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Peatlands and the carbon cycle: from local processes to global implications – a synthesis

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Abstract

Although peatlands cover only 3% of the Earth's land surface, boreal and subarctic peatlands store about 15–30% of the world's soil carbon as peat. Despite their potential for large positive feedbacks to the climate system through sequestration and emission of greenhouse gases, peatlands are not explicitly included in global climate models and therefore in predictions of future climate change. In April 2007 a symposium was held in Wageningen, the Netherlands, to advance our understanding of peatland C cycling through integration across disciplines and research approaches and to develop a more synthetic picture of the present and future role of peatlands in the global C cycle and their interactions with the climate system. This paper aims to synthesize the main findings of the symposium, focusing on (i) small-scale processes, (ii) C fluxes at the landscape scale, and (iii) peatlands and climate. The paper concludes with a summary of the main drivers of the C balance of peatlands, and proposes directions for new research to reduce key uncertainties in our knowledge of C cycling in peatlands in order to facilitate the explicit inclusion of these ecosystems in a new generation of earth system models.

1 Introduction

Despite covering only 3% of the Earth's land surface, boreal and subarctic peatlands store about 15–30% of the world's soil carbon as peat (200–400 10^{15} g C; Botch et al., 1995; Turunen et al., 2002), and this excludes the peat stored in the fast disappearing 16–27 million ha of tropical peatlands (Sorensen, 1993; Hooijer et al., 2006). These massive deposits are the legacy of peatlands acting as sinks of atmospheric carbon dioxide (CO₂) for millennia, but also illustrate the potential for large CO₂ and methane (CH₄) fluxes to the atmosphere if peatlands were to be destabilized by global warming and changes in land use. Up to now, peatlands have contributed to global cooling on the millennium scale (Frolking and Roulet, 2007) and, at present, undisturbed peat-

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lands are likely to continue functioning as net carbon (C) sinks at the decadal scale, despite the large interannual variability of individual peatlands (Moore et al., 1998). Whether peatlands will continue their function as net C sinks remains uncertain, and depends on the impact of environmental and anthropogenic forcing on the C balance of these ecosystems (Moore, 2002; Page et al., 2002, 2008 this issue). Despite their proven role in past and present global cooling and their potential for large positive feedbacks to the climate system through sequestration and emission of greenhouse gases, peatlands are not explicitly included in global climate models and therefore in predictions of future climate change (IPCC, 2007).

In April 2007 a symposium was held in Wageningen, the Netherlands (Wieder et al., 2007), to advance our understanding of peatland C cycling through integration across disciplines and research approaches and to develop a more synthetic picture of the present and future role of peatlands in the global C cycle and their interactions with the climate system. This paper aims to synthesize the main findings of the symposium, with special focus on the key drivers of the C balance of peatlands at different spatial scales. We do not cover carbon stocks and processes for arctic tundra ecosystems involving permafrost, as they are discussed by Hayes et al. (2007).

With a process based approach we hope to contribute to the integration of research results across climatic zones, improving future predictions of the response of the peatland C balance to environmental and climate change. This paper presents a new synthesis on (i) small-scale processes, (ii) C fluxes at the landscape scale, and (iii) peatlands and climate. The paper concludes with a summary of the main drivers of the C balance of peatlands, and proposes directions for new research to reduce key uncertainties in our knowledge of C cycling in peatlands in order to facilitate the explicit inclusion of these ecosystems in a new generation of earth system models.

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2 Small scale processes and plant-soil feedbacks

Understanding the mechanisms controlling aerobic and anaerobic respiration at small spatial scales is particularly valuable for improving our predictions of potential effects of climate changes and perturbations, such as N deposition, on the peatland C flux. Furthermore, more insight in the feedbacks between vegetation, soil physical processes and aerobic and anaerobic respiration may allow us to better understand the high spatial and temporal variability of peatland C fluxes to water and atmosphere, particularly the production and oxidation of CH₄ (Sects. 3 and 4, Schrier et al., 2008 this issue) and generation and export of DOC (Sects. 3 and 4).

2.1 Biogeochemistry

At small spatial scales a close interaction exists between physical factors controlling transport processes of gases and soil microorganisms that use either oxygen or other electron acceptors as energy sources to breakdown organic material to final products such as CO₂, CH₄ and dissolved organic carbon (DOC). The availability of electron acceptors and the quality of the organic material in terms of nutrient content and degradability regulate the decomposition processes and influence the final product of decomposition. In addition, environment-enzyme interactions pose additional limitations as most soil microorganisms are dependent on the activity of extra cellular enzymes. Changes in the environment may either directly affect microbial activity by acting on the availability of electron acceptors or indirectly through changes in vegetation or soil physical structure. Direct impacts are, for example, caused by the deposition of nitrogen (N) and sulphur (S), or oxygenation after water table draw-down during summer drought. Indirect impacts comprise the change towards plant species with more decomposable litter or more root exudates (see Sect. 2.2).

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2.1.1 Biogeochemical processes and drivers

Understanding the drivers of below-ground carbon cycling, irrespective of peatland type, may be facilitated by describing the C cycle in terms of electron transfer processes (Fig. 1). Primary production provides reduced compounds that are buried as litter or released below-ground by vascular root activity creating a redox gradient to the atmosphere, which results in below-ground oxygen consumption and transfer by gas diffusion, advection and aerenchymatic transport in roots (Shannon and White, 1994; Chanton and Whiting, 1996). Oxidative capacity can further be stored in the form of electron acceptors, i.e. nitrate, ferric iron hydroxides, sulfate, and humic substances, which can be used as oxidants for organic matter in respiration, and whose utilization is broadly regulated by differences in the Gibbs free energy of the respective respiration processes and the concentrations of electron acceptors and donors (Achnich et al., 1995; Keller and Bridgham, 2007).

It is furthermore important that the electron transfer processes proceed in an environment that is strongly vertically structured (Fig. 1D). The relative importance of root respiration versus heterotrophic respiration generally decreases with depth. Fine roots of shrubs, for example, are often restricted to the acrotelm (i.e. unsaturated zone) of ombrotrophic peatlands (Moore et al., 2002). The ongoing decomposition produces increasingly decomposed and recalcitrant litter residues with burial; however, this is not a uniform process, because litter input occurs from both the surface and the root system, and because root exudates and litter leachates are also transported (Chanton et al., 1995). The transport of gases and solutes slows with depth, as diffusion coefficients and hydraulic conductivities of the peat decrease with water saturation and compaction (Waddington and Roulet, 1997; Fraser et al., 2001). Finally, the concentrations of electron acceptors, in particular oxygen, decrease with distance from their atmospheric source and with slowing transport and deplete rapidly in the saturated zone (Blodau et al., 2004; Fig. 1).

The emission of methane is a function of its rate of production, transport and oxida-

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tion. High peat decomposition rates in warm and poorly decomposed peat, provision of substrates by roots, and rapid transport by ebullition and root conduits generally lead to high methane emissions (Shannon and White, 1994; Fechner-Levy and Hemond, 1996; Coles and Yavitt, 2004). The coupling between carbon, nitrogen, iron, and sulfur transformations is also of importance. Iron and sulfate reducing bacteria can suppress methane production even at low concentrations of these alternative electron acceptors (Kristjansson et al., 1982; Achnich et al., 1995). Increased sulfate deposition rates have thus been conjectured to be the cause for relatively small CH₄ production and large sulfate reduction rates in oligotrophic peatlands in eastern North America and Europe (Nedwell and Watson, 1995; Gauci et al., 2002; Vile et al., 2003).

