Greenhouse gas dynamics in degraded and restored tropical peatlands

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SUMMARY

Agricultural and other land uses on ombrotrophic lowland tropical peat swamps typically lead to reduced vegetation biomass and water table drawdown. We review what is known about greenhouse gas (GHG) dynamics in natural and degraded tropical peat systems in south-east Asia, and on this basis consider what can be expected in terms of GHG dynamics under restored conditions. Only limited *in situ* data are available on the effects of restoration and the consequences for peat carbon (C) dynamics. Hydrological restoration seeks to bring the water table closer to the peat surface and thus re-create near-natural water table conditions, in order to reduce wildfire risk and associated fire impacts on the peat C store, as well as to reduce aerobic peat decomposition rates. However, zero emissions are unlikely to be achieved due to the notable potential for carbon dioxide (CO_2) production from anaerobic peat decomposition processes. Increased vegetation cover (ideally woody plants) resulting from restoration will increase shading and reduce peat surface temperatures, and this may in turn reduce aerobic decomposition rates. An increase in litter deposition rate will compensate for C losses by peat decomposition but also increase the supply of labile C, which may prime decomposition, especially in peat enriched with recalcitrant substrates. The response of tropical peatland GHG emissions to peatland restoration will also vary according to previous land use and land use intensity.

KEY WORDS: fire, organic carbon, temperature, vegetation cover, water table.

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INTRODUCTION

In south-east Asia, population growth and the depletion of existing agricultural land - especially by erosion and through industrial and urban expansion - have provided compelling drivers for peatland reclamation[1] over the last three decades. The total area of lowland peatland in the region is 24.8 million hectares (Mha), which stores 68.5 Gt of carbon (C) and thus accounts for 77 % of the tropical and 11–14 % of the global peatland C store (Page *et al*. 2011).

Between 1990 and 2015, 50 % of the 15.7 Mha of peat swamp forest land in Peninsular Malaysia and on the islands of Borneo and Sumatra was converted to managed land, which included 22.4 % by smallholders and 27.4 % by industrial plantations. In 2015, about 20 % (3.2 Mha) of the area's peatlands were classified as 'open undeveloped' and 'secondary regrowth' while only 6 % of the forests showed no evidence of human influence (Miettinen *et al*. 2016). The largest single peatland reclamation scheme, i.e. the Mega Rice Project (1996–1998) in Central Kalimantan, intended for agricultural production, was alone responsible for deforestation and drainage of nearly one Mha of peatland, most of which was abandoned soon after reclamation.

The reclamation of peatland for agriculture usually leads to reduced vegetation biomass and water table (WT) drawdown (IPCC 2014). Typically, the original evergreen broadleaf forest is removed to make way for production of palm oil, *Acacia* pulp, vegetables *etc*. Because the root systems of most crop species - apart from sago (*Metroxylon sagu*), the source of sago flour - do not tolerate the anoxic conditions created by prolonged flooding, the seasonal soil surface flooding that occurs in undisturbed peat swamp forests is prevented by installing permanent drainage. Abandoned (degraded) peatlands are not under active management and are typically characterised by large annual fluctuations in WT level due to uncontrolled drainage, modest biomass in secondary shrub and fern dominated vegetation, and the impacts of wildfire on peat and vegetation (e.g. Jauhiainen *et al*. 2008, Page *et al*. 2009, Hoscilo *et al*. 2011, Ritzema *et al*. 2014).

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[1] The term 'reclamation' is used here in the following sense: the conversion of natural peatlands to agricultural, forestry and other uses by deliberate human actions, which usually involve making fundamental changes to vegetation biomass, vegetation type and/or hydrology.

The creation of a deeper oxic peat profile following drainage improves the conditions for aerobic decomposition and results in enhanced peat C removal to the atmosphere, both in gaseous form and through fluvial losses in drainage waters (IPCC 2014). Peat surface subsidence in drained areas, resulting from peat structural rearrangement and mass loss (e.g. Hooijer *et al*. 2012, Couwenberg & Hooijer 2013), is a further consequence. Annual net greenhouse gas (GHG) emissions arising from peat decomposition (i.e. heterotrophic respiration) are estimated at *ca.* 600 Mt carbon dioxide equivalents (CO_{2e}) (Hooijer *et al*. 2010) and a further 640 Mt CO_{2e} are released to the atmosphere from fires on peatlands in south-east Asia (GFED 2016).

