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Modelling effects of seasonal variation in water table depth on net ecosystem CO_2 exchange of a tropical peatland

M. Mezbahuddin[1], R. F. Grant[1], and T. Hirano[2]

[1]Department of Renewable Resources, University of Alberta, Alberta, Canada
[2]Research Faculty of Agriculture, Hokkaido University, Sapporo, Japan

Correspondence to: M. Mezbahuddin (mezbahud@ualberta.ca)

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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 CO_2 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 process-based mathematical model *ecosys* to study effects of seasonal variation in WTD on net ecosystem productivity (NEP) of a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Simulated NEP suggested that the peatland was a C source (NEP $\sim -2\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$, where a negative sign represents a C source and a positive sign a C sink) during rainy seasons with shallow WTD, C neutral or a small sink (NEP $\sim +1\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$) during early dry seasons with intermediate WTD and a substantial C source (NEP $\sim -4\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$) during late dry seasons with deep WTD from 2002 to 2005. These values were corroborated by regressions ($P < 0.0001$) of hourly modelled vs. eddy covariance (EC) net ecosystem CO_2 fluxes which yielded $R^2 > 0.8$, intercepts approaching 0 and slopes approaching 1. We also simulated a gradual increase in annual NEP from 2002 ($-609\,\mathrm{g\,C\,m^{-2}}$) to 2005 ($-373\,\mathrm{g\,C\,m^{-2}}$) with decreasing WTD which was attributed to declines in duration and intensity of dry seasons following the El Niño event of 2002. This increase in modelled NEP was corroborated by EC-gap filled annual NEP estimates. Our modelling hypotheses suggested that (1) poor aeration in wet soils during shallow WTD caused slow nutrient (predominantly phosphorus) mineralization and consequent slow plant nutrient uptake that suppressed gross primary productivity (GPP) and hence NEP (2) better soil aeration during intermediate WTD enhanced nutrient mineralization and hence plant nutrient uptake, GPP and NEP and (3) deep WTD suppressed NEP through a combination of reduced GPP due to plant water stress and increased ecosystem respiration (R_e) from enhanced deeper peat aeration. These WTD effects on NEP were modelled from basic eco-hydrological processes including microbial and root oxidation-reduction reactions driven by soil and root O_2 transport and uptake which in turn drove soil and plant carbon, nitrogen and phosphorus transformations within a soil-plant-atmosphere water transfer scheme driven by water potential gradients. Including these processes in ecosystem models should therefore provide an improved predictive capacity for WTD management programs intended to reduce tropical peat degradation.

1 Introduction

Seasonal and interannual fluctuations in water table depth (WTD) can affect peatland net CO_2 exchange through complex effects on soil oxidation-reduction reactions and hence on nutrient 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 of reduced C coupled to reduction of O_2 under aerobic conditions exceeds that from oxidation coupled

to reduction of alternative electron acceptors (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 when WTD is shallow. 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 (Couwenberg et al., 2009; Flanagan and Syed, 2011; Limpens et al., 2008; Sulman et al., 2010). 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; Flanagan and Syed, 2011; Murphy and Moore, 2010; 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 sustain with further WTD drawdown in the later part of a prolonged dry season when WTD falls below a critical depth. This critical WTD is highly site-specific depending upon peat forming vegetation and artificial drainage. For instance, this critical WTD may vary from as shallow as 0.4 m (Sonnentag et al., 2010) for pristine peatlands dominated by moss with shallow rhizoids to as deep as 0.9 m (Schwärzel et al., 2006) for drained peatlands dominated by vascular plants with deep root systems. When WTD falls below the critical depth for a particular peatland, near surface peat desiccation occurs. This desiccation can 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 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 (Dimitrov et al., 2010; Lafleur et al., 2005; Strack and Waddington, 2007). However, plant water stress from near surface peat desiccation might also cause a decline in GPP during deep WTD hydroperiods (Dimitrov et al., 2011; Sulman et al., 2010), thereby lowering net ecosystem productivity (NEP). Therefore, responses of peatland ecosystem net CO_2 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 CO_2 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 review of 7 widely used ecosystem models, Sulman et al. (2012) found only *ecosys* (Grant, 2001) included processes to limit both CO_2 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. Kurbatova et al., 2009; St-Hilaire et al., 2010; van Huissteden et al., 2006), (2) parameterizing models with empirical rate constants and/or scalar functions for aerobic vs. anaerobic decomposition (e.g. Bond-Lamberty et al., 2007; Frolking et al., 2002; 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. Bond-Lamberty et al., 2007; Frolking et al., 2002) instead of simulating nutrient limitations to CO_2 fixation imposed by reduced nutrient availability and root nutrient uptake caused by slower oxidation-reduction reactions resultant of slower O_2 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 have 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 CO_2 fluxes against WTD (e.g. Couwenberg et al., 2009; Hirano et al., 2009; Hooijer et al., 2010; Jauhiainen et al., 2008, 2012b; Melling et al., 2005) 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 tropical peatlands is particularly important since climates in tropical peatlands are very different from those in northern temperate and boreal peatlands. 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 as C dated and measured by Page et al., 2004) tropical peat deposits (Couwenberg et al., 2009; Hirano et al., 2009, 2012; Jauhiainen et al., 2008). 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-dominated by mosses and vascular plants. Trees have well developed root systems and stomatal regulations that are lacking in bryophytes. These differences can alter plant water and nutrient uptake processes in tree dominated peatlands from those in bryophyte dominated peatlands. Consequently WTD effects on productivity of tropical peatlands may be very different than of those in northern boreal and temperate peatlands. Besides, tropical peat deposits formed by tree remains can have very different substrate quality for microbial decomposition than boreal and temperate moss peatlands and hence may have a different WTD – peat respiration interaction. This difference in peat forming materials can also cause different hydrological characteristics thereby producing very different water retention and transport phenomena between tropical and temperate/boreal peatlands. Variations in climate and peat forming vegetation thus necessitate rigorous testing of process models against measurements across peatlands developed under very different climate (e.g. boreal vs. tropical) and vegetation (e.g. moss vs. tree) to improve predictive capacity for eco-hydrological controls on peatland C balance.

The process-based hourly time step ecosystem model *ecosys* previously simulated the effects of WTD fluctuations on net CO_2 exchange of northern boreal peatlands (Dimitrov et al., 2011; Grant et al., 2012a). Testing the same model against site measurements of a tropical peatland 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 current understanding of peatland water, nutrient and C interactions is sufficiently robust to capture complex WTD effects on peatland R_e and GPP over a wide range of climates (boreal to tropical). Our study hereby uses *ecosys* to simulate WTD effects on net CO_2 exchange of a drainage affected tropical peat swamp forest at Palangkaraya, Central Kalimantan, Indonesia (Hirano et al., 2007). These effects are 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 slower CO_2 fixation due to reduced nutrient availability and uptake caused by slower nutrient transformation and root growth and uptake resulting from slower O_2 diffusion through wet soils.

2. When WTD increases during the early dry season (May–July), more rapid O_2 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 CO_2 fixation which contributes to a higher NEP. Increased O_2 availability 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 CO_2 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 (nitrogen, phosphorus) 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 CO_2 exchange that are directly 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 brackets with the letter representing a particular appendix in the supplementary materials.

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 transport 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 (A21), 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 nitrogen and phosphorus (A7) and production of dissolved organic nitrogen (DON) and phosphorus (DOP), which causes slower uptake of microbial nitrogen and phosphorus (A22) and hence growth of M (A29). This slower growth causes slower mineralization of organic nitrogen and phosphorus, and hence lower aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (A26).

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 hastens 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 nitrogen and phosphorus (A7) and production of DON and DOP, which increases uptake of microbial nitrogen and phosphorus (A22) and hence growth of M (A29). This rapid growth causes rapid mineralization of organic nitrogen and phosphorus, and hence greater aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (A26).

However, desiccation of surface litter and near surface soil resulting from deepening WTD decreases litter and soil water contents and potentials (ψ_s) which cause an increase in aqueous microbial concentrations ($[M]$) (A15). This reduces microbial access to the substrate for decomposition through an algorithm for competitive inhibition of microbial exoenzymes (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 CO_2 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 O_2 reduction (C14b) which is driven by root O_2 demand to sustain C oxidation and nutrient uptake (C14e), and constrained by O_2 uptake controlled by concentrations of aqueous O_2 in the soil ($[O_{2s}]$) and roots ($[O_{2r}]$) (C14d). Values of $[O_{2s}]$ are maintained by convective-dispersive transport of O_2 through soil gaseous and aqueous phases and by dissolution of O_2 from soil gaseous to aqueous phases. Values of $[O_{2r}]$ are maintained by convective-dispersive transport of O_2 through the root gaseous phase (D16d) and by dissolution of O_2 from root gaseous to aqueous phases (D14b) through processes analogous to those described under Sect. 2.1.2. 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 O_2 transport, forces root O_2 uptake to rely more on $[O_{2r}]$ and hence on root O_2 transport determined by θ_{pr}. If this transport is inadequate, decline in $[O_{2r}]$ slows root O_2 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 O_2 demand to be almost entirely met from $[O_{2s}]$ (C14c, d).

2.1.4 Gross primary productivity

By reducing root O_2 uptake, shallow WTD slows root growth (C20b) and root nitrogen and phosphorus uptake (C23b, d, f). Root nitrogen and phosphorus uptake in this hydroperiod is further slowed by reductions in aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (C23a, c, e) from slower mineralization of organic nitrogen and phosphorus as described in Sect. 2.1.2. Slower root nitrogen and phosphorus uptake in turn reduces concentrations of non-structural nitrogen and phosphorus products of root 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 $[O_{2s}]$ with WTD drawdown during the dry season hastens root O_2 uptake and so enables more rapid root growth and nitrogen and phosphorus uptake as discussed in Sect. 2.1.3. Increased root growth and nitrogen and phosphorus uptake is further stimulated by increased aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (C23a, c, e) from more rapid mineralization of organic nitrogen and phosphorus during this hydroperiod as described in Sect. 2.1.2. Greater root nitrogen and phosphorus 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 less 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 critical depth (Sect. 1), 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 potentials (ψ_r, ψ_c and ψ_t) (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 a drainage affected tropical peat swamp forest at Palangkaraya, Central Kalimantan, Indonesia (2°20′42″ S and 114°2′11″ E). The site is a tropical ombrotrophic 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 over-storey trees and dense under-storey of dominant tree seedlings with no mosses. These peatlands were drained by excavating drainage canals during 1996–1997, approximately 5 yr before the measurements started at a flux station established in Palangkaraya Drained Peat Swamp Forest (PDPSF). Peat depth around the flux tower site was about 4 m. Detail description of edaphic and vegetation characteristics as well as management history of the site can be found in Hirano et al. (2007) and Jauhiainen et al. (2008).

