 4).

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4.5 Drained vs. undrained seasonal variation in modelled WTD and NEP

Large negative simulated and EC-gap filled annual NEPs modelled and measured during 2002–2005 (Table 4) may reflect disturbance effects of drainage in 1998 which increased WTD. In order to examine the drainage effects on modelled NEP we performed a model sensitivity test to drained vs. undrained conditions as described in Sect. 2.2.4. During the rainy seasons (November–April) from 2002–2005, simulated undrained WTD was always above the hollow surface as opposed to the simulated drained WTD where water table never rose above the hollow surface (Fig. 8). The undrained WTD remained ~ 0.5 m shallower than the drained WTD, and so altered the timing and intensity of the different hydroperiods (Fig. 8). The seasonal variation in simulated undrained WTD followed that in a nearby similar undrained tropical peat swamp forest (Fig. 8).

NEP modelled in the undrained peatland was higher than that in the drained peatland during the rainy seasons (November–April) (Fig. 9). During 2002 and 2003 undrained WTDs during the late dry seasons were deep enough to simulate negative NEPs similar to those with drained WTDs (Fig. 9). However in 2004 and 2005, shallower WTD during late dry seasons in the undrained simulation caused higher NEPs (less negative) than those in the drained simulation (Fig. 9). Hirano et al. (2012) also found higher NEPs in the undrained site than in the drained site mainly during the rainy seasons. They also found almost similar NEPs for drained vs. undrained peatland during the prolonged dry seasons with deep WTD. Late dry season NEPs in the undrained site in their study were higher than those in drained site only during the wettest dry seasons (e.g. 2005). Seasonality in WTD is thus a key control of net CO_2 exchange over PPSF irrespective of drainage further highlighting the research needs that led to the present modelling effort. Large spikes of simulated negative NEPs during the transitions of WTD from above to below the hollow surface (e.g. between DOY 130 and 140, 140 and 150, 170 and 180, and 140 and 150 during 2002, 2003, 2004 and 2005 respectively in Fig. 9) arose from large flushes of soil CO_2 due to rapid degassing of soil

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the hollow surface could bring the undrained peatland ecosystem to C neutrality. In line with their simple prediction, a much more sophisticated process-based undrained simulation by *ecosys* in our study resulted in a near C neutral NEP during the wettest year 2005 with a mean annual WTD of 0.10 m above the hollow surface (Table 5).

C losses modelled in the undrained simulation and observed in the undrained peat swamp forest, however, may be a recent phenomenon since a long term apparent C accumulation study showed that Central Kalimantan peatlands have been accumulating C at a rate of $31 \text{ g C m}^{-2} \text{ yr}^{-1}$ for last $\sim 12\,000$ yr (Dommain et al., 2011) and that the peatlands around our study site have been accumulating C at a rate of $56 \text{ g C m}^{-2} \text{ yr}^{-1}$ for last $\sim 20\,000$ yr (Page et al., 2004). One of the main reasons behind the modelled negative NEPs even in the undrained simulation may be that the precipitation within our study period (2002–2005) was less than the long term average, which led to deeper WTD than the long term mean. The wettest year in our study period (2005) experienced a total annual precipitation which was considered as “normal” annual precipitation (2570 mm yr^{-1}) measured over Indonesian Borneo during 1994–2004 (Takahashi et al., 2004). The year 1999 was the wettest within their measurement period with an annual precipitation of 3788 mm that caused the water table to remain above the ground throughout the year (Wösten et al., 2008). This speculation of large C losses due to reduced precipitation and consequent deeper WTD in recent years can be further corroborated by the cessation of Central Kalimantan peat growth during last ~ 5000 yr as reported by Dommain et al. (2011) due to WTD drawdowns caused by increased El Niño frequency and intensity.

5 Conclusions

Ecosys successfully simulated the effects of WTD fluctuations on seasonal and inter-annual variations in net ecosystem CO_2 exchange over PPSF (Table 2). In order to simulate key responses of GPP and R_e to variations in WTD, *ecosys* required sophis-

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ticated coupling of basic ecosystem processes parameterized by independent basic research as follows:

1. Shallow WTD during rainy seasons reduced productivity by explicitly modelling slower convective-dispersive O_2 transport through soils and roots and hence slower root O_2 uptake, slower soil N and P transformations [A26], slower root N and P uptake and growth [C23], and consequently lower leaf nutrient status [C11] and slower CO_2 fixation [C6] (Sects. 2.1.3. and 2.1.4) (Figs. 5 and 6b).
2. WTD drawdown during early dry seasons increased deeper peat respiration due to better aeration by explicitly modelling higher $[O_{2s}]$ [A17] due to more rapid O_2 transport through soils, and hence more rapid microbial and root oxidation-reduction reactions [A3, A5], greater microbial O_2 uptake and energy yields [A20] driving more rapid microbial growth [A25] and respiration [A13, A14, A20] (Sect. 2.1.2) (Figs. 5 and 6c).
3. Deeper WTD during late dry seasons suppressed productivity through plant water stress by explicitly modelling declines in g_s and their effects on CO_2 fixation from hydraulically driven water transport along soil-plant-atmosphere water potential gradients [B1-B14] (Sect. 2.1.4) (Figs. 5 and 6b).