The oxidation processes, following water table draw down, that lead to the recycling of electron acceptor pools in wetland soils have not been extensively investigated, which currently hampers our ability to assess the impact of drought-rewetting cycles on subsequent CO₂ and CH₄ production across a range of peatland types. Generally, a production of a particular electron acceptor is possible by oxygen transfer into the saturated zone by root conduit transport and by drying-rewetting cycles, and by the utilization of reservoirs of other electron acceptors with a more positive redox potential. Electron acceptors contained in dissolved organic matter (DOM) may also allow for the chemical oxidation of hydrogen sulfide (H₂S) and thus maintain anaerobic sulfur cycling (Fig. 1C; Heitmann and Blodau, 2006).

2.1.2 Novel controls on biogeochemical processes

Potentially important and more recently identified controls on organic matter decomposition and methanogenesis are the effects of extracellular enzyme activity and of transport and associated accumulation of decomposition products in peat. The electron transfer processes that finally lead to, or influence, CO₂, CH₄ and DOC fluxes are almost exclusively microbially mediated and proceed following exo-enzymatic cleavage of complex litter and soil organic matter molecules (Conrad 1999; Fig. 2D). Direct, enzyme mediated constraints on decomposition have been identified. Extracellular mi-

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crobial phenol oxidase enzymes – oxidative copper containing enzymes that catalyse the release of reactive oxygen-radicals (Hammel, 1997; Claus, 2004) – produced by fungi (Hammel, 1997; Burke and Cairney, 2002), bacteria (Hullo et al., 2001; Fenner et al., 2005) and actinomycetes (Crawford, 1978; Endo et al., 2003) have been recognised to play a pivotal role in the pathways involved with the breakdown of complex organic matter and the cycling of phenolic compounds that may interfere with extracellular enzymes (Benoit and Starkey, 1968; Albers et al., 2004). Changes in the activity of extracellular phenol oxidases may affect the retention of carbon in the soil environment directly via the breakdown of otherwise highly recalcitrant organic matter and indirectly by releasing extracellular hydrolase enzymes from phenolic inhibition (Pind et al., 1994; Freeman et al., 2001a, 2004); consequently playing an important role in the stability of peatland carbon stores. The activity of extracellular phenol oxidases has been found to be constrained by low oxygen availability (McLatchey and Reddy, 1998), low temperatures (Freeman et al., 2001b) and low pH (Criquet et al., 1999). Such conditions are characteristic of northern peatlands, and the release of phenol oxidase activity from one or a combination of these inhibitory factors can therefore release an “enzymic latch mechanism” (Freeman et al., 2001a) allowing destabilization of peatland carbon storage.

Recent studies also suggest that the impact of full saturation, anaerobiosis and associated accumulation of decomposition products may be larger than previously derived from laboratory incubations, and can result in a near shut down of hetero- and autotrophic respiration deeper into the saturated zone of ombrotrophic peat soils (Beer and Blodau, 2007; Blodau et al., 2007). If such findings could be generalized, heterotrophic respiration could be explained mainly by the depth of the “active” unsaturated layer, the distribution of the aerobic decomposition constant and the soil temperature, and photosynthetically driven root respiration. Most of the uncertainties related to rates and pathways of below-ground carbon cycling are tightly coupled to insufficient knowledge of the spatiotemporal distribution of in situ physical and chemical parameters, such as air filled porosity, that drive the processes. Given the interdependency

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of respiration rates, transport, and air filled porosity, changes in water content near saturation most likely have a strong impact on rates of respiration in the unsaturated zone of many peat soils. Changes in water contents of the uppermost 'active' peat will likely determine if larger impacts of intensified drought and rewetting on respiration and redox processes may occur at such sites in the future.

2.2 Vegetation-mediated feedbacks

Plants differ in important characteristics such as productivity, litter decomposability and association with fungi, resulting in many different ways by which they affect the carbon balance of peatlands at a local to ecosystem scale, depending on their abundance and spatial arrangement. As plants and vegetation types generally form easily recognizable units for both land-based and airborne assessments and are closely coupled to soil processes, vegetation changes are both convenient predictors for environmental changes to come as well as monitoring tools for changes underway.

As a result of differences in plant characteristics we can distinguish a number of vegetation-biogeochemistry feedbacks: (1) There is a general trade-off between hummock and hollow inhabiting *Sphagnum* species, with lower decomposability among the former, and higher productivity among the latter (Rydin et al., 2006); (2) Plants produce peat with different structure and hydraulic conductivity, features that in turn affect redox status and other physico-chemical conditions. For instance, for the same degree of humification, the hydraulic conductivity generally increases in the order *Sphagnum* peat < *Carex* peat < woody peat (Päivänen, 1982); (3) Ombrotrophic growing *Sphagnum* species are usually difficult to decompose compared with most co-inhabiting vascular plants (Limpens and Berendse, 2003; Dorrepaal et al., 2005); (4) The decrease in litter C:N ratio following from N deposition may enhance decomposition (Limpens and Berendse, 2003; Bragazza et al., 2006); and (5) An increasing sedge cover will increase CH₄ emission through aerenchymatic tissue (Thomas et al., 1996; Nilsson et al., 2001).

On the whole, the vegetation that dominates a peatland will not only affect photo-

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synthetic and respiration rates, but also the amount of carbon available for mobilisation as DOC from the peatland at a landscape scale. Research undertaken in Alaska for example suggests that vegetation type may be more important than regional climate in determining DOC fluxes from peatlands (Neff and Hooper, 2002). Figure 2 presents results from a survey across UK blanket peats showing that DOC concentrations are significantly greater where woody *Calluna* dominates when compared to *Eriophorum*-dominated sites or *Sphagnum-Eriophorum* sites (all differences between categories are significant at $p < 0.01$). Additionally Holden (2005) has shown that the growth of woody *Calluna* plants are a causative factor in pipe development in peats thereby opening up more routes for carbon release from the peatland.

2.2.1 Vegetation responses to environmental change

Apart from the obvious destruction of peatlands by drainage, climatic changes that affect water availability are, together with N deposition, the most important factors altering peatland vegetation in temperate and boreal regions. There is quite a good understanding from ecological experiments how different peatland plant species react to water table position and wetness (Rydin and Jeglum, 2006). The future challenge is to understand how various climate scenarios affect the wetness of the peatlands, and how this in turn leads to vegetation changes through differential growth and interspecific competition. This research field, which will require a new modeling approach, is just starting to emerge.