2.2.2 Field datasets

CO_2 fluxes used for model validation in our study were measured by Hirano et al. (2007) at a flux station established in PDPSF during November 2001. Hourly NEP (a negative sign represents an upward flux or a flux out of the ecosystem and a positive sign represents a downward flux or a flux into the ecosystem) over PDPSF was estimated by a combination of eddy and storage CO_2 flux measured using a micrometeorological approach (Hirano et al., 2007). NEP along with latent heat (LE) and sensible heat (H) fluxes were measured by using an open path CO_2 / H_2O analyzer mounted at 41.3 m height, about 15 m above the forest canopy (Hirano et al., 2007). A CO_2 profile was also measured by using a closed path analyzer at six heights between 2.0 and 41.3 m. Hourly weather variables (e.g. incoming longwave and shortwave radiation, wind speed, relative humidity, air temperature, precipitation etc.) were also measured at the flux station. Soil moisture content (θ) at a depth from 0–0.2 m and soil temperature (T_s) at 0.05 m depth were measured in hummocks. Hourly WTD measurements at the site were started from April 2004. Ground reference point for WTD measurements was a hollow surface.

A u^* (friction velocity) threshold of 0.17 m s^{-1} was used to screen out the NEP in a calm night hour. However, no u^* threshold screening was performed for daytime NEP. NEP measured in the rain was also excluded (Hirano et al., 2005, 2012). Nighttime NEP that survived the quality control was used as a measure of nighttime R_e. Daytime R_e was extrapolated by using nighttime R_e. GPP was then calculated by adding daytime R_e to daytime NEP that survived the quality screening.

Flux gaps due to quality control were filled by Hirano et al. (2007) through look up tables (LUT) created for four periods of 3 months each (November–January, February–April, May–July and August–October). Hourly measured θ, WTD and T_s were used to incorporate environmental controls in LUTs for filling nighttime NEP ($= R_e$) gaps. No hourly WTD measurement was available at the site before April 2004. Therefore, only θ was used as hydrological control in LUTs from January 2002–March 2004. In order to balance the number of original data in each cell, θ was grouped into six classes from below 0.23 m^3 m^{-3} to above 0.35 m^3 m^{-3}

with an interval of $0.03\,m^3\,m^{-3}$. T_s was also grouped into five classes from 25 to 30 °C with an interval of 1 °C. In filling GPP gaps, photosynthetic photon flux density (PPFD) and vapour pressure deficit (D) were used as environmental factors to create LUTs similar to those used for R_e. PPFD and D were grouped into eight classes from 5–250 to above $1750\,\mu mol\,m^{-2}\,s^{-1}$ at intervals of $250\,\mu mol\,m^{-2}\,s^{-1}$ and three classes of below 1.2, 1.2–1.8 and above 1.8 kPa, respectively. Finally, NEP gaps during daytime hours were calculated by the differences between gap-filled GPP and estimated daytime R_e.

A more detailed description of eddy covariance (EC) methodology, measurement techniques, quality control, and partitioning and gap filling of fluxes can be found in Hirano et al. (2007, 2012).

2.2.3 Model run

For our modelling experiment, the PDPSF landscape was represented by one hummock and one hollow grid cell each of which had a dimension of 1 m × 1 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 PDPSF 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 PDPSF (Mezbahuddin et al., 2014). Very high carbon and nitrogen to phosphorus ratios (C : N and C : P) 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 an earlier study on an Amazonian rainforest (Grant et al., 2009), but selecting 0.2 for root porosity (θ_{pr}) used in root O_2 transport (D17d) to represent wetland 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 (40 yr of spin up and 4 yr of simulation run) 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. The spin up period allowed CO_2 exchange in the model to achieve stable values through successive weather sequences. Model results for the 4 yr of simulation run were compared with measurements at PDPSF from 2002–2005.

2.2.4 Model validation

Hourly CO_2 fluxes modelled over the hummock and the hollow were spatially averaged to represent 50 : 50 hummock-hollow ratios as described by Jauhiainen et al. (2008), and then regressed on hourly measured EC CO_2 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 EC measured as well as between modelled and gap-filled CO_2 fluxes. This test is very important since any small divergence between hourly modelled and EC measured as well as between hourly modelled and gap-filled CO_2 fluxes can result in a large divergence between modelled and EC-gap filled annual estimates.

2.2.5 Analyses of model results

In order to examine WTD effects on seasonal variations in NEP as proposed in hypotheses 1, 2 and 3 of our study, we chose daily modelled and EC-gap filled NEP for 30 days each from the three WTD hydroperiods, i.e. shallow, intermediate and deep, for 2002–2005. These 30 day periods were chosen based on the greatest availability of EC measured CO_2 fluxes that passed the quality control procedure described in Sect. 2.2.2. We then performed single factor analyses of variance (ANOVA) for the modelled and EC-gap filled NEP to test whether the means of daily NEP significantly differed among different hydroperiods. A significant difference in mean NEP between two particular hydroperiods meant the variation in mean NEP between those hydroperiods was larger than the day to day variation in NEP within each of those hydroperiods. This test would signify the consistency of seasonal variations in NEP as a result of WTD fluctuations.

2.2.6 Model sensitivity to drained vs. undrained WTD

WTD in the modelled grid cells 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 a surface boundary and in the forms of recharge and discharge with an adjacent ecosystem through lateral boundaries. The distance (L_t) and hydraulic gradient between modelled WTD and a set external water table depth (WTD_x, representing mean WTD of the adjacent watershed) generally governs the rate of lateral recharge and discharge (D10, D10a). All modelled WTDs were spatially averaged for the hummock and the hollow grid cell with reference to 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 measured for our drained site (Hirano et al., 2012). L_t was set to 400 m in all directions which was the nearest distance from the study site to the drainage canal (Hirano et al., 2012). Since drainage is a key disturbance reported to alter WTD and hence C balance of Southeast Asian peatlands (Couwenberg et al., 2009; Hooijer et

Table 1. Key soil properties as *ecosys* inputs to represent a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia *.

D_{humm} (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		500	18 000	238	3.78	37.5
0.15				192		
0.16	0.01					
0.20	0.05	500	18 000	143	3.78	37.5
0.25	0.10					
0.40	0.25					
0.60	0.45	500	14 000	115	3.75	37.5
0.80	0.65					
1.00	0.85					
1.20	1.05					
1.40	1.25	500	14 000	49	3.75	37.5
1.60	1.45					
1.80	1.65					
4.00	3.85					

* D_{humm} = 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 top 4 m of a 9 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).

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_xs 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 NEP to the difference in drained vs. undrained WTD. A more detailed description of how subsurface hydrology, water balance and surface energy exchange over PDPSF was simulated can be found in our concurrent paper on modelling seasonal variation in WTD and surface energy exchange over PDPSF (Mezbahuddin et al., 2014).

3 Results

3.1 Modelled vs. measured ecosystem net CO_2 fluxes

Regressions of hourly modelled vs. measured net ecosystem CO_2 fluxes gave intercepts within 1.0 $\mu mol\,m^{-2}\,s^{-1}$ 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 $\mu mol\,m^{-2}\,s^{-1}$ (Table 2). Values for coefficients of determination (R^2) and root-mean-square for errors (RMSE) were ~ 0.8 ($P < 0.0001$) and $\sim 5.0\,\mu mol\,m^{-2}\,s^{-1}$ (Table 2). Much of the unexplained variance in EC-measured CO_2 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 random errors (RMSRE) in EC measurements, calculated for forests with similar CO_2 fluxes from Richardson et al. (2006) that were similar to RMSE. 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 CO_2 fluxes gave larger slopes than those of modelled vs. EC-measured CO_2 fluxes despite higher R^2 and lower RMSEs, indicating the diurnal variation of the modelled CO_2 fluxes was systematically larger than that of the gap-filled CO_2 fluxes (Table 2). Further investigation into hourly simulated vs. gap-filled and simulated vs. EC measured net ecosystem CO_2 fluxes suggested that modelled nighttime fluxes were systematically larger than the gap-filled nighttime fluxes particularly in the rainy season when valid EC measured data were scarce (Fig. 1). However, modelled nighttime fluxes showed good agreement with more available valid EC measured nighttime fluxes during the dry season (Fig. 1).

3.2 Seasonal variation in WTD and daily net ecosystem CO_2 exchange

WTD in PDPSF showed distinct seasonality in each year from 2002 to 2005 (Mezbahuddin et al., 2014). 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. 2–5). During late dry seasons (August–October) observed WTD fell below 1.0 m from the hollow surface (Figs. 2–5). Increasing amounts and declining seasonality of precipitation caused the wet to dry season drawdown of WTD to be more and more gradual from the driest year 2002 to the wettest year 2005 (Figs. 2–5).

NEP (a negative sign represents C source and a positive sign represents C sink) modelled and measured over PDPSF showed a distinct seasonality, with negative values over shallow WTD (within 0.3 m below the hollow surface) during the rainy season, near zero 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. 2–5). These values indicated that the ecosystem was a C source when the WTD was shallow, became C neutral or a small sink when WTD receded to an intermediate position, and again became a large source of C when WTD further deepened (Figs. 2–5).