There is general and increasing interest in the active utilisation of abandoned peat areas as plantations, reforested areas and for ecological restoration. However, *in situ* studies providing comparisons of hydrology, vegetation or peat GHG fluxes between degraded and rehabilitated conditions are mostly lacking from tropical peatland studies. In this review, we aim to provide insights on the GHG flux dynamics of rehabilitated degraded tropical peatlands. We focus on literature sources to provide an understanding of how peat C and nitrogen (N) dynamics could potentially change following the manipulation of hydrology and vegetation in degraded areas that are undergoing active restoration.

FACTORS AFFECTING GHG DYNAMICS

Greenhouse gas dynamics in tropical peat systems involve CO_2 uptake *via* photosynthesis and C losses through autotrophic respiration of the vegetation, heterotrophic respiration of soil animals and microbiota, and fluvial removals of C as particulates (POC) and dissolved organic matter (DOM) (e.g. Hirano *et al*. 2009, Jauhiainen *et al*. 2012a, Moore *et al*. 2013). Vegetation adds C to the peat surface as litter and into the peat from the rhizosphere, and thus contributes to maintenance of the peat C store by compensating for C losses that result from concurrent decomposition. Peat swamp forest litter is composed largely of coarse and fine roots, woody debris and leaf litter, and is rich in both cellulosic and more complex ligneous substrates (Miyajima *et al*. 1997). Because lignin is resistant to decomposition, the amount of cellulosic substrates decreases more and more rapidly as peat decomposition advances (Melillo *et al*. 1982, Brady 1997, Harmon *et al*. 2009). Also, tree roots excrete organic acids, amino acids and other C- and N-containing short-chained organic compounds, which may be important for

maintenance of the peat microbial community.

Over time, and with increasing peat depth, the fraction of decomposition-resistant substrates in the peat increases, particularly in the water-saturated (anoxic) zone away from the peat surface. In reclaimed peatlands, lower average WT, slower rates of litter deposition and less decomposition-resistant substrate types (e.g. Miyajima *et al*. 1997, Yule & Gomez 2009, Hertel *et al*. 2009, IPCC 2014) may be expected to lead to conditions whereby the deposited litter is more readily decomposed and decomposition resistant substrates become increasingly dominant close to the peat surface. Recent peat C compound composition studies in reclaimed and degraded swamp systems indicate that microbial degradation is enhanced under such circumstances (Könönen *et al*. 2016), and that similar consequences can arise from pyrolysis during fires (Milner 2013). Therefore, deforested, drained, and fire impacted peat systems are extreme environments for microbes because the surface peat is high in decomposition resistant C compounds, pH is low (< 4), and there can be extreme variations in oxygen supply, moisture content and peat surface temperatures (Iiyama *et al*. 2012, Sundari *et al*. 2012, Adji *et al*. 2014, Hirano *et al*. 2014, Jauhiainen *et al*. 2014). The most extreme conditions are likely to be found in severely fire affected deforested and drained peatlands, where previous recurrent fires have consumed the topmost peat exposing older and thus more decomposition resistant peat to aerobic decomposition (Figure 1) (Könönen *et al*. 2016). Combustion processes are also responsible for the replacement of labile C compounds with more resistant ones (Milner 2013). Recurrent fires can erase several decimetres of the topmost peat and keep vegetation regrowth (and litter deposition) modest (Page *et al*. 2002, Hoscilo *et al*. 2011, Konecny *et al*. 2016).