N deposition above ca. $1-1.5 \text{ g m}^{-2} \text{ yr}^{-1}$ generally increases vascular plant cover, and decreases *Sphagnum* cover, although changes may be slow, and experimentally difficult to demonstrate, especially in regions with low background deposition where the *Sphagnum* layer is not yet saturated with N. Where vegetation changes were reported within 4 years at high background deposition in the Netherlands (Limpens et al., 2004), it took 5-8 years for the first effects to emerge in N Sweden and Canada (Bubier et al., 2007; Wiedermann et al., 2007). An increase in cover of vascular plants beyond a critical limit inevitably leads to a decrease in *Sphagnum* cover (Berendse et al., 2001),

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and this alteration in dominance of the different groups of plants is driven by positive feedbacks mediated by increased light competition and decreased uptake of N by the *Sphagnum* mosses (Limpens et al., 2006; Rydin and Jeglum, 2006). Long-term monitoring has shown that nitrogen demanding species have increased on ombrotrophic peatlands in SW Sweden over the last decades (Gunnarsson and Flodin, 2007).

Increased temperature probably affects vegetation more by indirect effects such as increased evaporation and reduced snow cover than by direct, differential effects on plant species performance (Weltzin et al., 2001). There are some experimental indications of temperature-nitrogen interactive effects on vascular plant cover (Wiedermann et al., 2007), and it appears that temperature may have different effects on growth of different *Sphagnum* species (Robroek et al., 2007), but it is unclear if this eventually may shift the balance among species to such extent that carbon cycling is affected.

While increased concentrations of CO₂ in the air may affect the physiology and growth of plants (Jauhiainen et al., 1998), most studies have failed to demonstrate strong effects on peatland species composition (Berendse et al., 2001; Heijmans et al., 2002). In contrast, Fenner et al. (2007a) showed increased vascular plant cover at the expense of *Sphagnum* in weakly minerotrophic peatland vegetation subjected to elevated CO₂. Increased C turnover in vascular plants, particularly *Juncus effusus*, resulted in higher DOC concentrations via exudation and accelerated decomposition of litter and peat. Moreover, a more than additive effect was found due to the interaction between CO₂ and warming, leading to even greater increases in vascular plant dominance, decomposition and DOC release (Fenner et al., 2007b).

A field experiment in Switzerland showed a differential effect on N and CO₂ on the growth of peatland bryophytes (Mitchell et al., 2002): height growth of *Polytrichum strictum* was favored by N addition, whereas *Sphagnum fallax* was favored by increased CO₂ concentration. Such contrasting effects on height growth may be more important than effects on biomass accumulation for competition and changes in species composition, since competitive outcome in bryophytes to a large extent is determined by overtopping and shading effects (Rydin, 2008). The results indicate that even for such

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a “nitrogen-tolerant” species as *S. fallax*, the negative effects of N deposition are more important than any positive CO₂ effects.

There is very little data about the natural changes in peatland vegetation as a result of climate variability. In the absence of human impact the species composition of temperate and boreal ombrotrophic peatlands (bogs) appears to be very stable. This holds for fine-scale (less than 1 m) persistence of *Sphagnum* species over centuries-millennia (Rydin and Barber, 2001), and also for stability of microtopographic structure (hummock-hollow patterns over 40–60 yr (Backéus, 1972; Rydin et al., 2006). However, recent re-analyses of bogs that were studied in detail in the 1940s and 1950s reveal larger changes. In a peatland in central Sweden with low levels of air pollution there were clear indications of acidification and associated changes in bryophyte composition (Gunnarsson et al., 2000, 2002). Novel approaches based on remote sensing data, such as mapping the leaf area index of trees and shrubs (Sonnentag et al., 2007) or the plant functional type fractional cover in peatlands (Schaeppman-Strub et al., 2008 this issue) allow a spatially continuous assessment of the current status and the detection of changes in ecosystem functioning and vegetation composition.

3 Carbon fluxes at the landscape scale

3.1 Land-aquatic carbon fluxes

The aquatic export from temperate and boreal peatlands ranges between 1 and 50 g DOC m⁻² yr⁻¹ (Dillon and Molot, 1997), which typically represents around 10% of the total carbon release, and are currently showing widespread increases (Freeman et al., 2001b; Worrall et al., 2003). For some mires, CO₂ outgassing from the streams may comprise additional losses of 2 to 13 g C m⁻² yr⁻¹ (Buffam et al., 2007). In the most severely eroding peat catchments in the UK, particulate organic carbon (POC) losses may exceed 100 g C m⁻² yr⁻¹ (Evans and Warburton, 2007).

Wherever peatlands appear in the landscape they will dominate the fluvial fluxes of

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dissolved carbon in inorganic (DIC), DOC or POC form. Given the flashy nature of stream response (Bay, 1969; Price, 1992; Holden and Burt, 2003a) this can mean most of the aquatic carbon losses from peatlands can occur during relatively short periods (during high flow), for example following heavy rain or snow melt. The dominant pathways for water movement in most ombrotrophic peatlands are near surface flow through the upper peat layers and saturation-excess overland flow (Holden and Burt, 2002, 2003a) while matrix flow in deeper peat layers is severely limited (Rycroft et al., 1975; Holden and Burt, 2003b). Nevertheless, large preferential pathways are common in many peatlands and these form conduits (called pipes, Fig. 3) for water and carbon bypassing near-surface and matrix flow. Baird (1997) and Holden et al. (2001) have shown that over 30% of runoff in fens and blanket peats moves through macropores, which results in water and nutrients being transferred between deep and shallow layers of the peat profile.

What is often ignored on a landscape scale is the variability in water table and runoff that can occur wherever peatlands are subject to any significant topographic variation. Underestimated is also the speed with which the dominant overland and near-surface flow in many peatlands may accelerate peat exposure after degradation of the vegetation cover, resulting in enhanced POC efflux and reduced NPP as a result of vegetation loss (Holden et al., 2007b). Furthermore, increased subsurface erosion of preferential pathways leading to larger pipes and enhanced preferential water flow, may lead to unexpected aquatic carbon and nutrient losses in some catchments (Holden, 2006).

DOC is important in peatlands because any change in the flux of DOC will result in a significant regional redistribution of terrestrial carbon. In downstream ecosystems, DOC exerts significant control over productivity, biogeochemical cycles and attenuation of visible and UV radiation (Pastor et al., 2003). In addition, DOC impacts water quality in terms of color, taste, safety, and aesthetic value, as well as altering the acid-base and metal complexation characteristics of soil water and streamwater. Together with the carbon losses considerable nutrient export may occur as well, potentially increasing impacts on aquatic diversity downstream (Waldron et al., 2008 this issue).

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DOC accumulates in peat pore waters and is flushed out by water movement, with concentrations often greatest following periods of warm, dry conditions when DOC has had time to accumulate. DOC concentrations are usually between 20 and 60 mg l⁻¹ in northern peatlands (Blodau, 2002) but concentrations are higher during low flow periods. Despite this the total flux of dissolved carbon (DC; DC = DOC + DIC) exported is likely to be higher during storm flows but many sampling programmes do not take this into account (Schiff et al., 1998). Recent strong interest in water-borne carbon exports from peatlands has focused mainly on concentrations and fluxes of carbon, especially DOC within the drainage system of peat dominated catchments (Dawson et al., 2002; Billett et al., 2006). Buffam et al. (2007) reported DOC export for 15 Swedish streams at 2–10 g C m⁻² yr⁻¹ while DIC was between 0.2 and 2 g C m⁻² yr⁻¹. However, we still know little about what controls the transport of DOC and particulate carbon release within peatlands themselves and the hydrological processes leading to their delivery to rivers.