Modelled and EC-gap filled NEP during intermediate WTD hydroperiods were significantly ($P < 0.01$) higher than those during shallow WTD hydroperiods during 2002–2003 (Fig. 6). Both the modelled and EC-gap filled NEP showed similar trend of increasing NEP from shallow to intermediate WTD hydroperiods during 2004–2005. However, only the increases in modelled NEP from shallow to intermediate WTD hydroperiods in those years were statistically significant ($P < 0.01$) (Fig. 6). Both modelled (in 2002–2004) and EC-gap filled (in 2002–2005) NEP during deep WTD hydroperiods was significantly ($P < 0.01$) lower than that during intermediate WTD hydroperiods (Fig. 6). This seasonal trend in NEP also varied interannually depending upon the duration and intensity of dry seasons. For instance, NEP during the deep WTD hydroperiod was more negative in a drier dry season (2002–2004, Figs. 2–4 and 6) than that in a wetter dry season (2005, Figs. 5–6).

In addition to the successful simulations of interannual variation in seasonal cycles 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. 2), DOY 258–262 in 2003 (Fig. 3), DOY 143–146 in 2004 (Fig. 4), DOY 259–262 in 2005 (Fig. 5) etc. caused by smaller CO_2 influxes and larger CO_2 effluxes on cloudy and rainy days. These dips were modelled from less CO_2 fixation under lower R_n and/or from flushes of soil CO_2 effluxes due to rewetting surface residues from a rainfall following a dry period (Grant et al., 2012b).

3.3 Seasonal variation in WTD and diurnal CO_2 exchange

In order to examine WTD effects on ecosystem diurnal net CO_2 exchange, we compared hourly modelled net CO_2 fluxes against EC-gap filled CO_2 fluxes binned for the three WTD hydroperiods, i.e. shallow, intermediate and deep from 2002–2005 (Fig. 7). During 2002–2003, modelled downward CO_2 fluxes were suppressed over shallow WTD during the rainy seasons, became larger over intermediate WTD during the early dry seasons, and again suppressed over deeper WTD during the late dry seasons, as were also apparent in EC-gap filled CO_2 fluxes (Fig. 7). During 2004, modelled downward fluxes followed the same seasonal pattern as in 2002–2003 but EC-gap filled fluxes showed clear suppression in only the deep WTD hydroperiod (Fig. 7). Both modelled and EC-gap filled downward CO_2 fluxes during 2005, however, increased with deepening WTD with no suppression during late dry season (Fig. 7). Suppressions of downward CO_2 fluxes during deep WTD periods varied interannually depending upon the duration and intensity of the hydroperiods. For instance, suppression of modelled and EC-gap filled downward CO_2 fluxes during the deep WTD hydroperiods was stronger during the drier late dry seasons of 2002 and 2004, less strong in wetter late dry season of 2003 and absent in the wettest late dry season of 2005 (Fig. 7)

Limited precision and frequency of EC-measured nighttime CO_2 fluxes caused by insufficient nighttime turbulence made the comparison of modelled vs. EC-gap filled upward CO_2 fluxes more difficult than that for downward CO_2 fluxes. EC-gap filled upward CO_2 fluxes (= R_e) showed no significant change except a small decrease during 2003 with WTD drawdown from rainy to early dry seasons and marked increases with further deepening of WTD in late dry seasons during 2002–2005 (Fig. 7). These effects of seasonal WTD variation on upward CO_2 fluxes (= R_e) were reasonably well simulated except that the modelled decrease in upward CO_2 fluxes from shallow to intermediate WTD hydroperiod in 2003 was smaller than that in EC-gap filled fluxes (Fig. 7). Moreover, modelled upward CO_2 fluxes (= R_e) had a small decrease from rainy to dry season in 2005 which was not apparent in EC-gap filled fluxes (Fig. 7). Increase in EC-gap filled upward CO_2 fluxes (= R_e) from intermediate to deep WTD hydroperiod was not prominent in modelled upward fluxes during 2002 (Fig. 7).

Both modelled and EC-gap filled downward CO_2 fluxes increased from shallow to intermediate WTD hydroperiods during 2002, 2003 and 2005 while upward CO_2 fluxes (= R_e) decreased little or not at all, suggesting that GPP was raised by gradual drawdown of WTD from the rainy to early dry season (Fig. 7). An increase in R_n from the rainy to early dry season may have contributed to the increase in downward CO_2 fluxes during 2002 (Figs. 2b and 7). However, a similar increase in R_n from the rainy to early dry seasons during 2003 and 2004 did not coincide with a similar

Table 2. Modelled vs. measured net ecosystem CO_2 fluxes over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia*.

Year	Precipitation (mm yr^{-1})	n	a	b	R^2	RMSE	RMSRE
Modelled vs. EC measured CO_2 fluxes recorded at $u^* > 0.17$ m s^{-1}							
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
Modelled vs. gap-filled CO_2 fluxes							
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 RMSE = root-mean-square for errors from simple linear regressions of measured on modelled. All measured values were recorded at u^* (friction velocity) > 0.17 m s^{-1}. RMSRE = root-mean-square for random errors in EC measurements calculated by inputting EC fluxes recorded at $u^* > 0.17$ m s^{-1} into algorithms for estimation of random errors in EC measurements developed for forests by Richardson et al. (2006).

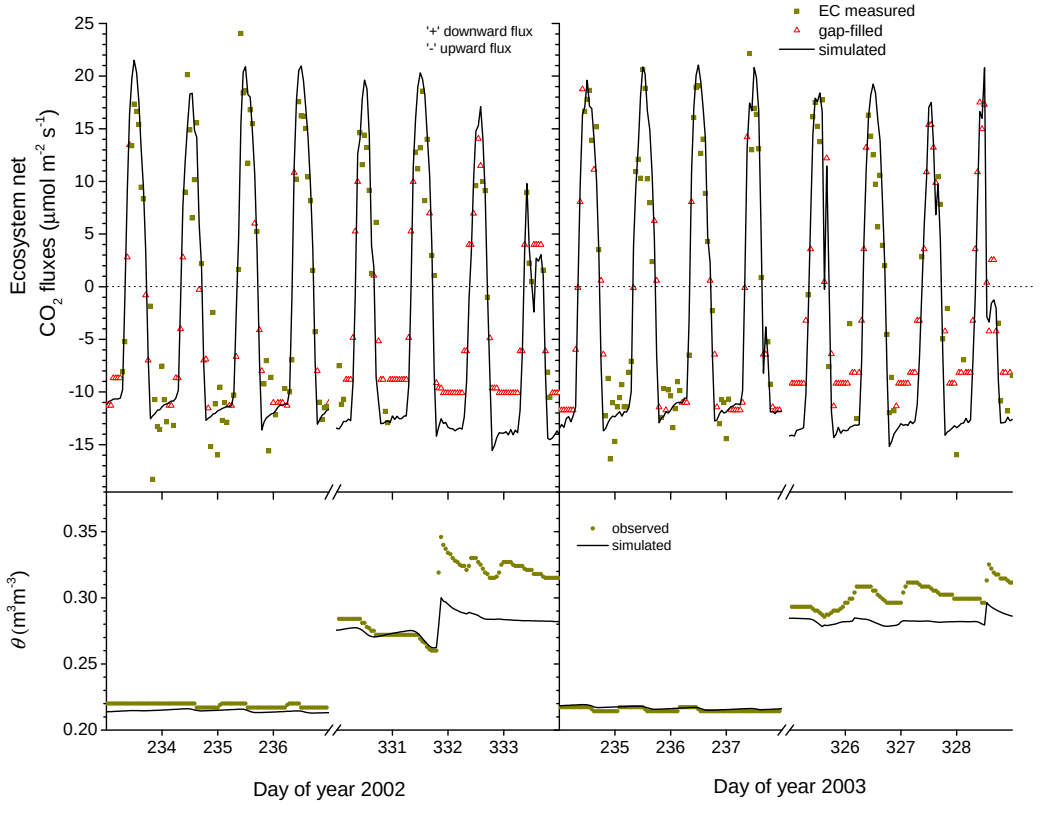

Fig. 1. Hourly EC measured, gap-filled and simulated net ecosystem CO_2 fluxes and observed and simulated soil water contents (θ) from 0–0.20 m depth of the hummock during 2002 and 2003 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia.

increase in downward flux, whereas no change in R_n between those hydroperiods during 2005 coincided with an increase in downward CO_2 fluxes (Figs. 3–5 and 7). Moreover, an increase in D from rainy to early dry season (Fig. 6f) did not cause a decline in downward CO_2 fluxes during 2002–2005 (Fig. 7). These confounding effects of R_n and D on

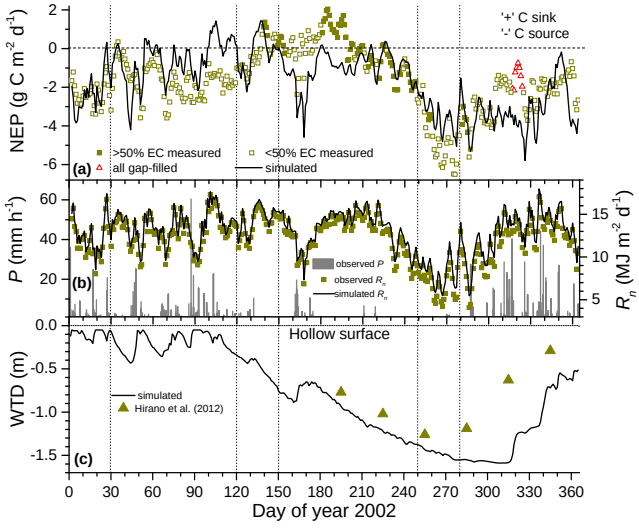

Fig. 2. (a) Three day moving averages of simulated and EC-gap filled estimates of net ecosystem productivity (NEP). Solid squares indicate sums of 24 values more than 1/2 of which were recorded at u^* (friction velocity) > 0.17 m s^{-1}, open squares indicate sums of 24 values more than 1/2 of which were gap-filled, and open triangles indicate sums of 24 values all of which were gap-filled; **(b)** hourly measured precipitation (P) and three day moving averages of simulated and measured net radiation (R_n); and **(c)** monthly measured (values digitally obtained from Hirano et al., 2012) and daily modelled water table depths (WTD) from hollow surface during 2002 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Negative values of WTD mean depths below the ground.