In addition to gaseous emissions of C from the peat surface, C is also lost from peatlands through off-site fluvial transport, principally in the form of DOC. In intact peat swamp forests, DOC arises from the decomposition of plant litter at the peat surface, as evidenced by the near-recent radiocarbon (^{14}C) age of the C, which indicates that the DOC does not come from long-term storage (Evans *et al*. 2007, Moore *et al*. 2013, Müller *et al*. 2015). In contrast, the thicker peat profile over which aerobic decomposition is active in drained peatlands gives rise to a higher DOC flux involving much older C derived from deeper-lying peat (Moore *et al*. 2013, Evans *et al*. 2014). In combination with drainage, burning has also been shown to increase the magnitude of the DOC flux during the post-fire period (V. Gauci personal communication). There have been few investigations

Figure 1. Surface peat in peat swamp forest (left) and in degraded burned peatland (right) in Central Kalimantan. Photos: Jyrki Jauhiainen.

of the fate of tropical DOC once it enters a fluvial system, although a recent study by Müller *et al.* (2015) indicates that in a short blackwater river system in northern Borneo, about one third of the DOC-C was outgassed as CO_2 following in-stream processing, while the remainder was discharged to the ocean. Evasion of CO_2 from DOC in peat-draining rivers is likely to be increased by drainage but this aspect of peatland fluvial C dynamics is the subject of ongoing studies.

The position of the WT in the peat, which reflects the balance between water gains (from precipitation) and losses (by evapotranspiration and outflow) over time, determines the volume of sub-surface peat that is subject to oxic conditions. Under oxic conditions, peat-forming organic polymers in litter can be decomposed by aerobic bacteria and fungi. In contrast, a succession of bacteria decompose the organic matter anaerobically in water-saturated peat, with methanogens producing methane (CH_4) as the terminal product, either from acetate and/or from CO_2 and hydrogen (H_2). Methanotrophic bacteria can consume upward-diffusing CH_4 in oxic conditions, releasing the C as CO_2 (Arai *et al.* 2014a).

The rate, seasonal distribution and volume of precipitation, which influence peat moisture and oxygen availability, have also been used to explain the GHG dynamics of tropical peat decomposition (e.g. Inubushi *et al.* 2003, Takakai *et al.* 2006, Arai *et al.* 2014b), although WT level in peat as a proxy for soil moisture is the most commonly applied abiotic factor (Figure 2) (IPCC 2014). Other factors that influence organic matter decomposition and GHG flux, such as peat temperature (influenced by vegetation cover) and peat substrate composition, have received less attention in tropical peatland studies (Brady 1997, Jauhiainen *et al.* 2014); although peat temperature, in particular, is likely to be an important co-factor. A few studies have included fertilisation in experimental designs for monitoring GHG emissions close to cultivated plants (e.g. Hadi *et al.* 2000, Takakai *et al.* 2006) or from bare peat (Jauhiainen *et al.* 2014) but, despite the widespread use of fertilisers on these agricultural peatlands, information on the effect of nutrient additions on organic matter decomposition is still limited.

Carbon dioxide is clearly the main GHG released by decomposition of tropical peat in both drained and natural conditions (Table 1) (IPCC 2014). Methane plays only a minor role in the peat GHG balance of
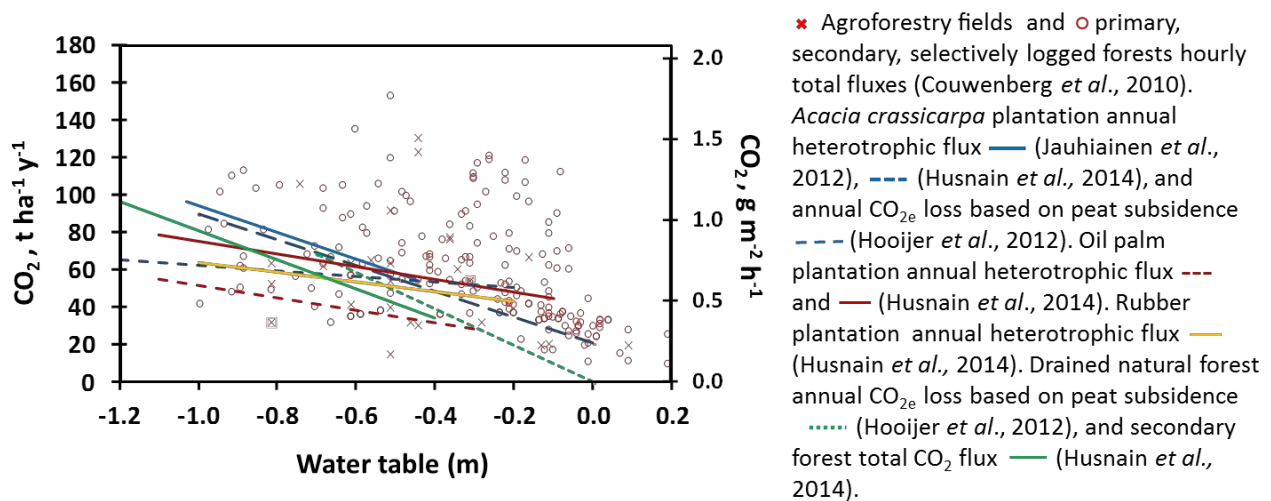
Figure 2. Relationship between peat carbon dioxide (CO_2) loss and peat water table level in (short-term) fluxes and in annual emission estimates. Total soil flux (g CO_2 m^{-2} h^{-1}) for agroforestry and primary, secondary and selectively logged forests from Couwenberg *et al*. (2010), modelled annual heterotrophic emission (t CO_2 ha^{-1} y^{-1}) for *Acacia crassicarpa* plantation (Jauhiainen *et al*. 2012a, Husnain *et al*. 2014) and rubber plantation (Husnain *et al*. 2014), CO_{2e} emissions modelled from peat subsidence for *Acacia* plantation and drainage-affected forest (Hooijer *et al*. 2012), and modelled total annual CO_2 emissions for secondary forest (Husnain *et al*. 2014).