This study showed for the first time the application of detailed process based modelling in capturing non-linear WTD-tropical peatland CO_2 exchange interactions, as recommended by Murdiyarso et al. (2010). The findings of this study showed that the duration and intensity of the dry season with deeper WTD had profound effects on tropical peatland CO_2 emissions irrespective of disturbance (e.g. drainage). This has an important implication in terms of the fate of tropical peatland C storage under future climate change scenarios since Li et al. (2007) predicted a general drying trend and consequent WTD drawdown over Southeast Asian peatlands during this century using 11 land surface models. Moreover, the response of tropical peatland CO_2 exchange to disturbance (e.g. drainage) was also investigated by our model sensitivity test for

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drained vs. undrained peatlands. Insights gained from our modelling effort thus can improve our predictive capacity for the effects of WTD fluctuations arising from interactions between seasonality in precipitation and artificial drainage on tropical peatland C balance. This capacity might be very important for planning long term tropical peatland rehabilitation projects and mapping peat C sequestration for current REDD+ scheme.

Supplementary material related to this article is available online at <http://www.biogeosciences-discuss.net/10/13353/2013/bgd-10-13353-2013-supplement.pdf>.

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Table 1. Key soil properties as *ecosys* inputs, Palangkaraya Peat Swamp Forest, Indonesia*.

D_{hummm} (m)	D_{holl} (m)	TOC (g kg ⁻¹)	TON (g Mg ⁻¹)	TP (g Mg ⁻¹)	pH	CEC (cmol+ kg ⁻¹)
0.01				256		
0.05				238		
0.15			18 000	192	3.78	
0.16	0.01					
0.20	0.05			143		
0.25	0.10					
0.40	0.25			115		
0.60	0.45	500				37.5
0.80	0.65					
1.00	0.85			49		
1.20	1.05		14 000		3.71	
1.40	1.25					
1.60	1.45					
1.80	1.65					
4.00	3.85					

* D_{hummm} = depth from hummock surface, D_{holl} = depth from hollow surface, TOC = Total organic C (maximum limit of input for TOC concentration in *ecosys* is used from an average of TOC values for a 4 m deep tropical peat column measured by Page et al., 2004), TON = Total organic nitrogen and TP = total phosphorus (Values obtained from Page et al., 1999), pH and CEC = Cation exchange capacity (Values obtained from Sayok et al., 2007).

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Table 2. Modelled vs. measured net ecosystem CO₂ fluxes, Palangkaraya Peat Swamp Forest, Indonesia*.

Year	Precipitation (mm yr ⁻¹)	<i>n</i>	<i>a</i>	<i>b</i>	<i>R</i> ²	RMSD	RMSE
<i>Modelled vs. EC measured CO₂ fluxes recorded at <i>u</i>* > 0.17 ms⁻¹</i>							
2002	1852	3007	0.82	1.03	0.77	5.7	5.5
2003	2291	2595	0.11	1.05	0.83	4.9	5.9
2004	2560	3299	0.61	1.01	0.83	4.9	5.8
2005	2620	3164	1.09	1.01	0.81	5.2	5.6
<i>Modelled vs. gap-filled CO₂ fluxes</i>							
2002	1852	5753	0.23	1.19	0.93	2.5	–
2003	2291	6165	–0.51	1.14	0.92	2.8	–
2004	2560	5485	–0.76	1.08	0.92	2.6	–
2005	2620	5494	–0.35	1.10	0.93	2.3	–

* (*a*, *b*) from simple linear regressions of modelled on measured. *R*² = coefficient of determination and RMSD = root mean square for differences from simple linear regressions of measured on simulated. All measured values were recorded at *u** > 0.17 ms⁻¹. RMSE = root mean square for random errors in EC measurements calculated by inputting EC fluxes recorded at *u** > 0.17 ms⁻¹ into algorithms for estimation of random errors due to EC measurements developed for forests by Richardson et al. (2006).

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Table 3. Periodical changes in simulated (sim) and observed (obs) net ecosystem productivity (NEP) with variations in water table depth (WTD), Palangkaraya Peat Swamp Forest, Indonesia*.