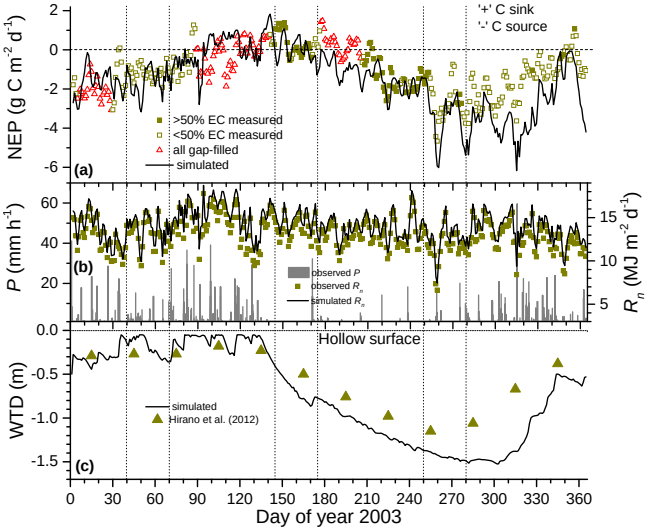

Fig. 3. (a) Three day moving averages of simulated and EC-gap filled estimates of net ecosystem productivity (NEP). Solid squares indicate sums of 24 values more than 1/2 of which were recorded at u^* (friction velocity) > 0.17 m s^{-1}, open squares indicate sums of 24 values more than 1/2 of which were gap-filled, and open triangles indicate sums of 24 values all of which were gap-filled; **(b)** hourly measured precipitation (P) and three day moving averages of simulated and measured net radiation (R_n); and **(c)** monthly measured (values digitally obtained from Hirano et al., 2012) and daily modelled water table depths (WTD) from hollow surface during 2003 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Negative values of WTD mean depths below the ground.

modelled and EC-gap filled downward CO_2 fluxes further indicated that there was a consistent increase in GPP from shallow to intermediate WTD hydroperiods which was driven by eco-hydrology rather than micrometeorology. Larger declines in downward modelled and EC-gap filled CO_2 fluxes than the increases in upward CO_2 fluxes (= R_e) from intermediate to deep WTD hydroperiods during 2002–2004 indicated GPP suppression by deep WTD (Fig. 7). Higher D (e.g. during 2002–2004 in Fig. 6f) and lower R_n (e.g. due to smoke haze shading from surrounding forest and peat fires during 2002 in Fig. 2b as mentioned by Hirano et al., 2007) may have further contributed to GPP suppression during deep WTD hydroperiods (Fig. 7). However, interannual variation in the intensity of GPP suppression (Fig. 7) coincided with that in the duration and intensity of dry seasons irrespective of changes in D and R_n (Figs. 2–6), as described earlier, further suggested the significance of hydrological control over micrometeorological control in suppressing GPP during deep WTD hydroperiods.

Therefore, a gradual drawdown of WTD from rainy to early dry season resulted in higher NEP mainly by raising GPP with no change or little decrease in R_e (Figs. 2–7). Further drawdown of WTD during late dry season forced NEP to decline by a combination of reduced GPP and increased R_e (Figs. 2–7). This seasonal effect of WTD on NEP through its effects on GPP and R_e can also be corroborated by the quadratic curve fittings between monthly modelled and EC-derived NEP, GPP and R_e vs. monthly modelled and observed WTD. Such curve fittings between NEP and WTD yielded goodness of fits (R^2) of 0.61 (modelled NEP vs. modelled WTD) and 0.53 (EC-derived NEP vs. observed WTD) indicating a small increase in NEP from shallow to intermediate WTD hydroperiods and a remarkable decline in NEP from intermediate to deep WTD hydroperiods during 2002–2004 (Fig. 8). The quadratic relationships between GPP and WTD ($R^2 = 0.14$ for modelled GPP vs. modelled WTD and $R^2 = 0.10$ for EC-derived GPP vs. observed WTD) indicated that increases in GPP from shallow to intermediate WTD hydroperiods contributed to increases in NEP and declines in GPP from intermediate to deep WTD hydroperiods contributed to declines in NEP (Fig. 8). R_e and WTD relationships ($R^2 = 0.53$ for modelled R_e vs. modelled WTD and $R^2 = 0.60$ for EC-derived R_e vs. observed WTD) indicated that no change or small decreases in R_e from shallow to intermediate WTD hydroperiods contributed little to increases in NEP, and large increases in R_e from intermediate to deep WTD hydroperiods contributed substantially to declines in NEP (Fig. 8). Though monthly modelled

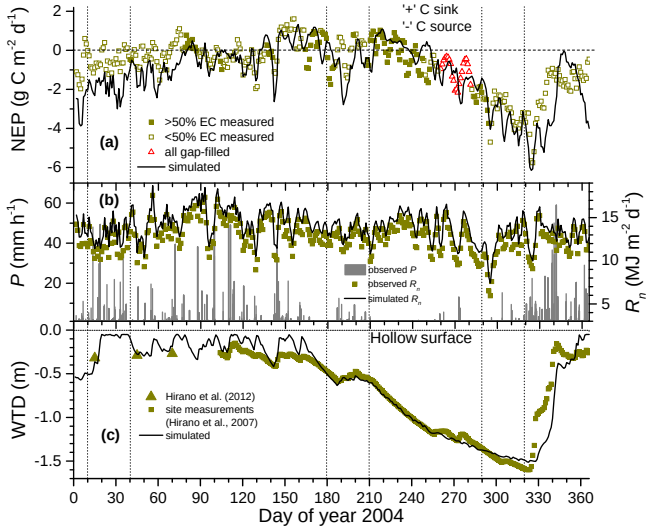

Fig. 4. (a) Three day moving averages of simulated and EC-gap filled estimates of net ecosystem productivity (NEP). Solid squares indicate sums of 24 values more than 1/2 of which were recorded at u^* (friction velocity) $> 0.17\,\mathrm{m\,s^{-1}}$, open squares indicate sums of 24 values more than 1/2 of which were gap-filled, and open triangles indicate sums of 24 values all of which were gap-filled; **(b)** hourly measured precipitation (P) and three day moving averages of simulated and measured net radiation (R_n); and **(c)** monthly measured (values digitally obtained from Hirano et al., 2012), daily measured (site measurements mentioned in Hirano et al., 2007) and daily modelled water table depths (WTD) from hollow surface during 2004 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Negative values of WTD mean depths below the ground.

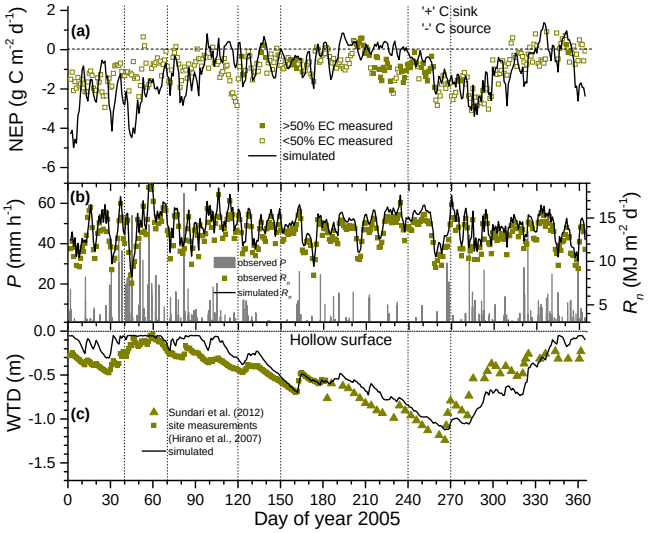

Fig. 5. (a) Three day moving averages of simulated and EC-gap filled estimates of net ecosystem productivity (NEP). Solid squares indicate sums of 24 values more than 1/2 of which were recorded at u^* (friction velocity) $> 0.17\,\mathrm{m\,s^{-1}}$ and open squares indicate sums of 24 values more than 1/2 of which were gap-filled; **(b)** hourly measured precipitation (P) and three day moving averages of simulated and measured net radiation (R_n); and **(c)** daily measured (values digitally obtained from Sundari et al., 2012 and measured in situ as mentioned in Hirano et al., 2007) and modelled water table depths (WTD) from hollow surface during 2005 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Negative values of WTD mean depths below the ground.

NEP values were similar to EC-gap filled NEP values, both monthly modelled GPP and R_e were systematically larger than EC-derived GPP and R_e (Fig. 8).

3.4 Interannual variation in WTD and NEP

Interannual variation in WTD over PDPSF from 2002 to 2005 was mainly caused by differences in annual precipitation. Increasing amount of annual precipitation from the driest year 2002 to the wettest year 2005 drove a gradually shallower average annual modelled and measured WTD from 2002 to 2005 (Table 3). Variation in annual estimates of neither modelled nor EC-gap filled evapotranspiration (ET) from 2002 to 2005 did correlate with that in average annual modelled or observed WTD (Table 3). However, modelled lateral discharge increased from 2002 to 2005 with decreasing WTD (Table 3). This interannual variation in WTD caused interannual variation in NEP over PDPSF from 2002 to 2005. A gradual rise in both modelled and EC-gap filled annual NEP was found from 2002 to 2004 with progressively shallower WTD (Table 3). However, modelled NEP was considerably lower than the EC-gap filled estimates of NEP in 2003 and 2004 (Table 3). The decreasing WTD from 2002 to 2005 reduced modelled annual GPP, R_a and R_h and hence R_e (Table 3), although this reduction could not be corroborated from EC-derived estimates. In contrast, EC-derived annual GPP increased with decreasing WTD from 2002–2004 but EC-derived R_e showed no response (Table 3). Moreover, modelled annual GPP and R_e were consistently larger than the EC-derived estimates during 2002–2004 (Table 3). Similar declines in modelled GPP and R_a with shallower WTD left modelled NPP almost unchanged throughout the study period (Table 3). However, greater suppression of annual R_h by shallow WTD caused annual NEP to become gradually less negative from 2002 to 2005 (Table 3).