3.2 Land-atmosphere carbon fluxes

The mass exchange of carbon between peatlands and the atmosphere is dominated by the fluxes of CO₂ and CH₄, but due to the difference in radiative properties between CO₂ and CH₄ the much smaller mass exchange of CH₄ can have a disproportional effect on climate forcing.

3.2.1 Net Ecosystem Exchange of CO₂ (NEE)

NEE from ombrotrophic peatlands (bogs) ranges from a net loss of >100 g C m⁻² yr⁻¹ for a permafrost dominated Siberian bog (Friborg et al., 2003) and Russian European boreal bogs (Arneeth et al., 2002) to large uptakes of about 90 g C m⁻² yr⁻¹ (Alm et al., 1997). However, most studies report mean annual NEE in a much smaller range with multiple year averages between 20 and 60 g C m⁻² yr⁻¹ (Sottocornola and Kiely, 2005; Dunn et al., 2007; Roulet et al., 2007). The NEE from minerotrophic peatlands (fens),

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particularly mineral poor fens, shows a similar range and interannual variability as that of bogs (Shurpali et al., 1995; Joiner et al., 1999; Aurela et al., 2001, 2007). While all these studies show large differences among years and peatland types in annual NEE the observed ranges are relatively smaller than those observed among other major ecosystem types. Humphreys et al. (2006) did a comparative analysis of NEE from seven quite contrasting bogs and fens and found, despite large differences in water table depth, water chemistry, and plant community structure, that the summer daily NEE was about $1.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ for all peatlands. From this result it seems that the differences in cumulative annual NEE between individual peatlands are more a function of broad scale geographic location and physical setting rather than internal factors such as the hydrology, community structure and biogeochemistry. However, more long-term, continuous records of NEE from a more diverse set of peatlands covering a wider range of geographical locations are required before this broad conjecture can be evaluated. An analysis by Lindroth et al. (2007) shows that photosynthetic radiation (PAR) is the dominant controller by far on the gross and net uptake of CO_2 . When analyzing the relationship between PAR and NEE, Frohking et al. (1998) found that in comparison with other upland ecosystems, such as closed forest, grasslands and croplands, just one NEE-PAR relationship with smaller ecosystem respiration and NEE rates applied to the two broad groups of ombrotrophic and minerotrophic peatlands. At a landscape scale, internal factors such as moisture, temperature, vegetation composition and nutrient status all seem to play secondary roles. This may be partly due to the confounding effects that some environmental factors have on the components of NEE. A modest increase in temperature, for example, may both stimulate C assimilation and C respiration, diminishing or even cancelling out its net effect on NEE. If it is confirmed that the range of NEE among peatland types is much smaller than initially expected then it will simplify the task of modeling peatland CO_2 exchange at coarse scales in global models.

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3.2.2 Exchange of CH_4 between peatlands and the atmosphere

There are many comprehensive reviews of CH_4 flux from peatlands (Moore et al., 1998). These show that the temporal and spatial variability of CH_4 exchange is much more variable, by several orders of magnitude, than that of peatland NEE. In some cases the CH_4 flux is very small ($<1 \text{ g C m}^{-2} \text{ yr}^{-1}$) in drier bogs with persistently low water tables with or without permafrost (Roulet et al., 2007; Christensen et al., 2004) to intermediate fluxes ($5\text{--}8 \text{ g C m}^{-2} \text{ yr}^{-1}$) for wetter bogs (Laine et al., 2007), but in wetter fens, particularly when there is significant cover of sedges the annual flux can exceed $15 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Shurpali et al., 1993; Suyker et al., 1996). In a boreal landscape, Bubier et al. (2005) estimated the regional flux to be about $7 \text{ g C m}^{-2} \text{ yr}^{-1}$, but the fluxes from individual peatlands types differed by a factor 10 or more. Back calculating from the recent estimates of the atmospheric burden of CH_4 from high latitude wetlands ($8\text{--}20 \cdot 10^{12} \text{ g CH}_4 \text{ yr}^{-1}$, Mikaloff Fletcher et al., 2004; Chen and Prinn, 2006) yields an average emission of $2\text{--}5 \text{ g C m}^{-2} \text{ yr}^{-1}$.

3.3 Putting the fluxes together: the annual carbon budget of peatlands

There are very few examples of net ecosystem carbon balances (NECB) for peatlands, where both the atmospheric fluxes of CO_2 and CH_4 and the water borne fluxes of DOC, POC and DIC have been measured at the same time. In this assessment of the carbon balance of a peatland it is important to be very clear on the terms. We adapt the terminology discussed by Lovett et al. (2006) and Chapin et al. (2006): $\Delta_{\text{org}}\text{C}$ (Lovett et al., 2006) or NECB (Chapin et al., 2006) is the accumulation of carbon in the sediments of an ecosystem after all the inputs and outputs are balanced. The NECB for northern peatlands from measurements is quite conservative ranging between 10 to $30 \text{ g C m}^{-2} \text{ yr}^{-1}$. NEE is the largest term ranging between 0 and $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ inputs and the approximate losses via the CH_4 flux and DC range respectively between 0 and 12, and 2 and $70 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 4). However, the high end of the range of DC export comes from peatlands that have been disturbed or used extensively throughout

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part of their history for grazing and/or subjected to other forms of land-use (Worrall et al., 2003).

Examining these composite carbon balances it is clear that without the inclusion of the CH₄ and dissolved losses, balances based on the NEE only could be in error in excess of 100%. This means not only does the CH₄ and DC flux need to be measured but the simulation of the response of northern peatlands to environmental changes will also need to include these loss mechanisms to make the predictions of use.

3.4 Perturbations

3.4.1 Fire and drainage

Currently many large peatlands are undergoing major changes due to human alteration, often involving burning, particularly forested tropical peatlands in Southeast Asia. These peatlands store at least 42 10¹⁵ g of soil C but are more and more under threat from drainage and fires associated with plantations such as palm oil crops (Page et al., 2002). Hooijer et al. (2006) estimated that current CO₂ emission resulting from the destruction of peatlands in Southeast Asia (90% emitted by Indonesia) through drainage and burning alone is equal to 8% of global fossil fuel emissions. Furthermore, the burning of peat and vegetation in Indonesia during the El Niño-Southern Oscillation (ENSO) in 1997 released an estimated 0.81–2.57 10¹⁵ g C, an equivalent amount of 13 to 40% of the mean annual global carbon emissions from fossil fuels (Page et al., 2002).

A large proportion of the temperate peatlands are also subject to both wildfire and prescribed burning (Yallop et al., 2006; Buytaert et al., 2005, 2006; Holden et al., 2007a). Wildfires might increase on peatlands under future climate change as temperatures increase and rainfall patterns change (Li et al., 2007). The fires themselves release carbon into the atmosphere through the burning process and are likely to result in short to longer-term changes, at least, to hydrology caused by decreased albedo and changes in near-surface peat properties. Additionally there is diminished net primary productivity in the aftermath of the fire that may last for about 20 years (Wieder

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et al., 2007). In peatlands with discontinuous permafrost, severe fire events may contribute to permafrost melt leading to more permanent vegetation changes (Kuhry, 1994, Myers-Smith et al., 2008 this issue).