Hydroperiod	Units		Year							
			2002		2003		2004		2005	
			sim	obs	sim	obs	sim	obs	sim	obs
SWT	T_a	°C	26.3		27.1		25.3		26.0	
IWT			27.8		26.6		25.4		26.6	
DWT			26.9		26.7		26.9		26.6	
SWT	P	mm 30d ⁻¹	270		147		466		606	
IWT			49		57		105		100	
DWT			11		108		73		105	
SWT	WTD	m	0.10		0.38	0.27	0.22	0.28	0.06	0.14
IWT			0.50		0.69	0.5	0.58	0.53	0.36	0.46
DWT			1.48	1.26	1.44	1.25	1.44	1.49	1.00	1.04
SWT	NEP	gCm ⁻² 30d ⁻¹	-65	-69	-49	-35	-54	-16	-71	-30
IWT			-6	-7	-1	8	-23	-6	-18	-19
DWT			-103	-138	-108	-79	-105	-94	-29	-41

* SWT = shallow WTD (DOY 1–30, 41–70, 11–40 and 41–70 during 2002, 2003, 2004 and 2005 respectively), IWT = intermediate WTD (DOY 121–150, 146–175, 181–210 and 121–150 during 2002, 2003, 2004 and 2005 respectively) and DWT = deep WTD (DOY 251–280, 251–280, 291–320 and 241–270 during 2002, 2003, 2004 and 2005 respectively) hydroperiods with comparable weather condition differing mainly by WTDs (Figs. 1–4); T_a = mean air temperature for each hydroperiod of 30 days; P = total precipitation per hydroperiod; WTD = mean water table depth in each hydroperiod; NEP = net ecosystem productivity in each hydroperiod, observed NEPs are calculated from hourly EC-gap filled net ecosystem CO₂ fluxes mentioned by Hirano et al. (2007).

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Table 4. Simulated (sim) and observed (obs) annual C balance, Palangkaraya Peat Swamp Forest, Indonesia^a.

	Units	Year								Values from other studies
		2002		2003		2004		2005		
		sim	obs	sim	obs	sim	obs	sim	obs	
Precipitation	mm yr ⁻¹	1852		2291		2560		2620		
Avg. WTD	m	0.77		0.73	0.56	0.59	0.52	0.45	0.52	
GPP		4201	3254	4164	3466	4109	3631	4040		
R_a		2909		2823		2760		2778		
NPP		1292		1341		1349		1262		900 ^b
										1200 ^c
R_h	g C m ⁻² yr ⁻¹	1901		1918		1777		1635		2182 ^d
R_e		4810	3848	4741	3844	4537	3907	4413		
NEP		-609	-594	-577	-378	-428	-276	-373		
CH ₄		21		12		13		19		0.2–15.5 ^e

^a WTD = water table depth, simulated and observed WTDs are averages of data used in Figs. 1c, 2c, 3c and 4c for 2002, 2003, 2004 and 2005 respectively, observed mean WTD for 2002 was not calculated due to the absence of any field observations for the first six months (Fig. 1c); GPP = gross primary productivity, observed GPP for each year was partitioned from EC-gap filled net ecosystem productivity estimates as found in Hirano et al. (2007); R_a = autotrophic respiration; NPP = net primary productivity (NPP = GPP - R_a); R_h = heterotrophic respiration; R_e = ecosystem respiration, observed R_e for each year was partitioned from EC-gap filled net ecosystem productivity estimates as found in Hirano et al. (2007); NEP = net ecosystem productivity (NEP = NPP - R_h), observed NEP for each year was calculated from hourly EC-gap filled CO₂ flux data mentioned by Hirano et al. (2007); and CH₄ = methane emissions.

^b for Amazonian rainforest (Chambers et al., 2004).

^c for oil palm plantations in tropical peatlands of Malaysia (Melling et al., 2008).

^d for a mature Acacia plantation in a drained Indonesian peatland with an average WTD of 0.8 m (Jauhiainen et al., 2012b).

^e average range for tropical southeast Asian peatlands (Hergoualc'h and Verchot, 2011).

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Table 5. Sensitivity of modelled annual C balance to drainage, Palangkaraya Peat Swamp Forest, Indonesia*.

Units		Year									
		2002		2003		2004		2005		Mean	
		dr	undr	dr	undr	dr	undr	dr	undr	dr	undr
WTD	m	0.77	0.22	0.73	0.17	0.59	0.11	0.45	-0.10	0.59	0.10
GPP		4201	3578	4164	3780	4109	3695	4040	3665	4123	3680
R_a		2909	2412	2823	2455	2760	2431	2778	2396	2818	2423
NPP		1292	1166	1341	1325	1349	1264	1262	1269	1311	1256
R_h	gCm ⁻² yr ⁻¹	1901	1595	1918	1636	1777	1382	1635	1320	1808	1483
R_e		4810	4007	4741	4091	4537	3813	4413	3716	4625	3907
NEP		-609	-429	-577	-311	-428	-118	-373	-51	-497	-227
CH ₄		21	35	12	23	13	30	19	44	16	33

* dr = drained condition with external water table depth (WTD_x) in the model set at 0.45 m below the hollow surface; undr = undrained condition with WTD_x set at 0.15 m above the hollow surface (i.e. level with the hummock surface); WTD = water table depth, values are the annual means of simulated WTD data in Fig. 8, positive values represent WTDs below hollow surface and the negative value represents WTD above the hollow surface; GPP = gross primary productivity; R_a = autotrophic respiration; NPP = net primary productivity (NPP = GPP - R_a); R_h = heterotrophic respiration; R_e = ecosystem respiration; NEP = net ecosystem productivity (NEP = NPP - R_h); and CH₄ = methane emissions.