3.5 Seasonal and annual variations in simulated drained vs. undrained WTD and NEP

Large negative simulated and EC-gap filled annual NEP during 2002–2005 (Table 3) may reflect disturbance effects of drainage in 1996–1997 which increased WTD. In order to examine the drainage effects on modelled NEP, we performed a drained vs. undrained model sensitivity test as described in Sect. 2.2.6. During the rainy seasons (November–April) from 2002–2005, simulated undrained WTD was always above the hollow surface as opposed to the simulated drained

Table 3. Simulated (sim) and observed (obs) annual water and C balance over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia [a].

	Units	Year								Values from other studies
		2002		2003		2004		2005		
		sim	obs	sim	obs	sim	obs	sim	obs	
Precipitation			1852		2291		2560		2620	
ET	mm yr^{-1}	1485	1325	1607	1366	1545	1324	1558	1310	
Q		390		708		918		1067		
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	g C	2909		2823		2760		2778		
NPP	m^{-2}	1292		1341		1349		1262		900[b], 1200[c]
R_h	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		

[a] ET = evapotranspiration, observed ET for each year was calculated from EC-gap filled hourly latent heat fluxes measured by Hirano et al. (2005); Q = total lateral discharge; WTD = water table depth, simulated and observed WTDs are averages of data used in Figs. 2c, 3c, 4c and 5c for 2002, 2003, 2004 and 2005 respectively, observed mean WTD for 2002 was not calculated due to the lack of site measurements and/or literature values for the first six months (Fig. 2c); GPP = gross primary productivity, observed GPP values were derived by Hirano et al. (2007) from EC-gap filled net CO_2 flux partitioning (Sect. 2.2.2); R_a = autotrophic respiration; NPP = net primary productivity (NPP = GPP − R_a); R_h = heterotrophic respiration; R_e = ecosystem respiration, observed R_e values were derived by Hirano et al. (2007) from EC-gap filled net CO_2 flux partitioning (Sect. 2.2.2); and NEP = net ecosystem productivity (NEP = NPP − R_h), observed NEP values were derived from hourly EC-gap filled net ecosystem CO_2 fluxes measured and gap-filled by Hirano et al. (2007) (Sect. 2.2.2),

[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).

WTD where water table never rose above the hollow surface (Fig. 9). The undrained WTD remained ∼ 0.5 m shallower than the drained WTD, and so altered the timing and intensity of the different hydroperiods (Fig. 9). The seasonal variation in simulated undrained WTD followed that in a nearby similar undrained tropical peat swamp forest (Fig. 9).

NEP modelled in the undrained condition was higher (less negative) than that in the drained condition during the rainy seasons (November–April) but similar during the late dry seasons (August–October) (Fig. 10). However in 2004 and 2005, NEP modelled in the undrained simulation was higher than in the drained simulation during late dry season (Fig. 10). Large spikes of negative NEP were simulated in the undrained simulation at the end of the rainy seasons when WTD first declined below the hollow surface (Fig. 10). This decline suddenly increased contact between atmosphere and aqueous CO_2 in the previously saturated soil, causing rapid degassing. Such spikes were not found in the drained simulation where WTD remained below the hollow surface.

On an annual basis, the undrained simulation produced a shallower average WTD by ∼ 0.5 m than the drained simulation over four years i.e. 2002–2005. This reduction in WTD in undrained vs. drained simulation decreased GPP and R_a slightly, but decreased R_h much more, thereby increasing mean annual NEP throughout the study period (Table 4).

4 Discussion

4.1 Modelling hypotheses of WTD effects on seasonal variation in tropical peatland NEP

Reduction of NEP during both shallow and deep WTD hydroperiods with respect to that in the intermediate WTD hydroperiods was established during 2002–2005 in Sects. 3.2 and 3.3. Reduction of NEP during the shallow WTD hydroperiods was mainly attributed to reduction in GPP that was independent of changes in R_n and D (Sect. 3.3). Reduction of NEP during the deep WTD hydroperiods, however, was attributed to reduction in GPP irrespective of changes in R_n and D, and to increase in R_e irrespective of changes in temperature (variations in mean daily air temperature and mean daily soil temperature measured at 0.05 m depth of the hummocks were less than 3 °C among the hydroperiods) (Sect. 3.3). The absence of a decline in GPP during the deep WTD hydroperiod in the wettest year 2005 also suggested that there was a considerable interannual variation in WTD effect on tropical peatland NEP that depended on the intensity and duration of dry vs. wet seasons (Sect. 3.3). Seasonal variation in WTD thus affected that in NEP through its effect on both GPP and R_e as mentioned above independent of variations in other micrometeorological controls such as R_n, D and temperature. These effects suggested that tropical peatland NEP was reduced by plant processes as affected by soil

Table 4. Sensitivity of modelled annual C balance to drainage over a drainage affected tropical peat swamp forest at Palangkaraya, 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	g C	2909	2412	2823	2455	2760	2431	2778	2396	2818	2423
NPP	m^{-2}	1292	1166	1341	1325	1349	1264	1262	1269	1311	1256
R_h	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

* dr = drained simulation; undr = undrained simulation (Sect. 2.2.6); WTD = water table depth, values are the annual means of simulated WTD data in Fig. 9, 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; and NEP = net ecosystem productivity (NEP = NPP − R_h).

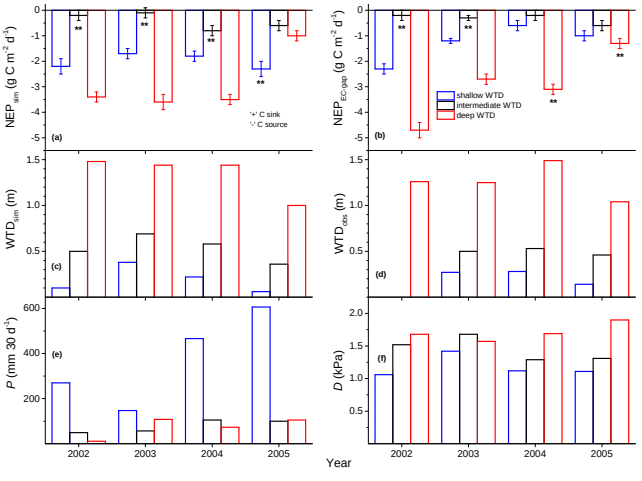

Fig. 6. (a) Average simulated daily net ecosystem productivity (NEP_{sim}) **(b)** average EC-gap filled daily net ecosystem productivity (NEP_{EC-gap}) **(c)** average simulated water table depths (WTD_{sim}) **(d)** average observed water table depths (WTD_{obs}) **(e)** total observed precipitation (P), and **(f)** average mid-day (10:00–14:00 LT) vapour pressure deficit (D) during shallow (DOY 1–30, 41–70, 11–40 and 41–70 in 2002, 2003, 2004 and 2005 respectively), intermediate (DOY 121–150, 146-1-75, 181–210 and 121–150 in 2002, 2003, 2004 and 2005 respectively) and deep (DOY 251–280, 251–280, 291–320 and 241–270 in 2002, 2003, 2004 and 2005 respectively) water table depth (WTD) hydroperiods (delineated by vertical dotted lines in Figs. 2–5) over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Bars represent standard errors of means. Asterisks (**) at the top of a column represent significant ($P < 0.01$) difference from the adjacent column(s).

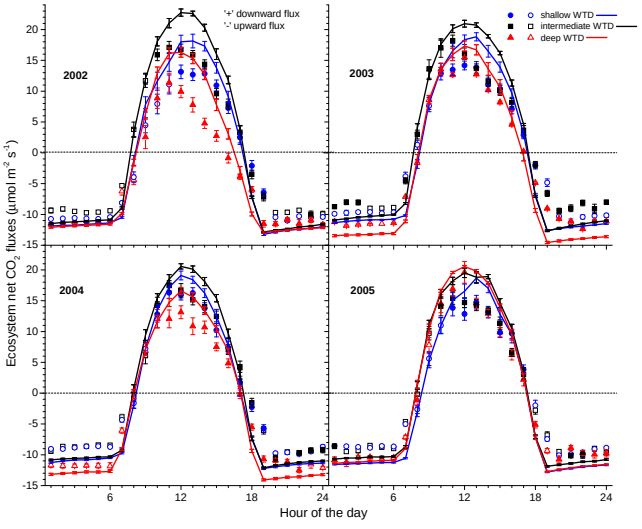

Fig. 7. Hourly binned simulated (lines) and EC-gap filled (symbols) ecosystem net CO_2 fluxes during shallow (DOY 1–30, 41–70, 11–40 and 41–70 in 2002, 2003, 2004 and 2005 respectively), intermediate (DOY 121–150, 146–175, 181–210 and 121–150 in 2002, 2003, 2004 and 2005 respectively) and deep (DOY 251–280, 251–280, 291–320 and 241–270 in 2002, 2003, 2004 and 2005 respectively) water table depth (WTD) hydroperiods (delineated by vertical dotted lines in Figs. 2–5) over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Solid symbols are averages of 30 hourly values more than 1/3 of which were EC measured CO_2 fluxes recorded at u^* (friction velocity) $> 0.17\,m\,s^{-1}$. Open symbols are averages of 30 hourly values less than 1/3 of which were EC measured CO_2 fluxes recorded at $u^* > 0.17\,m\,s^{-1}$. Bars represent standard errors of means.

processes influenced by both shallow and deep WTD. Since our modelling could reasonably simulate seasonal variation in WTD as well as its effects on that in NEP (Sects. 3.2 and 3.3), we hereby discuss the modelling hypotheses proposed at the beginning of our study to explain the underlying causes of these WTD effects on tropical peatland NEP.