Table 1. Carbon and greenhouse gas emission factors for drained tropical peatlands (IPCC 2014).

Source	Forest	Shrubland	Grassland	Rice	Cropland	Plantation	General[§]	Units
CO_2	5.3	5.3	9.6	9.4	14	15[*]	–	t C ha^{-1} yr^{-1}
DOC	–	–	–	–	–	–	0.82	t C ha^{-1} yr^{-1}
CH_4 (land)	4.9	4.9	7	143	7	2.7 – 26.2	–	kg ha^{-1} yr^{-1}
CH_4 (ditch)	–	–	–	–	–	–	2259	kg ha^{-1} yr^{-1}
N_2O	2.4	–	5	0.4	5	1.2 – 3.3	–	kg ha^{-1} yr^{-1}

[§]All land uses where data from ditches were available.
[*]Specific for plantation type; 20 t C ha^{-1} yr^{-1} for *Acacia crassicarpa* and 11 t C ha^{-1} yr^{-1} for oil palm.

south-east Asian peatlands, even when the peat is saturated with water. It is likely that the high lignin content of peat deposits in this region (Andriesse 1988, Brady 1997, Könönen *et al*. 2016) restricts the potential for CH_4 production from decomposition. However, the trunks of some adapted wetland tree species are known to facilitate egress of CH_4 from anoxic soils, although the contribution of tree-mediated emissions to total ecosystem CH_4 flux remains unknown (Pangala *et al* 2012). Data on nitrous oxide (N_2O) emissions exist but these are generally quite low from unfertilised peat (e.g. Hadi *et al*. 2000, Inubushi *et al*. 2003, Takakai *et al*. 2006, Jauhiainen *et al*. 2012b). In general, GHG emissions

from degraded tropical peatland forests are at the lower end of the range for reclaimed land uses (cf. shrublands in Table 1 derived from IPCC 2014).

EFFECTS OF HYDROLOGY RESTORATION ON GHG EMISSIONS

Restoration aims to revive the original resource functions of degraded ecosystems, thus re-establishing their environmental and economic services (Page *et al*. 2009). Re-wetting the peat (restoration of hydrology) is fundamental to both restoration of the vegetation and protection of the

remaining peat C stocks. The soil water regime of an undamaged peat swamp forest is typically characterised by inundation of the forest floor for several months during the wet season, alternating with more aerated conditions due to WT drawdown (to a depth of several decimetres) during the dry season (e.g. Sundari *et al.* 2012, Lampela *et al.* 2016). Artificial drainage systems increase water runoff and, thus, also the depth and duration of deeper WT conditions, especially towards the end of the dry season (e.g. Jauhiainen *et al.* 2008, Sundari *et al.* 2012, Ritzema *et al.* 2014). According to Ritzema *et al.* (2014), dams built in drainage canals in peat can reduce WT drawdown in upstream canal sections and the surrounding peatland during the dry season and ensure rapid re-establishment of higher (i.e. nearer the peat surface) WT levels after onset of the wet season, but cannot maintain WTs close to the peat surface during prolonged dry periods.