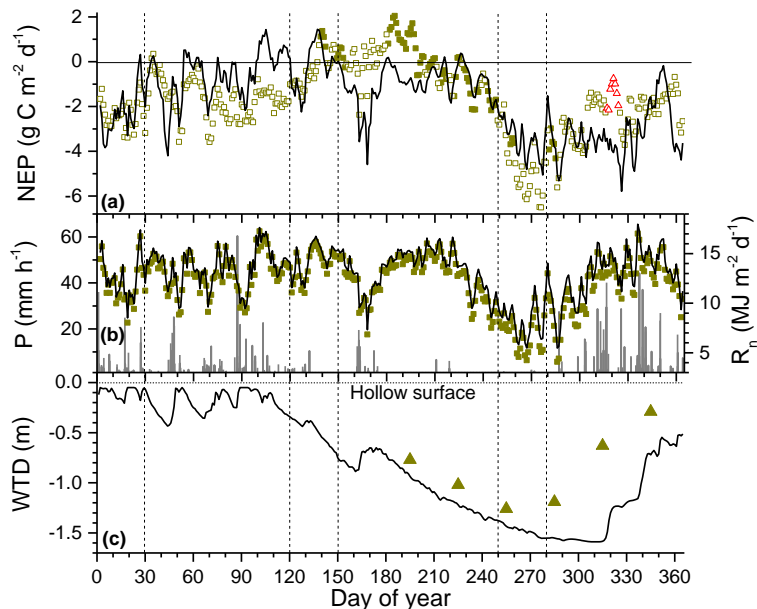


Fig. 1. (a) Three day moving averages of simulated (line) and EC-gap filled estimates (symbols) of net ecosystem productivity (NEP) (negative NEP means the ecosystem is a source and positive NEP means the ecosystem is a sink of C. Closed squares indicate sums of 24 values more than 1/2 of which were recorded at $u^* > 0.17 \text{ ms}^{-1}$, open squares indicate sums of 24 values more than 1/2 of which were gap-filled, and open triangles mean sums of 24 values all of which were gap-filled); (b) hourly measured precipitation (bars on left y-axis) and three day moving averages of simulated (line on right y-axis) and measured (symbols on right y-axis) net radiation (R_n); and (c) monthly measured (triangles) (values digitally obtained from Hirano et al., 2012) and daily modelled (line) water table depths (WTD) from hollow surface during 2002 over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. Negative values of WTD mean depths below the ground.

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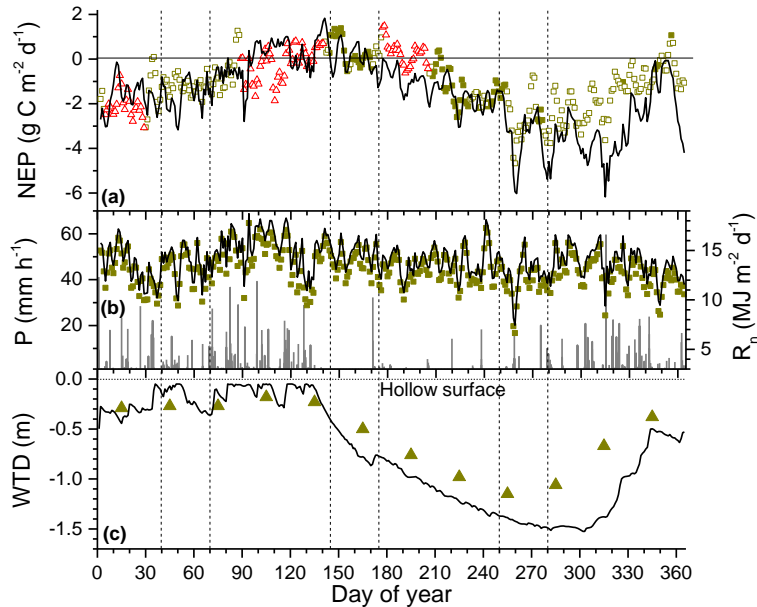


Fig. 2. (a) Three day moving averages of simulated (line) and EC-gap filled estimates (symbols) of net ecosystem productivity (NEP) (negative NEP means the ecosystem is a source and positive NEP means the ecosystem is a sink of C. Closed squares indicate sums of 24 values more than 1/2 of which were recorded at $u^* > 0.17 \text{ m s}^{-1}$, open squares indicate sums of 24 values more than 1/2 of which were gap-filled, and open triangles mean sums of 24 values all of which were gap-filled); (b) hourly measured precipitation (bars on left y-axis) and three day moving averages of simulated (line on right y-axis) and measured (symbols on right y-axis) net radiation (R_n); and (c) monthly measured (triangles) (values digitally obtained from Hirano et al., 2012) and daily modelled (line) water table depths (WTD) from hollow surface during 2003 over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. Negative values of WTD mean depths below the ground.