Many peatlands have been drained for commercial exploitation (improvements in grazing, forestry or preparations for extraction), resulting in profound effects on peatland biogeochemistry, vegetation and C loss (Strack et al., 2006). In addition, drainage not only encourages significantly enhanced POC loss through concentrated flow in the drainage channels but also increases subsurface peat erosion and soil piping, depending on time since drainage (Holden et al., 2006).

3.4.2 Restoration

Many degraded peats are the subject of restoration projects. Management practices are varied but include raising the water table through gully and ditch blocking (Evans et al., 2005) and reseeded or planting bare surfaces (Petrone et al., 2004). This has an immediate impact in that it can rapidly reduce the losses of particulate carbon from a peatland. Holden et al. (2007a) for example, demonstrated an almost two orders of magnitude decrease in POC release for a restoration project in northern England. A drain blocking monitoring project conducted by Worrall et al. (2007) showed that in the short-term (one year) there was limited change in DOC concentrations while Wallage et al. (2006) have shown that DOC production can be significantly reduced through drain blocking and water table recovery within five years. Quick re-vegetation is often possible and peat formation can be fast in revegetated gullies and drains, even without water table restoration measures, thereby still having positive effects on carbon storage (Evans and Warburton, 2007). In some places where water tables have been artificially raised to restore a peatland, this has led to the development of fresh biomass but also to increases in CH₄ emissions (Chojnicki et al., 2007).

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4 Peatlands and climate

Climate change is largely driven by the accumulation of C in the atmosphere which is the net balance between emissions from human activities and the removal of C by natural sinks on land and in the ocean. Over the last 50 years, the efficiency of natural
5 CO₂ sinks has been declining (Canadell et al., 2007) and model projections show a further decline throughout the 21st century (Friedlingstein et al., 2006). High latitude and tropical peatlands have been identified as potential key vulnerabilities of the terrestrial carbon cycle likely to lead to positive feedbacks to climate change (Freeman et al., 1993; Fenner et al., 2005; Canadell et al., 2004). Particularly global warming for
10 the high latitude peatlands and deforestation in tropical peatlands are major drivers of the net C balance of these regions.

4.1 Modelling vegetation – climate feedbacks

Over the last eight years there has been considerable effort to couple global climate models with global carbon models to examine the magnitude and rate of potential feed-
15 backs as a result of changes in the cycling of carbon in the terrestrial biosphere and the oceans. Until now, all the simulations agree on a positive feedback between the terrestrial biosphere, the oceans and climate. The strength of this feedback, however, varies considerably, and results range between an additional 20–200 ppm of atmospheric CO₂ by 2100, using the A2-IPCC emission scenario (Friedlingstein et al.,
20 2006). Climate-carbon modelers acknowledge that there are major components, such as dynamic land-use change, nitrogen cycling, fire, and wetlands that have the potential for large feedbacks but are currently ignored. The uncertainty in the projections caused by these omissions is considerable. Recent carbon-nitrogen-climate simulations for example show that results are dramatically different between runs that include
25 nitrogen and those that do not (Thorton et al., 2007). If N availability is included, the feedback involving the terrestrial biosphere is greatly reduced because of the smaller responses of the C cycle to temperature and precipitation variations and reduced C

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uptake to elevated CO₂. The feedback potential of wetlands is equally large. A preliminary estimate suggests that up to 100 10¹⁵ g C of CO₂ equivalents could be released to the atmosphere from wetlands and peatlands over the next 100 years (Gruber et al., 2004). Yet, no global climate simulations, that we are aware of, include wetlands,
5 even though they store up to one-third of the terrestrial carbon (Gorham, 1995) and are recognized as significant contributors of atmospheric CH₄.

4.1.1 Including peatlands in earth system models

The inclusion of wetlands, particularly peatlands, in global models is severely constrained by the way hydrology is treated by the models. At a global scale the distribution
10 of wetlands is concentrated in areas where precipitation exceeds evapotranspiration. However, the actual hydrology of wetlands that controls ecosystem structure and function is largely a function of physical setting, substrates, and topographic location at a landscape level. At present, these factors are too local to be included, and the research community is still searching for an adequate way to parameterize the issue.
15 There have been attempts to use a topographic wetness index to simulate northern peatland distribution (Kirkby et al., 1995) and this has been extended globally by Gedney and Cox (2003). However, this approach only simulates where surface saturation occurs, whereas much of the biogeochemical processes in wetlands are a function of the seasonal water table changes over a range of 0.3–0.4 m (Moore et al., 1998).

For peatlands the two factors that may be globally significant are the fate of the large
20 mass of carbon stored as peat and the production and oxidation of CH₄. There have been no global simulations of the fate of stored carbon but a series of local peatland models have emerged that could, in principle, with simplification be used to examine this issue at the global scale. Results from simulations using the Peatland Carbon
25 Simulator (Frolking et al., 2001, 2002; Lafleur et al., 2003), the NUCOM-BOG model (Heijmans et al., 2008) and the newly developed McGill Wetland Model (Saint Hilaire et al., 2008 this issue) show that production and decomposition in peatlands are quite sensitive to both changes in moisture and temperature.

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There has been much more effort on modeling the potential feedbacks of CH₄ from wetlands, including northern peatlands. Walter et al. (2001a, b) developed a process based wetland-methane emissions model and Shindell et al. (2004) used this model to examine the potential feedback with climate change. They simulated a 78% increase in CH₄ emissions for a scenario involving a doubling of the ambient atmospheric CO₂ concentration. Although most of the increase came from tropical wetlands, emissions from high latitude wetlands doubled, showing an increase from 24 to 48 10¹⁵ g CH₄ yr⁻¹. Gedney et al. (2004) also estimated a doubling of CH₄ wetland emissions from about 300 to between 500 and 600 10¹⁵ g CH₄ yr⁻¹ by 2100, leading to a temperature increase of 0.14 to 0.2 K. They concluded the latter would involve a 3.5 to 5.0% increase in overall radiative forcing in comparison to the Cox et al. (2000) CO₂ feedback. The latter is a factor of 2 larger than any other couple carbon-climate simulation over the 21st century (Friedlingstein et al., 2006).

It is too early in the global research effort to draw any conclusions about the relative strengths of the CO₂ and CH₄ feedback involving peatlands. Much more work is required in this area and the links among peatland surface climate, hydrology, ecosystem structure and function, and trace gas biogeochemistry represent a major challenge for the global modeling community. However, the recent modeling of the role northern peatlands over the Holocene suggest that the stored carbon in peatlands represents a present day cooling of up to -0.5 W m⁻² when both CO₂ and CH₄ are considered (Frolking and Roulet, 2007). Short-term decreases in the wetness of peatlands, result in a reduction of this net cooling effect, with the size of the reduction depending on whether the change is dominated by changes in net CO₂ exchange (smaller) or CH₄ exchange (larger) (Frolking et al., 2006).