WT levels and emissions from decomposition
In both undrained and abandoned drained peatlands where the WT can rise up to the peat surface during periods when precipitation exceeds water runoff capacity, the lowest CO_2 flux rate occurs when the WT is close to the peat surface (Figure 2; Jauhiainen *et al.* 2005, 2008, 2012a; Hirano *et al.* 2009, 2014; Sundari *et al.* 2012). This can be explained by the reduced oxic space in the uppermost peat, which results in reduced rates of aerobic decomposition and the consequent CO_2 emissions. In drained peatlands the WT may sink far below the peat surface during periods with low rainfall, and such conditions result in a wide scatter of CO_2 flux data (Figure 2; Jauhiainen *et al.* 2008, Hirano *et al.* 2009, 2014). Because the number of observations in deeply drained peatlands is low, CO_2 flux models and projections (for both total and heterotrophic emissions) for exceptionally deep WT conditions have variously indicated a continued emission increase, emission saturation, or even an emission decrease after a peak emission level is reached (Jauhiainen *et al.* 2008, Hirano *et al.* 2009, 2014). Therefore, the duration of periods with WT some decimetres below the peat surface resulting in maximal CO_2 emission rates will be equally important in determining the annual emission budget.

Although CO_2 emissions from saturated peat are expected to be near zero (IPCC 2014, Wilson *et al.* 2016) and some models are forced through zero (e.g. Couwenberg *et al.* 2010), data from field studies show that CO_2 emissions can arise from water saturated and flooded peat surfaces, in both short- and long-term estimates (e.g. Figure 2, Inubushi *et al.* 2003, Furukawa *et al.* 2005, Jauhiainen *et al.* 2005,

2008). The CO_2 emissions from water-saturated peat are often thought to be derived from root respiration close to the monitoring location (especially when the total CO_2 flux is monitored) or from transported dissolved CO_2 that is released to the atmosphere from water moving slowly over the flooded peat surface (Jauhiainen & Silvennoinen 2012). Although it is often assumed otherwise, oxic conditions are not an absolute requirement for heterotrophic CO_2 release from peat, and comparable production rates can be reached under both oxic and anoxic conditions (e.g. Moore & Dalva 1997). Indeed, Hadi *et al.* (2001) suggest that the CO_2 production potential of water saturated tropical peat (rice paddy and rice paddy-soybean rotation) is high in *ex situ* conditions. A recent laboratory study demonstrated that the surface CO_2 production potential from decomposition of tropical peats differed by less than 50 % between oxic and anoxic conditions, which implies significant CO_2 production from anaerobic decomposition processes (Jauhiainen *et al.* 2016). The pathway, C-substrates and electron acceptors involved in this anaerobic CO_2 production have not yet been studied. If the CO_2 production rates under both oxic and anoxic (waterlogged) conditions were also substantial in the field situation, the emissions detected from the waterlogged soil surface would nonetheless be lower due to the restricted gas transfer capacity at the water-air boundary. Thus, if substantial CO_2 production from anaerobic decomposition under waterlogged conditions is a general phenomenon, fluvial export of this CO_2 in water flowing out from the peatland and degassing in waterways could form a large and integral part of the peat decomposition emissions derived from peatland areas (Moore *et al.* 2013, Jauhiainen & Silvennoinen 2012, Müller *et al.* 2015).

Methane is produced under anoxic conditions and flooded peat creates an optimal environment for its production with minimal potential for oxidation by methanotrophs before transfer to the atmosphere. Microcosm experiments show that woody ombrotrophic tropical peat has minor production potential for CH_4 relative to CO_2, even in anoxic conditions (Hadi *et al.* 2001), and this has been confirmed by concurrent CO_2 and CH_4 flux measurements in several *in situ* studies (e.g. Inubushi *et al.* 2003, Jauhiainen *et al.* 2005, 2008; Hirano *et al.* 2009, Arai *et al.* 2014a). Nitrous oxide emission rates over increasing WT levels usually reach a maximum when the WT is below the soil surface in drained peat (Jauhiainen *et al.* 2012b). It would appear that seasonal WT changes, particularly when the WT approaches the soil surface after the onset of the rainy season, enhance N_2O emissions (Takakai *et al.* 2006, Jauhiainen *et al.* 2012b, 2014). It is suggested that

this increase in emissions is due to enhanced microbial activity in litter that was deposited during previous drier conditions.