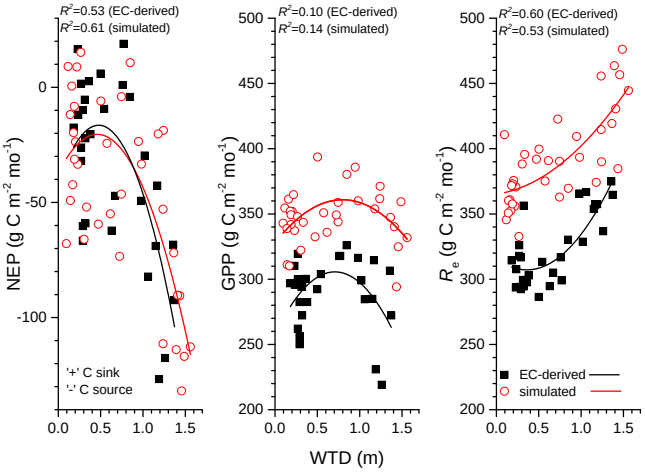

Fig. 8. Relationships between monthly simulated net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (R_e), and monthly averaged simulated water table depths (WTD) (from Figs. 2c, 3c and 4c for 2002, 2003 and 2004 respectively); and monthly EC-derived NEP (derived from EC-gap filled hourly CO_2 fluxes), GPP and R_e (calculated from monthly averaged daily values digitally obtained from Hirano et al., 2007), and monthly averaged observed WTDs (from Figs. 2c, 3c and 4c for 2002, 2003 and 2004 respectively) during 2002–2004 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia.

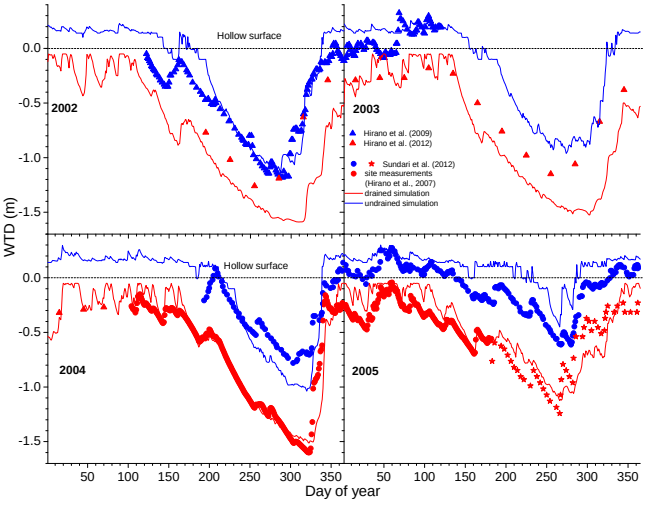

Fig. 9. Simulated daily drained vs. undrained water table depths (WTD) (Sect. 2.2.6) during 2002–2005 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Drained WTDs are the same as those in Figs. 2c, 3c, 4c and 5c for 2002, 2003, 2004 and 2005 respectively. Negative values of WTD mean depths below the hollow surface and positive values mean depths above the hollow surface.

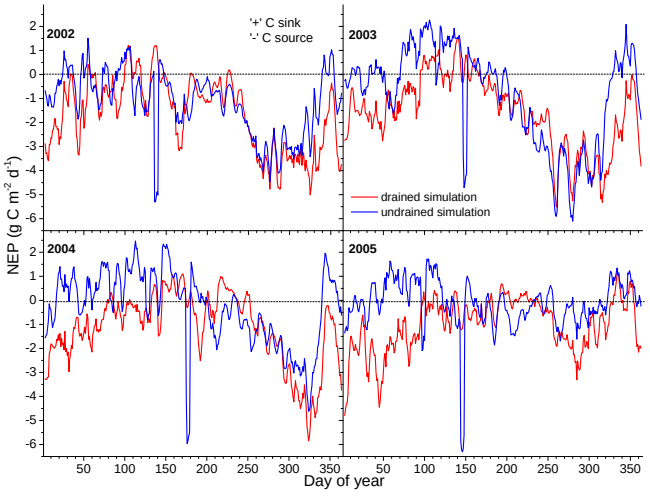

Fig. 10. Five-day moving averages of simulated daily net ecosystem productivity (NEP) for drained vs. undrained simulations (Sect. 2.2.6) during 2002–2005 over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. Drained values are the same as those in Figs. 2–5.

4.1.1 Hypothesis 1: WTD and NEP during rainy season

A shallower aerobic zone (Fig. 11) and resulting lower [O_{2s}] modelled during the 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 [O_{2s}] caused by shallow WTD forced [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 [O_{2r}] below the water table during this hydroperiod. Lower [O_{2r}] suppressed rates of C oxidation by root and mycorrhizal populations (C14a, b), thereby slowing root and mycorrhizal growth (C20b) below the water table. Consequently, root and mycorrhizal growth during this hydroperiod were largely confined to the shallow aerobic zone, thus limiting the soil volume from which nutrient (predominantly phosphorus) uptake (C23b, d, f) could occur. Slow phosphorus uptake reduced σ_P with respect to σ_C in leaves (C11), thereby slowing CO_2 fixation (C6) and hence GPP in the model as discussed in Sect. 2.1.4. The suppression of productivity with shallow WTD was also apparent in higher modelled and measured Bowen ratios ($\beta = H/\mathrm{LE}$) resulting from lower g_s required to conserve the ratio of CO_2 concentration at the photosynthetic site to that in the atmosphere ($C_c : C_a$) with slower CO_2 diffusion (Mezbahuddin et al., 2014). Reduction of GPP in our undrained simulation compared to our drained simulation was also caused by greater phosphorus limitation under shallower WTD (Table 4).

In tropical peatlands, phosphorus is likely to be more limiting to CO_2 fixation than nitrogen as indicated by foliar nitrogen to phosphorus ratios (N : P) ranging from 22 : 1 to 130 : 1 measured for different tree species growing in Indonesian peatlands (Tuah et al., 2000). A mass based foliar nitrogen to phosphorus ratio greater than 16 : 1 is thought to indicate phosphorus limitation to plant productivity over nitrogen limitation (Aerts and Chapin, 2000). This phosphorus limitation arises from low plant phosphorus availability resultant of high soil organic nitrogen to phosphorus ratios (N : P), low pH and high aluminum (Al) and iron (Fe) contents of these peats (Page et al., 1999, 2006; Rieley and Page, 2005). When site-specific inputs for soil pH, organic and inorganic nitrogen and phosphorus (Table 1), exchangeable Al (12 g Mg^{-1}) and Fe (21.6 g Mg^{-1}) were used in our modelling with site-independent algorithms for soil solute transformations (E1-E55) (Grant et al., 2009), soil solution phosphorus concentrations and hence root phosphorus uptake were forced to very low values. Low plant phosphorus availability and uptake in the model was reflected in lower modelled foliar phosphorus content ($\sim$ 2.5 g kg^{-1} C) during shallow WTD hydroperiods. Such low plant phosphorus status in our modelling was corroborated by even lower foliar phosphorus contents (0.2–1.4 g kg^{-1} C in matured leaves, assuming that 50 % of the dry matter was C) measured by Tuah et al. (2000) in the dominant tree species growing on our study site. Low foliar phosphorus contents in 150 tree species of tropical rain forests of Costa Rica and Brazil was also attributed to low phosphorus availability for plants growing on highly weathered phosphorus-deficient tropical soils (Townsend et al., 2007).

These results from the model are also consistent with those from Milner (2009) from a transect study on the effect of soil fertility on vegetation diversity of a tropical mixed swamp forest surrounding our study site. She found a reduction in basal area and tree growth in areas where the WTD was shallower by only $\sim$ 0.10 m. She speculated that the reduced tree growth was a result of low nutrient availability caused by anoxia under shallow WTD. Slow nutrient (phosphorus) mineralization in wet soils under shallow WTD may have reduced CO_2 diffusion and thereby fixation and productivity in her study site which supports the nutrient stress theory in our hypothesis 1. Moreover, a reduction in foliar phosphorus content during the rainy season with respect to mid-wet and dry seasons was also measured by Townsend et al. (2007) in tropical forest species of Costa Rica. Furthermore, tropical mangroves in Panama, Belize and Florida have shown significant increases in leaf CO_2 assimilation and plant growth with phosphorus enrichment indicating phosphorus stress to leaf gas exchange under anoxic conditions despite those species being well adapted to flooding stress (Lovelock et al., 2004, 2006a, b and c). Similar suppression of productivity caused by low nitrogen availability and uptake can also be found in boreal peatlands which are known to be more nitrogen than phosphorus limited as reported in experimental (Flanagan and Syed, 2011; Sulman et al., 2010) and modelling studies (Grant et al., 2012a; Sulman et al., 2012) across northern boreal peatlands.

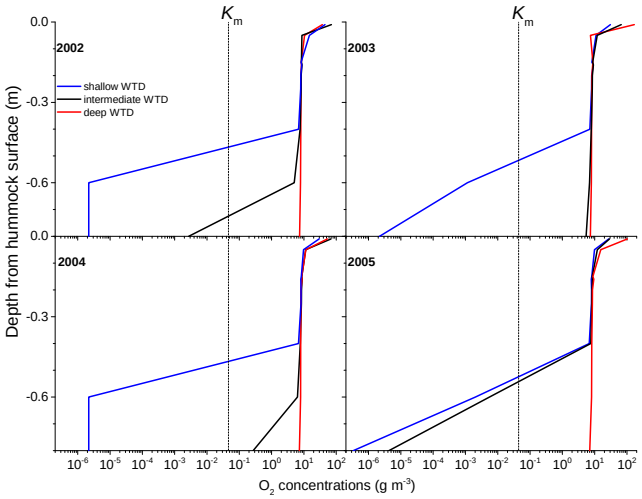

Fig. 11. Vertical profile distributions of peat soil aqueous oxygen concentrations ($[O_{2s}]$) simulated under hummock surface during shallow (DOY 15, 55, 25 and 55 of 2002, 2003, 2004 and 2005 respectively), intermediate (DOY 135, 160, 195 and 135 of 2002, 2003, 2004 and 2005 respectively), and deep (DOY 265, 265, 305 and 255 of 2002, 2003, 2004 and 2005 respectively) water table depth (WTD) hydroperiods over a drainage affected tropical peat swamp forest at Palangkaraya, Indonesia. K_m = Michaelis-Menten constant (0.064 g m^{-3}) for microbial, root and mycorrhizal uptake (A17a, C14c) in *ecosys*.