5 Conclusions—drivers of the carbon balance across different scales

The carbon economy of peatlands is tightly coupled to the water balance. Precipitation amount and frequency together with temperature strongly affect peatland water

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balance and thus the amounts of carbon taken up by the vegetation and lost through decomposition and export via water (Fig. 5). Moreover these same factors affect water availability at the peat surface where an important part of the carbon assimilation takes place. In addition, temperature directly affects the rate of many physical, chemical and biological processes. Fire frequency is tightly linked to climate through its direct relationships to ozone and oxygen concentrations as well as temperature. Its impacts on the carbon balance are both indirect through the release of aerosols and smoke or direct as large quantities of organically stored C are released to the atmosphere as CO₂. At the landscape and regional scale the percentage of peatlands (land cover), as well as their connections to other ecosystem types through subsurface and surface hydrology and topography affect carbon export via water and atmosphere. At an ecosystem scale water level and pH control the vegetation composition. In turn the vegetation composition, particularly *Sphagnum* cover, affects the C- balance through its effects on net primary productivity (NPP), the ratio of CO₂:CH₄ released into the atmosphere and peat physical properties. At a local scale water level also strongly controls soil respiration, through the availability of oxygen as well as other electron acceptors. Degradability of organic matter together with pH has a strong influence on decomposition rate as well as the ratio of CO₂:CH₄ produced and peat conductivity. Finally, the physical properties of the peat layers affect surface hydrology and the release of methane by ebullition.

Perturbations, such as high N deposition or drainage may affect the peatland carbon balance both directly or indirectly at different spatial scales. Enhanced N deposition for example may directly stimulate decomposition by increasing the availability of electron acceptors and indirectly through changes in vegetation composition and cover. Furthermore, combined perturbations may have an additional aggravating effect, leading to higher losses than expected from each disturbance separately. For tropical peatlands, for example, the interaction between drought (brought by the Southern Oscillation), deforestation, and fire is responsible for the dramatic losses of C to the atmosphere.

5.1 Ways forward

- Better understanding of the coupling between soil physical structure and aerobic and anaerobic respiration, with further model development at local and regional scales.
- 5 – Determining how vegetation change alters the C cycle and C mobilization in different forms (DOC, POC, gases).
- Understanding how various climate scenarios will affect the hydrology of peatlands, and how this will lead to vegetation changes and associated changes in C fluxes and stocks.
- 10 – Analyzing and establishing process studies in combination with ecosystem flux measurements to understand the key controls on fluxes in and out of the ecosystems (water table, temperature, etc).
- Incorporating in biogeochemical models key processes controlling landscape C fluxes such as fires regimes and vegetation shifts.
- 15 – Identifying possible thresholds in C dynamics of peatlands to prevent large scale vulnerability of C stocks and associated positive feedbacks to the climate system.
- Determining a more accurate global representation of the spatial distribution of C-pools and stocks in peatlands, with particular focus on peat depth, peat bulk density and the differentiation between ombrotrophic and minerotrophic peatlands.
- 20 – Including the treatment of organic soils, and particularly peat, in the carbon cycle components of fully coupled climate models.

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References

- 5 Achtnich, C., Bak, F., and Conrad, R.: Competition for electron-donors among nitrate reducers, ferric iron reducers, sulfate reducers, and methanogens in anoxic paddy soil, *Biol. Fert. Soils*, 19, 65–72, 1995.
- Albers, D., Migge, S., Schaefer, M., and Scheu, S.: Decomposition of beech leaves (*Fagus sylvatica*) and spruce needles (*Picea abies*) in pure and mixed stands of beech and spruce, *Soil Biol. Biochem.*, 36, 155–164, 2004.
- 10 Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykanen, H., and Martikainen, P. J.: Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland, *Oecologia*, 110, 423–431, 1997.
- Arneeth, A., Kurbatova, J., Kolle, O., Shibistova, O. B., Lloyd, J., Vygodskaya, N. N., and Schulze, E. D.: Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II. Interseasonal and interannual variability of CO₂ fluxes, *Tellus B*, 54, 514–530, 2002.
- 15 Aurela, M., Laurila, T., and Tuovinen, J. P.: Seasonal CO₂ balances of a subarctic mire, *J. Geophys. Res.-Atmos.*, 106, 1623–1637, 2001.
- 20 Aurela, M., Riutta, T., Laurila, T., Tuovinen, J. P., Vesala, T., Tuittila, E. S., Rinne, J., Haapanala, S., and Laine, J.: CO₂ exchange of a sedge fen in southern Finland – the impact of a drought period, *Tellus B*, 59, 826–837, 2007.
- Backeus, I.: Bog vegetation re-mapped after 60 years – studies on Skagershultamossen, central Sweden, *Oikos*, 23, 384–393, 1972.
- 25 Baird, A. J.: Field estimation of macropore functioning and surface hydraulic conductivity in a fen peat, *Hydrol. Process.*, 11, 287–295, 1997.
- Bay, R. R.: Runoff from small peatland watersheds, *J. Hydrol.*, 9, 90–102, 1969.
- Beer, J. and Blodau, C.: Transport and thermodynamics constrain belowground carbon turnover in a northern peatland, *Geochim. Cosmochim. Ac.*, 71, 2989–3002, 2007.

1402

- Benoit, R. E. and Starkey, R. L.: Inhibition of decomposition of cellulose and some other carbohydrates by tannin, *Soil Sci.*, 105, 291–296, 1968.
- Berendse, F., Van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M. R., Lee, J. A., Mitchell, E., Saarinen, T., Vasander, H., and Wallen, B.: Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs, *Glob. Change Biol.*, 7, 591–598, 2001.
- 5 Billett, M. F., Deacon, C. M., Palmer, S. M., Dawson, J. J. C., and Hope, D.: Connecting organic carbon in stream water and soils in a peatland catchment, *J. Geophys. Res.*, 111, doi:10.1029/2005JG000065, 2006.
- 10 Blodau, C.: Carbon cycling in peatlands – a review of processes and controls, *Environ. Rev.*, 10, 111–134, 2002.
- Blodau, C., Basiliko, N., and Moore, T. R.: Carbon turnover in peatland mesocosms exposed to different water table levels, *Biogeochemistry*, 67, 331–351, 2004.
- Blodau, C., Roulet, N. T., Heitmann, T., Stewart, H., Beer, J., Lafleur, P., and Moore, T. R.: Belowground carbon turnover in a temperate ombrotrophic bog, *Global Biogeochem. Cy.*, 15, 21, doi:10.1029/2005GB002659, 2007.
- Botch, M. S., Kobak, K. I., Vinson, T. S., and Kolchugina, T. P.: Carbon pools and accumulation in peatlands of the former Soviet-Union, *Global Biogeochem. Cy.*, 9, 37–46, 1995.
- Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., Ellis, T., Gerdol, R., Hajek, M., Lacumin, P., Kutnar, L., Tahvanainen, T., and Toberman, H.: Atmospheric nitrogen deposition promotes carbon loss from peat bogs, *P. Natl. Acad. Sci. USA*, 103, 19 386–19 389, 2006.
- Bubier, J., Moore, T., Savage, K., and Crill, P.: A comparison of methane flux in a boreal landscape between a dry and a wet year, *Global Biogeochem. Cy.*, 19, doi:10.1029/2004GB002351, 2005.
- 25 Bubier, J. L., Moore, T. R., and Bledzki, L. A.: Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog, *Glob. Change Biol.*, 13, 1168–1186, 2007.
- Buffam, I., Laudon, H., Oquist, M., Wallin, M., Agren, A., and Bishop, K.: Spatial and temporal dynamics of fluvial C export from Swedish boreal peatlands, in: *Proceedings of the 1st International Symposium on Carbon in Peatlands*, Wageningen, The Netherlands, 15–18 April, 29, 2007.
- 30 Burke, R. M. and Cairney, J. W. G.: Laccases and other polyphenol oxidases in ecto- and ericoid mycorrhizal fungi, *Mycorrhiza*, 12, 105–116, 2002.