WT levels and emissions from combustion
Fires typically occur in drained peatlands, but the amount of C released by fire events is temporally and spatially variable (Figure 3). Undrained peat swamp forest is at very low risk of fire, even during extreme drought conditions (Page *et al.* 2002), since the WT is close to the forest floor and the entire peat column, together with the living forest biomass, is almost permanently moist. Logged-over forest is at greater risk of ignition due to an altered microclimate that promotes drying of the peat surface and aboveground fuels (Siegert *et al.* 2001). Peatlands where the WT is maintained at an artificially low level by drainage, i.e. in or adjacent to agricultural land, is at greatest risk of combustion, and under severe drought conditions C emissions caused by peat fires can be larger than those arising from decomposition. The most severe peat fires of recent years can be linked to droughts driven by the ENSO climate anomaly (Page *et al.* 2002, Field *et al.* 2009), although peat fires are now a regular feature of all dry seasons, even short ones (Gaveau *et al.* 2014). It should be noted, however, that while peat fires lead to a rapid pulse of C to the atmosphere (e.g. Page *et al.* 2002), they are time limited (to weeks or, during prolonged droughts, months), while C loss from peat decomposition is a year-round process (Hooijer *et al.* 2010).

A key difference between the emissions arising from microbial decomposition and combustion of peat is that the latter have a different GHG signature. During peat fires, C is emitted both as CO_2 and as CH_4 (IPCC 2014), which has a much higher global warming potential. High emissions of CH_4 result from the smouldering nature of peat ground fires (i.e. incomplete combustion processes in the absence of sufficient oxygen) (Rein *et al.* 2008). Peat fire emissions also contain a cocktail of carbonaceous volatile organic compounds (VOCs) such as benzene, formaldehyde *etc.* and small particulates, all of which are harmful to human health (Johnston *et al.* 2012). In degraded peatlands with unregulated drainage, where up to three, four or even eight fires may occur within a relatively short time period (10–15 years), the scale of C loss reduces with each fire event as combustion progressively lowers the peat surface, bringing it closer to the WT (Konecny *et al.* 2016). It has also been shown that proximity to drainage features, i.e. locations in the landscape where the WT is lowest, increases both the frequency of fires and the amount of C emitted, an effect that extends over a distance of at least 800 m from the drainage feature (Konecny *et al.* 2016). Peat fires may also be expected to result in enhanced loss of fluvial C (DOC and POC; collectively referred to as total organic carbon, TOC) in waterways draining from fire-affected peatlands. In a recent unpublished study that compared total fluvial C fluxes from a peatland in Central Kalimantan, TOC fluxes were found to be

Figure 3. Wildfire degrading vegetation close to forest edge (left) and a recently burned site with exposed tree roots on the peat surface (above) in Central Kalimantan. Photos: Jyrki Jauhiainen.

32–68 % larger in catchment channels affected by fires when compared to fluxes over the same time interval in a previous non-fire year (V. Gauci personal communication.). It is likely that increased fluvial C export will initiate enhanced evasion of CO_2 and CH_4 to the atmosphere through in-stream processing, further augmenting GHG emissions derived from peat fires.

In addition to consuming peat, fires destroy the woody vegetation cover (i.e. the C sink) and promote a retrogressive succession towards increasingly herbaceous plant communities (Hoscilo *et al*. 2011), consume nutrients in the surface peat, and increase soil surface exposure to the sun, resulting in increased peat surface temperatures (Jauhiainen *et al*. 2014). While no large scale studies have as yet demonstrated the effect of rewetting on fire occurrence in tropical peatlands, work by Konecny *et al*. (2016) indicates that as the peat surface approaches the WT, the volume of peat combusted by each successive fire, and hence the magnitude of the C loss, is reduced. It is therefore assumed that the same principle will apply to rewetted peatlands if the WT can be maintained at or close to the peat surface throughout the year. There is still a risk, however, that peat fires may establish during periods of prolonged drought when a high WT cannot be maintained. Under these circumstances it will be essential to minimise anthropic sources of ignition.