During shallow WTD in rainy seasons, $[O_{2s}]$ below the water table was almost zero (Fig. 11) 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 $[O_{2s}]$. In these layers, DOC oxidation was coupled with DOC reduction by anaerobic heterotrophic fermenters, which yielded much less energy (4.4 vs. 37.5 kJ g C^{-1}) (A21) than did O_2 reduction and so resulted in slower microbial growth (A25) and R_h (A13) as discussed in Sect. 2.1.2. However, $[O_{2s}]$ above the water table during shallow WTD hydroperiod was well above K_m (Fig. 11) used for simulated microbial, root and mycorrhizal O_2 uptake so that R_h in this zone was not limited by $[O_{2s}]$. 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. This absence of suppression in modelled R_e during shallow WTD hydroperiods can further be corroborated by no significant decrease or even slight increase in nighttime EC-gap filled CO_2 fluxes during shallow compared to intermediate WTD hydroperiods (Fig. 7). Similar absence of suppression in soil respiration during shallow WTD hydroperiods compared to those in intermediate WTD hydroperiods were also measured by

Sundari et al. (2012) in our study site and Jauhiainen et al. (2008) in a nearby drained tropical peatland.

Shallow WTD during the rainy season thus caused lower NEP (Figs. 2–6) to be modelled over PDPSF through reducing GPP due to plant nutrient (phosphorus) stress and hence net CO_2 uptake (Figs. 7–8). This GPP suppression from nutrient stress during shallow WTD hydroperiod was well corroborated by EC-gap filled CO_2 fluxes (Fig. 7) (Table 2) as well as other biometric measurements (e.g. Townsend et al., 2007) and hence validated our hypothesis 1.

4.1.2 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 more rapid and deeper root growth (C20b) and hence phosphorus uptake (C23b, d, f). Uptake was further stimulated by more rapid mineralization of organic phosphorus (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 phosphorus uptake in turn increased σ_P:σ_C in leaves (C11), thereby facilitating rapid CO_2 fixation (C6) and hence GPP as discussed in Sect. 2.1.4. Rapid CO_2 fixation from improved plant phosphorus status was also apparent in larger EC-gap filled downward net CO_2 fluxes during intermediate WTD hydroperiods in 2002, 2003 and 2005 (Fig. 7). Rapid CO_2 fixation due to improved plant phosphorus status can further be corroborated by 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 PDPSF (Mezbahuddin et al., 2014).

Foliar phosphorus content was reported as a good indicator of soil phosphorus availability in many studies (e.g. Aerts and Chapin, 2000; Townsend et al., 2007). Modelled foliar phosphorus content increased from $\sim 2.5\,g\,kg^{-1}$ C in the wet season to $\sim 3\,g\,kg^{-1}$ C in the early dry season indicating increased soil phosphorus availability and subsequent increased plant phosphorus uptake in the early dry season with intermediate WTD. This increase in modelled foliar phosphorus content by $\sim 20\,\%$ from rainy to early dry season was consistent with a 25 % increase in foliar phosphorus content from wet to mid-wet and dry seasons measured by Townsend et al. (2007) in tropical forest species of Costa Rica. Similarly, higher foliar phosphorus content modelled in the drained simulation ($\sim 3\,g\,kg^{-1}$ C) than in the undrained simulation ($\sim 2.5\,g\,kg^{-1}$ C) during this hydroperiod raised GPP, further indicating improved phosphorus status due to deeper WTD (Table 4). Increased productivity resulting from improved nutrient (phosphorus) availability with WTD drawdown has been found in field studies for Indonesian peatlands (Milner, 2009), and Florida everglades wetlands (Saha et al., 2010). These field measurements further support our modelling hypothesis 2 of improved plant nutrient (phosphorus) status with improved soil aeration which increased GPP and hence NEP during intermediate WTD hydroperiods. Increased GPP with WTD drawdown was also measured by Sulman et al. (2009) and Flanagan and Syed (2011) for northern boreal peatlands. However, in those ecosystems, the drawdown of WTD could improve plant nitrogen rather than phosphorus availability and uptake and hence productivity as modelled with *ecosys* by Grant et al. (2012).

A deeper aerobic zone and resulting increase in $[O_{2s}]$ during the intermediate WTD hydroperiod in the early dry season (Fig. 11) 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 nighttime net CO_2 fluxes 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 to 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.

Intermediate WTD during the early dry season thus caused higher NEP (Figs. 2–6) over PDPSF by a combination of increased GPP and unchanged or slightly decreased R_e (Figs. 7–8). This trend of increased GPP with improved nutrient (phosphorus) status and unchanged R_e due to offsetting effects of surface vs. deep respiration was well corroborated by EC-gap filled CO_2 fluxes (Fig. 7) (Table 2) and other field measurements in our study site and in similar ecosystems and hence validated our hypothesis 2.

4.1.3 Hypothesis 3: WTD and NEP during late dry seasons

GPP during the 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 located (Mezbahuddin et al., 2014). These changes in turn forced higher Ω_r (B10), lower ψ_r, ψ_c, ψ_t (B4) and g_s (B2b) (Mezbahuddin et al., 2014) and hence slower CO_2 diffusion (C6) through stomata and consequently less GPP (Sect. 2.1.4). GPP suppression due to plant water stress can further be corroborated by higher measured and modelled β resulting from lower g_s as described in our

concurrent paper on modelling WTD effects on surface energy exchange over PDPSF (Mezbahuddin et al., 2014). Reductions in GPP resultant of plant water stress can also be corroborated by reductions in latent heat fluxes and consequent increases in βduring the late dry seasons as reported by Hirano et al. (2005) for our study site.

Deeper peat respiration during the deep WTD hydroperiod greatly increased due to abundant [O_{2s}] in the deeper aerobic zone (Fig. 11) 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. 4.1.2, 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. 2–6) by a combination of reduced GPP and increased R_e (Figs. 7–8). This trend of decreased GPP due to plant water stress and increased R_e due to enhanced deeper peat respiration during deep WTD hydroperiods was well corroborated by EC-gap filled CO_2 fluxes (Fig. 7) (Table 2) as well as by other field measurements over same site or similar ecosystems and hence validated our hypothesis 3.

4.2 Modelling WTD effects on annual tropical peatland C balance

4.2.1 Differences in annual EC-derived vs. modelled NEP, R_e and GPP

Modelled annual NEP was considerably lower than the EC-gap filled annual NEP in 2003 and 2004 (Table 3). These lower NEP estimates were mainly attributed to larger modelled vs. gap-filled R_e predominantly in the rainy seasons (Fig. 1) which was consistent throughout the study period and yielded larger slopes from modelled vs. gap-filled net CO_2 flux regressions (Table 2). During the rainy seasons throughout the study period, modelled water table never rose above the hollow surface leaving the top 0.05 m of hollow and the entire hummock unsaturated even when the WTD was the shallowest (Figs. 2–5). This trend was consistent with the observed daily WTDs (Figs. 4–5). Total porosity for the top 0.2 m of the modelled peat was 0.89 calculated from bulk density provided to the model (Mezbahuddin et al., 2014), consistent with field measurements in similar drained tropical peatlands (Couwenberg and Hooijer, 2013; Hooijer et al., 2012; Jauhiainen et al., 2012b; Takakai et al., 2006). Therefore, when θ in the top 0.2 m rose from $\sim 0.22\,m^3\,m^{-3}$ in the dry seasons to just above $0.30\,m^3\,m^{-3}$ in the rainy seasons, near surface peat in the model still had enough air filled porosity for soil respiration not to be suppressed (Fig. 1). Moreover, wet surface residue from frequent rainfall caused large flushes of modelled residue CO_2 effluxes during rainy seasons which were also apparent in soil respiration measurements by Sundari et al. (2012) at our study site. However, despite a similar rise in θ measured vs. modelled in the top 0.2 m, gap-filled CO_2 effluxes were much smaller than the modelled CO_2 effluxes during the rainy season (Fig. 1). Such smaller gap-filled vs. modelled nighttime NEP (Fig. 1) was consistent throughout the rainy seasons (November–April) of 2002–2005 as indicated by a slope of 1.24 from a regression of modelled on gap-filled net CO_2 fluxes ($n = 13218$). However, a slope of 0.98 from regression of modelled on EC-measured CO_2 fluxes ($n = 4464$) for the same hydroperiods indicated better model agreement with EC-measured fluxes. Since 75 % of the total hourly CO_2 fluxes during rainy seasons of 2002–2005 were gap-filled, larger modelled vs. gap-filled CO_2 fluxes during these hydroperiods could largely contribute to larger modelled vs. EC-derived annual R_e and hence lower modelled vs. EC-gap filled annual NEP estimates (Table 3).

Systematic uncertainties embedded in EC methodology were also thought to contribute to larger modelled vs. EC-derived monthly and annual R_e estimates (Fig. 8) (Table 3). Nighttime EC NEP decreased with u^* below $0.3\,m\,s^{-1}$ in our study site (Hirano et al., 2007) indicating the dependence of nighttime CO_2 flux measurements on above-canopy turbulent mixing (Miller et al., 2004). However, biological production of CO_2 by plant and microbial respiration was independent of u^* in the model. Possible underestimation of nighttime NEP resultant of uncertainty related to low u^* threshold can be as large as $\sim$ 45% of nighttime CO_2 fluxes estimated by Miller et al. (2004) for an Amazonian rainforest which would further contribute to larger modelled vs. EC-derived R_e estimates.

Larger modelled vs. gap-filled R_e contributed to larger modelled vs. gap-filled annual GPP (Fig. 8) (Table 3). In EC datasets, GPP was derived from extrapolated daytime R_e (Sect. 2.2.2) and hence smaller gap-filled vs. modelled nighttime R_e would cause smaller EC-derived GPP. A further cause of smaller EC-derived vs. modelled GPP could have been the incomplete ($\sim 80\,\%$) energy balance closure in EC measurements (Wilson et al., 2002) vs. complete energy balance closure in the model, which would reduce EC-derived ET and also possibly GPP (Table 3).