1403

- Buytaert, W., Wyseure, G., De Bievre, B., and Deckers, J.: The effect of land-use changes on the hydrological behaviour of Histic Andosols in south Ecuador, *Hydrol. Process.*, 19, 3985–3997, 2005.
- Buytaert, W., Celleri, R., De Bievre, B., Cisneros, F., Wyseure, G., Deckers, J., and Hofstede, R.: Human impact on the hydrology of the Andean paramos, *Earth-Sci. Rev.*, 79, 53–72, 2006.
- Canadell, J. G., Ciais, P., Cox, P., and Heimann, M.: Quantifying, understanding and managing the carbon cycle in the next decades, *Climatic Change*, 67, 147–160, 2004.
- Canadell, J. G., Le Quere, C., Raupach, M. R., Field, C. B., Buitenhuis, E. T., Ciais, P., Conway, T. J., Gillett, N. P., Houghton, R. A., and Marland, G.: Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks, *P. Natl. Acad. Sci. USA*, 104, 18 866–18 870, 2007.
- 10 Chanton, J. P., Bauer, J. E., Glaser, P. A., Siegel, D. I., Kelley, C. A., Tyler, S. C., Romanowicz, E. H., and Lazrus, A.: Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands, *Geochim. Cosmochim. Ac.*, 59, 3663–3668, 1995.
- 15 Chanton, J. P. and Whiting, G. J.: Methane stable isotopic distributions as indicators of gas transport mechanisms in emergent aquatic plants, *Aquat. Bot.*, 54, 227–236, 1996.
- Chapin, F. S., Woodwell, G. M., Randerson, J. T., Rastetter, E. B., Lovett, G. M., Baldocchi, D. D., Clark, D. A., Harmon, M. E., Schimel, D. S., Valentini, R., Wirth, C., Aber, J. D., Cole, J. J., Goulden, M. L., Harden, J. W., Heimann, M., Howarth, R. W., Matson, P. A., McGuire, A. D., Meilillo, J. M., Mooney, H. A., Neff, J. C., Houghton, R. A., Pace, M. L., Ryan, M. G., Running, S. W., Sala, O. E., Schlesinger, W. H., and Schulze, E. D.: Reconciling carbon-cycle concepts, terminology, and methods, *Ecosystems*, 9, 1041–1050, 2006.
- Chen, Y. H. and Prinn, R. G.: Estimation of atmospheric methane emissions between 1996 and 2001 using a three-dimensional global chemical transport model, *J. Geophys. Res.-Atmos.*, 25, 111, doi:10.1029/2005JD006058, 2006.
- Chojnicki, B. H., Augustin, J., and Olejnik, J.: Impact of reflooding on greenhouse gas exchange of degraded fen peatlands, in: *Proceedings of the 1st International Symposium on Carbon in Peatlands*, Wageningen, The Netherlands, 15–18 April, 2007, 33, 2007.
- 30 Christensen, T. R., Johansson, T. R., Akerman, H. J., Mastepanov, M., Malmer, N., Friborg, T., Crill, P., and Svensson, B. H.: Thawing sub-arctic permafrost: Effects on vegetation and methane emissions, *Geophys. Res. Lett.*, 31, doi:10.1029/2003GL018680, 2004.
- Claus, H.: Laccases: Structure, reactions, distribution, *Micron*, 35, 93–96, 2004.

1404

- Coles, J. R. P. and Yavitt, J. B.: Linking belowground carbon allocation to anaerobic CH₄ and CO₂ production in a forested peatland, New York State, *Geomicrobiol. J.*, 21, 445–455, 2004.
- Conrad, R.: Contribution of hydrogen to methane production and control of hydrogen concentrations in methanogenic soils and sediments, *Fems Microbiol. Ecol.*, 28, 193–202, 1999.
- 5 Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., and Totterdell, I. J.: Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, *Nature*, 408, 184–187, 2000.
- Crawford, D. L.: Lignocellulose decomposition by selected *Streptomyces* strains, *Appl. Environ. Microbiol.*, 35, 1041–1045, 1978.
- 10 Criquet, S., Tagger, S., Vogt, G., Iacazio, G., and Le Petit, J.: Laccase activity of forest litter, *Soil Biol. Biochem.*, 31, 1239–1244, 1999.
- Dawson, J. J. C., Billett, M. F., Neal, C., and Hill, S.: A comparison of particulate, dissolved and gaseous carbon in two contrasting upland streams in the UK, *J. Hydrol.*, 257, 226–246, 2002.
- 15 Dillon, P. J., and Molot, L. A.: Effect of landscape form on export of dissolved organic carbon, iron, and phosphorus from forested stream catchments, *Water Resour. Res.*, 33, 2591–2600, 1997.
- Dorrepaal, E., Cornelissen, J. H. C., Aerts, R., Wallen, B., and Van Logtestijn, R. S. P.: Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient?, *J. Ecol.*, 93, 817–828, 2005.
- 20 Dunn, A. L., Barford, C. C., Wofsy, S. C., Goulden, M. L., and Daube, B. C.: A long-term record of carbon exchange in a boreal black spruce forest: Means, responses to interannual variability, and decadal trends, *Glob. Change Biol.*, 13, 577–590, 2007.
- Endo, K., Hayashi, Y., Hibi, T., Hosono, K., Beppu, T., and Ueda, K.: Enzymological characterization of EpoA, a laccase-like phenol oxidase produced by *Streptomyces griseus*, *J. Biochem.*, 133, 671–677, 2003.
- Evans, M. G., Allott, T. E. H., Holden, J., Flitcroft, C., and Bonn, A.: Understanding gully blocking in deep peat, Derbyshire: Moors for the Future Report, 4, 2005.
- Evans, M. G. and Warburton, J.: Geomorphology of upland peat, erosion, form and landscape change, Blackwell, London, 280 pp., 2007.
- 30 Fechner-Levy, E. J. and Hemond, H. F.: Trapped methane volume and potential effects on methane ebullition in a northern peatland, *Limnol. Oceanogr.*, 41, 1375–1383, 1996.
- Fenner, N., Freeman, C., and Reynolds, B.: Hydrological effects on the diversity of phenolic