EFFECTS OF VEGETATION RESTORATION ON GHG EMISSIONS

Vegetation cover is essential for maintenance of the peat deposit as it provides the only source of C substrates to replace the C losses arising from peat decomposition. This C is derived from litter deposited both onto the peat surface (leaves and woody debris) and also directly into the rooting zone (dead root material) (e.g. Minkkinen *et al*. 2002). In peat swamp forests, the deposited litter is rich in both cellulosic and complex ligneous structural substrates (Miyajima *et al*. 1997), although lignin-rich and other decomposition-resistant substrates increase proportionally downwards in the peat profile due to faster depletion of the simpler cellulosic compounds (Melillo *et al*. 1982, Harmon *et al*. 2009). In a recent study, forest peat holocellulose content (dry mass basis) was found to decrease from 10 % in the topmost surface peat to 2 % at 80 cm depth and the Klason lignin content to increase correspondingly from 68 % to 72 % (Könönen *et al*. 2016). In reclaimed peatlands, the reduction in litter deposition and continued mineralisation of the peat under optimal conditions for aerobic decomposition also results in enrichment of decomposition-resistant substrates in the surface peat (*e.g.* Funakawa *et al*. 1996, Brady 1997). Indeed, the holocellulose content (1 % on a DW basis) of the topmost peat in degraded and burned land has been found to be only a fraction of the content (10 %) in topmost forest peat (Könönen *et al*. 2016). This can also be observed in the chemical characteristics of surface peat, which show increased C/N quotients (Könönen *et al*. 2015) and an increase in resistant organic compounds (e.g. aromatic- and aliphatic-derived compounds) in reclaimed peatlands (Milner 2013). The poorer peat substrate quality leads to lower GHG production in degraded and fire-affected peat in comparison to forest peat (Hirano *et al*. 2014).

Restoration activities on degraded tropical peatlands aim to increase both vegetation cover and biomass. This, in turn, will influence the C dynamics of the peat by increasing the supply (in litter) of substrates containing labile and structural C and N. This can be expected to enhance decomposition of the peat and thus to increase GHG emission rates. However, experimental field data showing how the peat C balance is affected are not available, and estimates of the contribution of litter turnover to peat GHG emissions are currently based only on data obtained from the literature (IPCC 2014). A recent study based on field data from boreal and temperate peatlands shows that vascular plants can prime the decomposition of existing decomposition-resistant substrates under rewetted conditions (Walker *et al*. 2016). Similarly, the results of a recent microcosm study by Jauhiainen *et al*. (2016) indicate that adding labile C (as glucose and glutamate) to tropical peat increases rates of CO_2 production from peat C mineralisation to 2–3 times the rates for non-augmented peat collected from typically waterlogged locations. Smaller or more variable changes in mineralisation rates were observed in surface peats from forested and degraded land.

Increased shading reduces the temperature of the uppermost peat. Thus, both daytime averages and diurnal ranges of peat surface temperature differ substantially between open and tree-covered areas (Jaya 2007, Jauhiainen *et al*. 2012a), even though seasonal differences in soil temperature are smaller in the lowlands of the humid tropics than in higher-latitude areas. Jaya (2007) reported diurnal averages of upper peat temperature in Central Kalimantan of 22.9 °C for intact peat swamp forest, 26.7 °C for heavily degraded forest and 30.2 °C for an agricultural area. Because shading affects peat temperature, decomposition-derived CO_2 flux budgets have been applied to emission budgets as a

correction for fluxes measured during daytime in *Acacia crassicarpa* plantations, where the difference between daytime and diurnal temperatures was concluded to lead to a 14.5 % reduction in heterotrophic fluxes monitored during the day when cooler night time peat temperature conditions were taken into account (Jauhiainen *et al.* 2012a).