Apart from above mentioned systematic errors, random errors in EC measurements and gap filling could also contribute to divergence between modelled and EC-gap filled annual NEP estimates. Hirano et al. (2012) estimated an uncertainty of about $\pm 25\,g\,C\,m^{-2}\,yr^{-1}$ in NEP estimates resultant of random errors in EC measurements and gap filling during 2002–2008 over our study site. Continuous data gaps due to instrumental failure can induce additional uncertainty in EC-gap filled annual NEP estimates. Richardson and Hollinger (2007) estimated an additional uncertainty of

$\pm 30\,g\,C\,m^{-2}\,yr^{-1}$ in NEP estimates for a week long gap in flux data over a range of forested FLUXNET sites. Additional uncertainties in EC-gap filled NEP estimates due to errors in filling continuous data gaps, however, were not quantified for the EC-gap filled NEP datasets used in our study. Such uncertainties could be substantial in EC-gap filled NEP estimates used in our study due to the presence of very long continuous data gaps (e.g. 11–22 November 2002, 3–31 January 2003, 29 March–22 May 2003, 24 June–26 July 2003 and 14 September to 9 October 2004) resultant of instrumental failures. Positive uncertainties due to above mentioned random errors could further contribute to larger EC-gap filled vs. modelled annual NEP, and hence smaller EC-derived vs. modelled annual R_e and GPP estimates.

All of these above mentioned sources of larger modelled vs. EC-derived R_e and GPP estimates were related to EC methodology and gap filling. These discrepancies between modelled and EC-derived R_e and GPP aggregates, however, could not be resolved in our modelling since, unlike EC datasets, every single mole of CO_2 that was modelled from fundamental ecosystem processes was counted in the modelled C budget.

4.2.2 Differences in annual WTD effects on EC-derived vs. modelled GPP and R_e

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 EC-gap filled net CO_2 fluxes by Hirano et al. (2007) (Sect. 2.2.2) (Table 3) although monthly partitioned GPP and R_e showed the similar seasonal trends as those modelled (Fig. 8). Accumulation of above-mentioned discrepancies between modelled and EC-gap filled fluxes (Sect. 4.2.1) over a larger time scale (e.g. from monthly to annual) obscured the agreement between the modelled and EC-gap filled trends in WTD effects on annual GPP and R_e. Furthermore, as opposed to EC-derived R_e that was used to calculate EC-derived GPP, modelled R_e ($R_a + R_h$) was driven by modelled GPP thereby contributing to deviation between WTD effects on modelled vs. EC-derived annual GPP and R_e. Modelled R_a was directly dependent on fixed C products during photosynthesis. Modelled R_h was also dependent on fixed C products in a diurnal time scale through root exudates as well as in a seasonal time scale through above and below ground litter fall.

Difference in flux partitioning methods may also produce variable agreements between modelled and EC-derived annual GPP and R_e aggregates. Desai et al. (2008) found a variability of $\sim 10\,\%$ in annual GPP and R_e estimates for 23 different flux partitioning methods over six European temperate forest. This difference was comparable to typical interannual variability in GPP and R_e over those sites. They also reported higher variability among those partitioning methods in estimating nighttime R_e that arose from frequent data gaps during calm night hours. Annual GPP and R_e aggregates for different partitioning methods in their study also varied abruptly for a Mediterranean site indicating spatial variability of partitioning method induced variation in annual GPP and R_e estimates. Moreover, artificially created data gaps of 10 % of total half-hourly net CO_2 fluxes in a year imparted additional 6–7 % variability in annual GPP and R_e aggregates in their study. These artificially created data gaps also contributed to a variability of $\pm 25\,g\,C\,m^{-2}\,yr^{-1}$ in annual NEP estimated for 15 different gap filling techniques (Moffat et al., 2007). Above mentioned partitioning method induced variations in annual GPP and R_e aggregates as estimated by Desai et al. (2008) could be more substantial over the drainage affected tropical peat swamp forest under this study due to longer growing season (i.e. tropical evergreen vs. temperate winter deciduous phenology) and larger soil CO_2 effluxes (i.e. tropical drained peat soils vs. temperate mineral soils).

We did not, however, examine whether a partitioning method other than the one used in this study (Sect. 2.2.2) could produce better agreement between modelled and EC-derived annual GPP and R_e aggregates. Inclusion of such a substantial study could obscure our main objective of portraying mechanistic relationships between seasonal variation in WTD and that in NEP which has been adequately corroborated by the regression analyses between hourly modelled vs. EC measured net ecosystem CO_2 fluxes (Table 2). However, comparing different flux partitioning methods along with sophisticated ecosystem modelling is likely to direct a separate future research that would offer increased confidence in annual GPP and R_e estimates over tropical peatland ecosystems.

Despite the above mentioned divergence between modelled vs. EC-derived R_e and GPP estimates, components of modelled annual C balance were 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 3). Modelled R_h was comparable with R_h measured for a mature *Acacia* plantation on drained Indonesian peatlands (Table 3).

4.3 Effects of WTD on modelled annual C balance in drained vs. undrained simulation

Reduced WTD by an average of ~ 0.5 m resulted in an increased mean NEP by $270\,g\,C\,m^{-2}\,yr^{-1}$ in undrained simulation compared to that in drained simulation over 2002–2005 (Table 4). This modelled trend was corroborated by measurements of Hirano et al. (2012) who found a larger mean NEP by $\sim 153\,g\,C\,m^{-2}\,yr^{-1}$ in a nearby undrained peat swamp forest than that in our drainage affected peat swamp forest site over 2004–2008. This increase in NEP in undrained simulation was modelled through greater suppressions of R_a and R_h than of GPP with reduced WTD (Table 4).

Apart from net vertical CO_2 exchange, drainage of tropical peatlands can also trigger substantial C losses through lateral transport of dissolved organic C (DOC). Moore et al. (2013) measured a drainage-induced additional C loss of $20\,g\,C\,m^{-2}\,yr^{-1}$ through the export of DOC in our study area. We, however, simulated a negligible additional increase in C losses through export of DOC ($1–2\,g\,C\,m^{-2}\,yr^{-1}$) due to drainage in this modelling study. Since transport of DOC heavily depends upon total amount of catchment discharge (Moore et al., 2013) this discrepancy between our point scale study and their watershed scale measurements on DOC transport is reasonable. However, up scaling our modelling to watershed scale might be a potential opportunity to examine the effects of drainage on C losses through export of DOC in drained tropical peatlands.

Even in the undrained simulation, NEP for 2002–2004 indicated substantial C losses from PDPSF (Table 4). Similarly large C losses were estimated from EC-gap filled NEP during 2004–2007 by Hirano et al. (2012) over a nearby similar undrained peat swamp forest. They also predicted from a simple linear regression analysis of NEP on WTD that maintaining a mean annual WTD within 0.03 m below 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 4).

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 $31\,g\,C\,m^{-2}\,yr^{-1}$ 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 $56\,g\,C\,m^{-2}\,yr^{-1}$ for last $\sim 20\,000$ yr (Page et al., 2004). One of the main reasons behind the modelled negative NEP 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 reduction of tropical peatland NEP during shallow and deep WTD hydroperiods with respect to those in intermediate WTD hydroperiods for four years, i.e. 2002–2005 over PDPSF (Figs. 2–5) (Table 2). Reduction of NEP during shallow WTD was modelled mainly through reduced GPP and that during deep WTD hydroperiods was modelled by a combination of reduced GPP and increased R_e (Figs. 6–8). Seasonal variation in NEP that was apparent in the measurements was thought to be caused by the following key responses that were modelled using following alogrithms of WTD effects on GPP and R_e from basic independent research fed by site specific inputs (Sect. 2.2.3):

1. Shallow WTD during rainy seasons reduced modelled NEP by explicitly simulating slower convective-dispersive O_2 transport through soils and roots and hence slower root O_2 uptake, slower soil nutrient (phosphorus) transformations (A26), slower root nutrient (phosphorus) uptake and growth (C23), and consequently lower leaf nutrient (phosphorus) status (C11) and slower CO_2 fixation (C6) (Sect. 4.1.1).

2. WTD drawdown during early and late dry seasons in the model increased deeper peat respiration due to better aeration by explicitly simulating higher $[O_{2s}]$ (A17) from 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) (Sects. 4.1.2. and 4.1.3).

3. Deeper WTD during late dry seasons in the model reduced NEP through plant water stress by explicitly simulating 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. 4.1.3).

Though our modelling effort reasonably well simulated seasonal WTD effects on NEP over PDPSF, the modelled GPP and R_e aggregates were systematically larger than the EC-derived estimates (Fig. 8) (Table 3). The possible reasons for these discrepancies are discussed in Sect. 4.2. Despite the modelled vs. EC-derived divergence in monthly and annual R_e and GPP aggregates, this study showed for the first time the application of a detailed process based model in gaining insights on nonlinear relationships between WTD and net ecosystem CO_2 exchange of tropical peatlands, 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 drained vs. undrained condition. 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.

Our point scale modelling reasonably delineated WTD effects on NEP over a homogeneous patch of drainage affected tropical peat swamp forest in terms of plant functional type (PFT) (i.e. tropical evergreen vascular vegetation) and land use (i.e. drained forest). However, this modelling can be up scaled to an ecosystem level by model inputs of weather data (Sect. 2.2.3); soil physical, hydrological, chemical and biological properties (Sect. 2.2.3) (Table 1) (Mezbahuddin et al., 2014); PFT (e.g. moss vs. vascular plants, evergreen vs. deciduous); and disturbance (e.g. drainage as discussed in Sect. 2.2.6, fire, logging etc.) representing a particular peatland ecosystem. Such up scaling studies over tropical peatlands could provide us with improved predictive capacity on management opportunities (e.g. undrained vs. drained, reforestation/afforestation vs. deforestation, unburnt vs. burnt) for reducing C emissions. This capacity might be very important for planning long-term tropical peatland rehabilitation projects and mapping peat C sequestration for current REDD+ (Reducing Emissions from Deforestation and forest Degradation) scheme.

Supplementary material related to this article is available online at http://www.biogeosciences.net/11/577/2014/bg-11-577-2014-supplement.pdf.

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