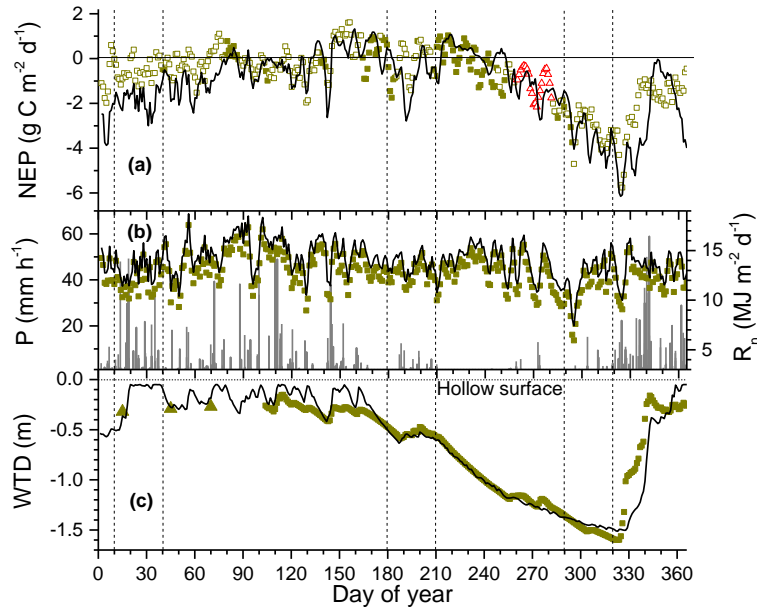


Fig. 3. (a) Three day moving averages of simulated (line) and EC-gap filled estimates (symbols) of net ecosystem productivity (NEP) (negative NEP means the ecosystem is a source and positive NEP means the ecosystem is a sink of C. Closed squares indicate sums of 24 values more than 1/2 of which were recorded at $u^* > 0.17 \text{ ms}^{-1}$, open squares indicate sums of 24 values more than 1/2 of which were gap-filled, and open triangles mean sums of 24 values all of which were gap-filled); (b) hourly measured precipitation (bars on left y-axis) and three day moving averages of simulated (line on right y-axis) and measured (symbols on right y-axis) net radiation (R_n); and (c) monthly measured (triangles) (values digitally obtained from Hirano et al., 2012), daily measured (squares) and daily modelled (line) water table depths (WTD) from hollow surface during 2004 over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. Negative values of WTD mean depths below the ground.

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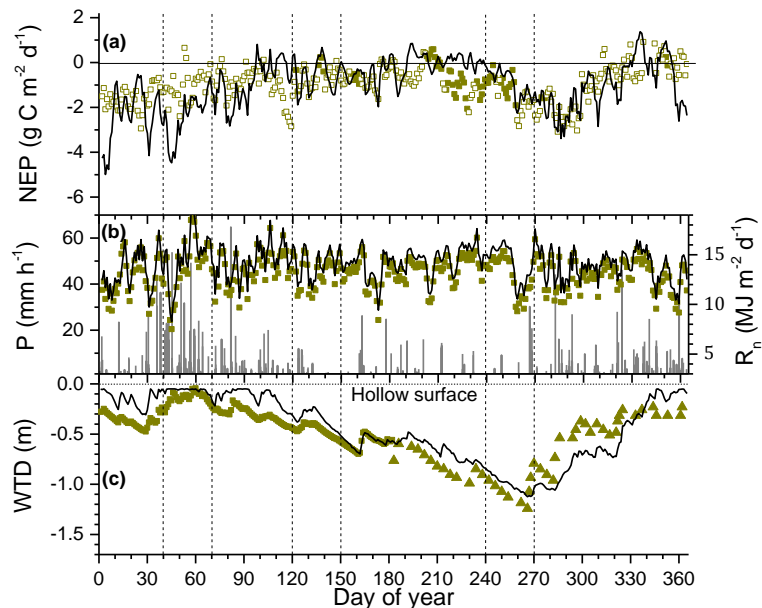


Fig. 4. (a) Three day moving averages of simulated (line) and EC-gap filled estimates (symbols) of net ecosystem productivity (NEP) (negative NEP means the ecosystem is a source and positive NEP means the ecosystem is a sink of C. Closed squares indicate sums of 24 values more than 1/2 of which were recorded at $u^* > 0.17 \text{ ms}^{-1}$ and open squares indicate sums of 24 values more than 1/2 of which were gap-filled); (b) hourly measured precipitation (bars on left y-axis) and three day moving averages of simulated (line on right y-axis) and measured (symbols on right y-axis) net radiation (R_n); and (c) daily measured (triangles were values digitally obtained from Sundari et al. (2012) and squares were measured in situ) and modelled (line) water table depths (WTD) from hollow surface during 2005 over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. Negative values of WTD mean depths below the ground.