To the best of our knowledge, only one study has directly measured the effect of temperature on tropical peat decomposition in field conditions. Jauhiainen *et al.* (2014) investigated GHG emissions from apparently similar open drained agricultural land and degraded land under four peat temperature conditions created by shading (levels between 0 % and 90 %). The correlation between peat temperature and CO_2 flux indicated that, without shading, the emission rate on the agricultural land changed by approximately 8 % (unfertilised) and 25 % (fertilised with NPK at 50 kg ha^{-1}) for each 1 °C temperature change at 5 cm depth; whereas higher shading levels, i.e. lower surface peat temperatures, resulted in lower CO_2 emission rates (Jauhiainen *et al.* 2014). Conversely, no response to surface peat temperature was observed in CO_2 emissions from the degraded land, and it was suggested that this may arise from differences in the characteristics of microbial communities between actively managed and degraded land.

The temperature dependence of the CH_4 flux rate in peat has been studied only in drained conditions, where the correlation remained low (Jauhiainen *et al.* 2014), and as yet no data are available on the response of CH_4 emissions to anoxic flooding conditions. For N_2O, the possible dependence of flux on temperature needs more clarification, as increased N availability appears to result in a negative flux-temperature correlation that is not present under unfertilised conditions (Jauhiainen *et al.* 2014). Nevertheless, studies from other terrestrial ecosystems show that microbial N_2O consumption (i.e. the reduction of N_2O to N_2) increases with temperature (Nömmik 1956, Maag & Vinther 1996, Holtan-Hartwig *et al.* 2002) and a similar relationship may apply in tropical peat soils.

In the tropics, successful restoration is far more challenging than in boreal and temperate zones where the peat is formed by sedges and/or *Sphagnum*. Rapid vegetation recovery occurs after rewetting of peatlands that were previously drained for forestry, as diaspores of mire plants are nearby and can spread faster and more easily than tree propagules in the tropics, which may require animal vectors for dispersal (Vasander *et al.* 2003, Page *et al.* 2009, Blackham *et al.* 2014). Under optimal hydrological conditions, even restored peat extraction areas in the early stages of revegetation can form a large CO_2 sink comparable to that of a pristine peatland ecosystem (Soini *et al.* 2010, Wilson *et al.* 2016). In general, the results of peatland restoration in temperate and boreal zones are usually promising provided that the ecohydrology of the area to be restored resembles that of the pre-drainage era (Bonn *et al.* 2016). These observations from northern peatlands may, in time, provide useful ground rules for peatland restoration in the tropical zone.

CONCLUSIONS

Land reclamation causes changes in biotic (e.g. vegetation and litter) and abiotic (e.g. WT, moisture, temperature) conditions, and as a consequence there is a change in both physical and chemical characteristics of the peat. Peatland restoration activities seek to achieve higher WTs and re-establish a high vegetation biomass in order to restore the pre-reclamation peat functions. Hydrological restoration seeks to maintain a WT closer to the peat surface and to create near-pristine WT conditions in order to (i) reduce wildfire risk and associated fire impacts on the peat C store, and (ii) reduce decomposition rates in the aerobic peat, although (iii) zero emissions may not be achieved due to potentially high anaerobic CO_2 production. The importance of fluvial C losses, which result in the export of relatively large amounts and differing types of C, has also recently gained recognition. An increase in vegetation cover, ideally a woody vegetation cover, will (i) reduce peat surface temperatures due to shading, which may in turn reduce aerobic decomposition rates; and (ii) increase the amount of labile C compounds in the surface peat, which may result in enhanced peat decomposition (priming), especially in peat enriched with decomposition-resistant substrates. For the continued existence of peat, C deposition in litter must outbalance C losses from organic matter decomposition. Land management activities prior to restoration may have changed the nutrient status, the C compound composition and the microbial community of the peat, and thus the response of GHG emissions to peatland restoration may vary according to the previous land use and land use intensity. The best prognosis for preservation of the peat C store is likely to be achieved by maintaining a sufficiently high WT to minimise CO_2 emissions from aerobic decomposition and establishing a high-biomass vegetation cover, such that the amount of C deposited as plant litter, both above and below ground level, eventually exceeds the amount of C removed from the system in gaseous and other forms.

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