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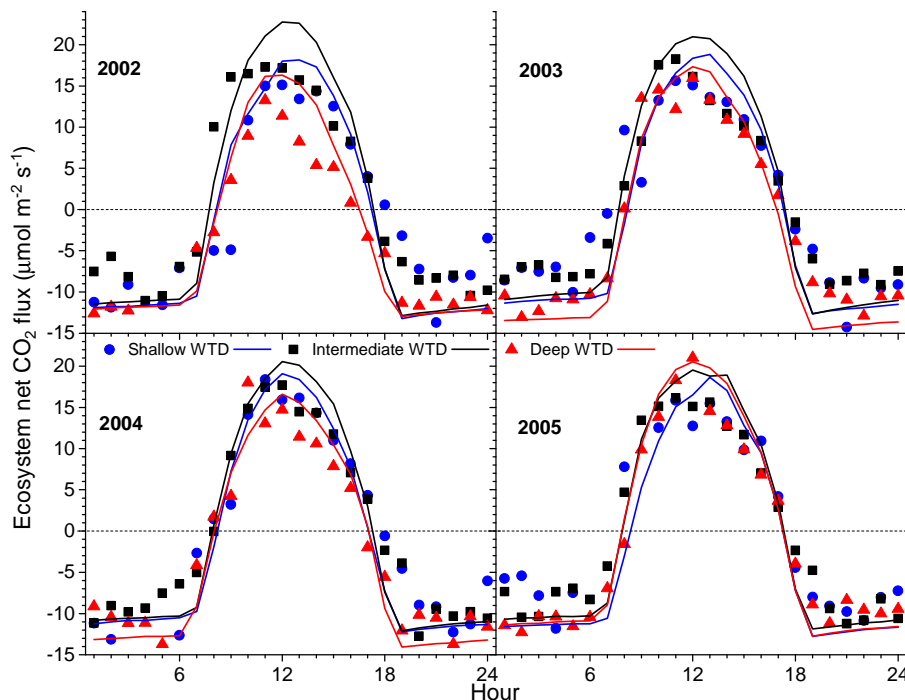


Fig. 5. Hourly binned simulated (lines) and EC measured (symbols) ecosystem net CO₂ fluxes during shallow water table depth (WTD) hydroperiods (DOY 1–30, 41–70, 11–40 and 41–70 during 2002, 2003, 2004 and 2005 respectively), intermediate WTD hydroperiods (DOY 121–150, 146–175, 181–210 and 121–150 during 2002, 2003, 2004 and 2005 respectively) and deep WTD hydroperiods (DOY 251–280, 251–280, 291–320 and 241–270 during 2002, 2003, 2004 and 2005 respectively) with comparable weather condition differing mainly by WTDs (Figs. 1–4) (Table 3) over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. Positive values represent influxes and the negatives represent effluxes. All EC values were recorded at $u^* > 0.17 \text{ ms}^{-1}$.

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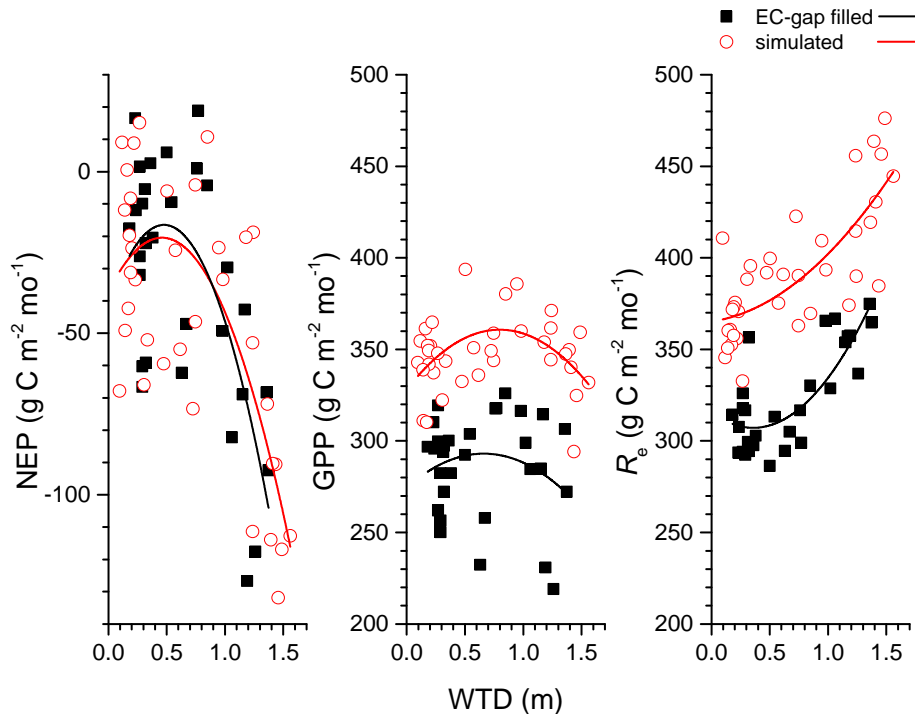


Fig. 6. Relationships between monthly simulated and EC-derived (calculated from monthly averaged daily values digitally obtained from Hirano et al., 2007) net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (R_e), and monthly averaged simulated and observed water table depths (WTD) from hollow surface (from Figs. 1c, 2c and 3c for 2002, 2003 and 2004 respectively) during 2002–2004 over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. Significant ($P < 0.0001$) quadratic curves were fit. Negative NEP means the ecosystem is a source and positive NEP means the ecosystem is a sink of C.

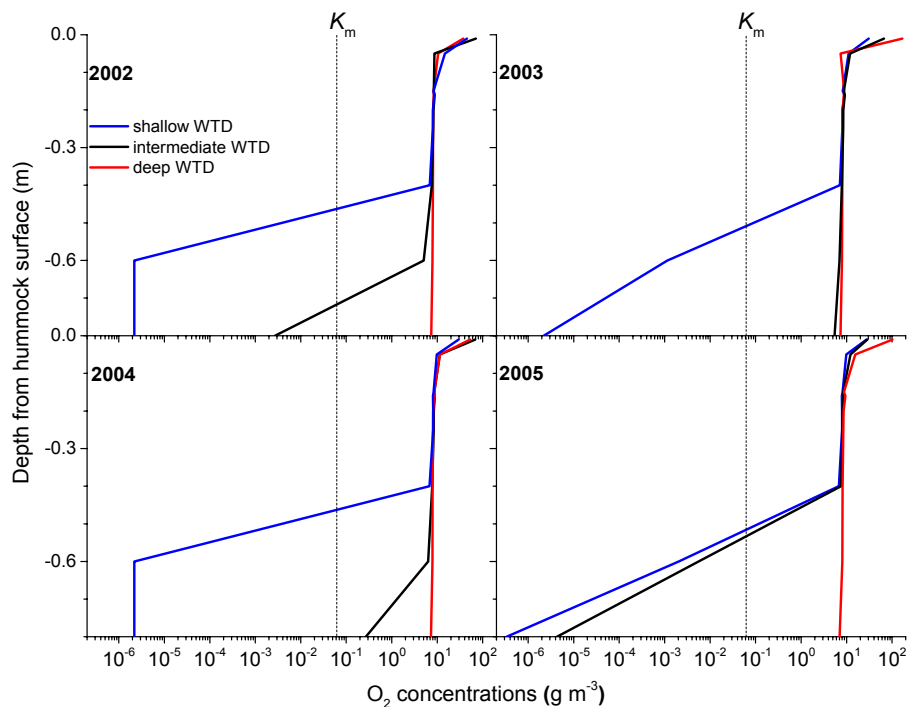


Fig. 7. Vertical profile distributions of peat soil aqueous oxygen concentrations simulated under hummock surface during shallow water table depth (WTD) hydroperiods (DOY 15, 55, 25 and 55 of 2002, 2003, 2004 and 2005 respectively), intermediate WTD hydroperiods (DOY 135, 160, 195 and 135 of 2002, 2003, 2004 and 2005 respectively), and deep WTD hydroperiods (DOY 265, 265, 305 and 255 of 2002, 2003, 2004 and 2005 respectively) over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. K_m = Michaelis–Menten constant (0.064 g m^{-3}) for microbial, root and mycorrhizal uptake [A17a, C14c] in *ecosys*.

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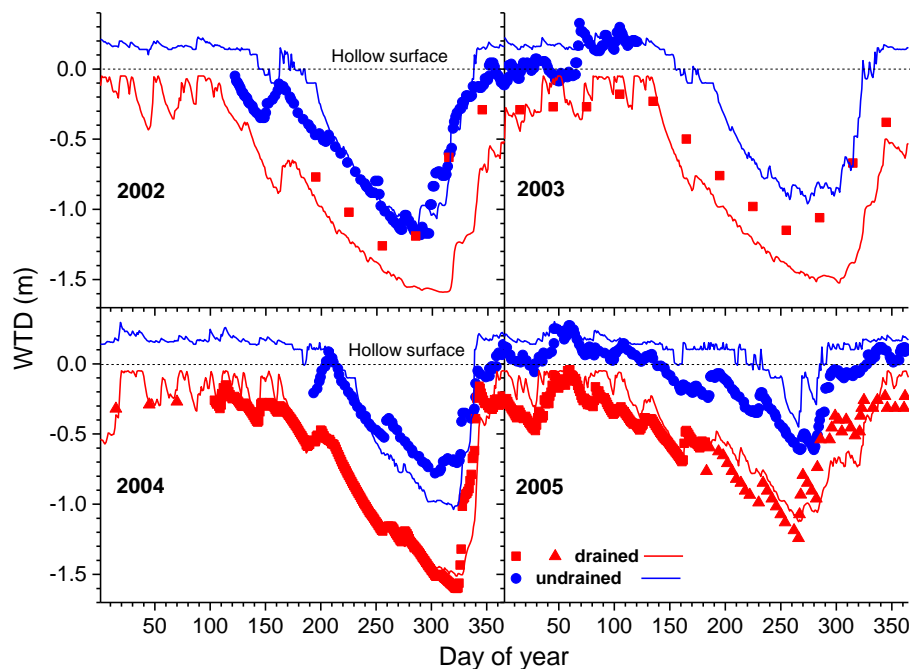


Fig. 8. Simulated (lines) daily drained (external water table depth (WTD_x) = 0.45 m below the hollow surface) vs. undrained (WTD_x = 0.15 m above the hollow surface) water table depths (WTD) during 2002–2005 over a tropical peatland at Palangkaraya Peat Swamp Forest, Indonesia. Observed WTDs (circles) at a nearby similar undrained peat swamp forest were obtained from Hirano et al. (2009) for 2002–2003 and Sundari et al. (2012) for 2004–2005. Simulated and observed drained WTDs are the same as those in Figs. 1c, 2c, 3c and 4c for 2002, 2003, 2004 and 2005 respectively. Negative values of WTD mean depths below the hollow surface and positive values mean depths above the hollow surface.

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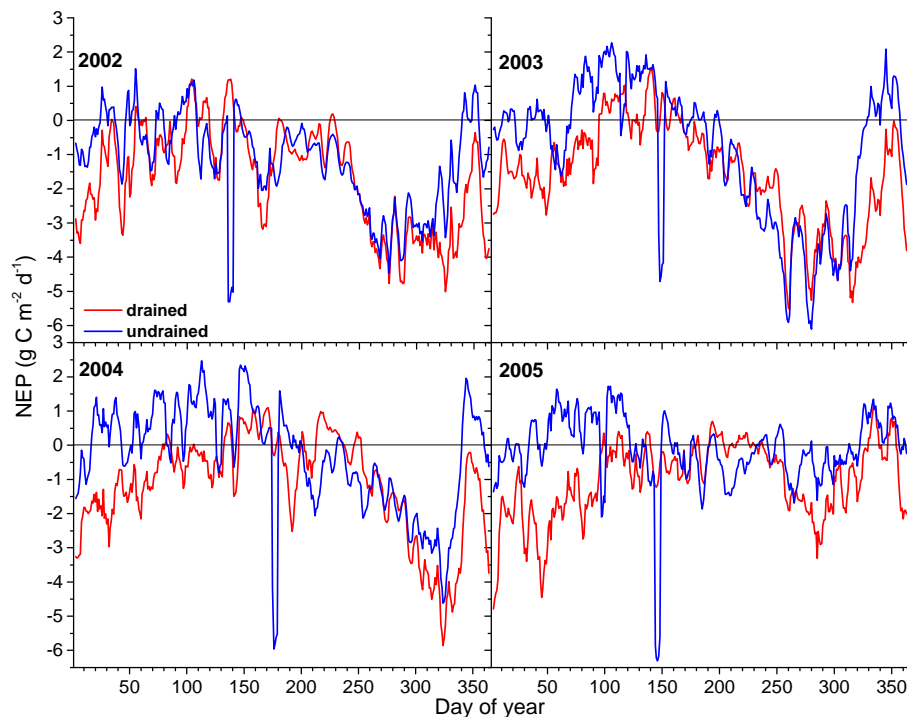


Fig. 9. Drained (external water table depth (WTD_x) = 0.45 m below the hollow surface) vs. undrained (WTD_x = 0.15 m above the hollow surface) five-day moving averages of simulated daily net ecosystem productivity (NEP) during 2002–2005 over Palangkaraya Peat Swamp Forest, Indonesia. Negative NEPs mean the ecosystem is a source of C and positive NEPs mean the ecosystem is a C sink. Drained values are the same as those in Figs. 1 to 4.

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