1405

- degrading bacteria in a peatland: Implications for carbon cycling, *Soil Biol. Biochem.*, 37, 1277–1287, 2005.
- Fenner, N., Freeman, C., Lock, M. A., Harmens, H., Reynolds, B., and Sparks, T.: Interactions between elevated CO₂ and warming could amplify DOC exports from peatland catchments, *Environ. Sci. Technol.*, 41, 3146–3152, 2007b.
- 5 Fenner, N., Ostle, N. J., McNamara, N., Sparks, T., Harmens, H., Reynolds, B., and Freeman, C.: Elevated CO₂ effects on peatland plant community carbon dynamics and DOC production, *Ecosystems*, 10, 635–647, 2007a.
- Fraser, C. J. D., Roulet, N. T., and Lafleur, M.: Groundwater flow patterns in a large peatland, *J. Hydrol.*, 246, 142–154, 2001.
- 10 Freeman, C., Lock, M. A., and Reynolds, B.: Fluxes of CO₂, CH₄ and N₂O from a Welsh peatland following simulation of water-table draw-down - potential feedback to climatic-change, *Biogeochemistry*, 19, 51–60, 1993.
- Freeman, C., Evans, C. D., Monteith, D. T., Reynolds, B., and Fenner, N.: Export of organic carbon from peat soils, *Nature*, 412, 785–785, 2001b.
- 15 Freeman, C., Ostle, N., and Kang, H.: An enzymic “latch” on a global carbon store – a shortage of oxygen locks up carbon in peatlands by restraining a single enzyme, *Nature*, 409, 149–149, 2001a.
- Freeman, C., Ostle, N. J., Fenner, N., and Kang, H.: A regulatory role for phenol oxidase during decomposition in peatlands, *Soil Biol. Biochem.*, 36, 1663–1667, 2004.
- 20 Friborg, T., Soegaard, H., Christensen, T. R., Lloyd, C. R., and Panikov, N. S.: Siberian wetlands: Where a sink is a source, *Geophys. Res. Lett.*, 30, doi:10.1029/2003GL017797, 2003.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K. G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N.: Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison, *J. Clim.*, 19, 3337–3353, 2006.
- 30 Frolking, S. E., Bubier, J. L., Moore, T. R., Ball, T., Bellisario, L. M., Bhardwaj, A., Carroll, P., Crill, P. M., Lafleur, P. M., McCaughey, J. H., Roulet, N. T., Suyker, A. E., Verma, S. B., Waddington, J. M., and Whiting, G. J.: Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands, *Global Biogeochem. Cy.*, 12, 115–

1406

- Frolking, S., Roulet, N. T., Moore, T. R., Richard, P. J. H., Lavoie, M., and Muller, S. D.: Modeling northern peatland decomposition and peat accumulation, *Ecosystems*, 4, 479–498, 2001.
- Frolking, S., Roulet, N. T., Moore, T. R., Lafleur, P. M., Bubier, J. L., and Crill, P. M.: Modeling seasonal to annual carbon balance of Mer Bleue bog, Ontario, Canada, *Global Biogeochem. Cy.*, 16, doi:10.1029/2001GB001457, 2002.
- Frolking, S., Roulet, N., and Fuglestedt, J.: How northern peatlands influence the earth's radiative budget: Sustained methane emission versus sustained carbon sequestration, *J. Geophys. Res.*, 111, doi:10.1029/2005JG000091, 2006.
- Frolking, S. and Roulet, N. T.: Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions, *Glob. Change Biol.*, 13, 1079–1088, 2007.
- Gauci, V., Dise, N., and Fowler, D.: Controls on suppression of methane flux from a peat bog subjected to simulated acid rain sulfate deposition, *Global Biogeochem. Cy.*, 16, doi:10.1029/2000GB001370, 2002.
- Gedney, N. and Cox, P. M.: The sensitivity of global climate model simulations to the representation of soil moisture heterogeneity, *J. Hydrometeorol.*, 4, 1265–1275, 2003.
- Gedney, N., Cox, P. M., and Huntingford, C.: Climate feedback from wetland methane emissions, *Geophys. Res. Lett.*, 31, doi:10.1029/2004GL020919, 2004.
- Gorham, E.: The biogeochemistry of northern peatlands and its possible responses to global warming, in: *Biotic feedbacks in the global climate system: Will the warming feed the warming?*, edited by: Woodwell, G. M., and Mackenzie, F. T., Oxford University Press, New York, USA, 169–187, 1995.
- Gruber, N., Friedlingstein, P., Field, C. B., Valentini, R., Heimann, M., Richey, J. E., Romero-Lankao, P., Schulze, D., and Chen, C. T. A.: The vulnerability of the carbon cycle in the 21st century: An assessment of carbon-climate-human interactions, in: *The global carbon cycle: Integrating humans, climate, and the natural world*, edited by: Field, C. B., and Raupach, M. R., Island Press, Washington, DC, USA, 45–76, 2004.
- Gunnarsson, U., Rydin, H., and Sjors, H.: Diversity and pH changes after 50 years on the boreal mire Skattlosbergs Stormosse, central Sweden, *J. Veg. Sci.*, 11, 277–286, 2000.
- Gunnarsson, U., Malmer, N., and Rydin, H.: Dynamics or constancy in Sphagnum dominated mire ecosystems? A 40-year study, *Ecography*, 25, 685–704, 2002.
- Gunnarsson, U. and Flodin, L. A.: Vegetation shifts towards wetter site conditions on oceanic ombrotrophic bogs in southwestern Sweden, *J. Veg. Sci.*, 18, 595–604, 2007.

- Hammel, K. E.: Fungal degradation of lignin, in: *Driven by nature: Plant litter quality and decomposition*, edited by: Cadish, G. and Giller, K. E., CAB International, 33–45, 1997.
- Hayes, D. J., Guo, L., and McGuire, A. D.: A scientific synthesis and assessment of the arctic carbon cycle, *EOS*, 88, 26, 270, 2007.
- Heijmans, M. M. P. D., Klees, H., de Visser, W., and Berendse, F.: Response of a Sphagnum bog plant community to elevated CO₂ and N supply, *Plant Ecol.*, 162, 123–134, 2002.
- Heijmans, M. M. P. D., Mauquoy, D., vanGeel, B., and Berendse, F.: Long-term effects of climate change on vegetation and carbon dynamics in peat bogs, *J. Veg. Sci.*, 19, doi: 10.3170/2008-8-18368, 2008.
- Heitmann, T. and Blodau, C.: Oxidation and incorporation of hydrogen sulfide by dissolved organic matter, *Applied and Environ Microbiol.*, 235, 12–20, 2006.
- Holden, J., Burt, T. P., and Cox, N. J.: Macroporosity and infiltration in blanket peat: The implications of tension disc infiltrometer measurements, *Hydrol. Process.*, 15, 289–303, 2001.
- Holden, J. and Burt, T. P.: Infiltration, runoff and sediment production in blanket peat catchments: Implications of field rainfall simulation experiments, *Hydrol. Process.*, 16, 2537–2557, 2002.
- Holden, J. and Burt, T. P.: Hydraulic conductivity in upland blanket peat: Measurement and variability, *Hydrol. Process.*, 17, 1227–1237, 2003b.
- Holden, J. and Burt, T. P.: Runoff production in blanket peat covered catchments, *Water Resour. Res.*, 39, doi:10.1029/2003WR002067, 2003a.
- Holden, J.: Piping and woody plants in peatlands: Cause or effect?, *Water Resour. Res.*, 41, doi:10.1029/2004WR003909, 2005.
- Holden, J.: Sediment and particulate carbon removal by pipe erosion increase over time in blanket peatlands as a consequence of land drainage, *J. Geophys. Res.*, 111, doi:10.1029/2005JF000386, 2006.
- Holden, J., Evans, M. G., Burt, T. P., and Horton, M.: Impact of land drainage on peatland hydrology, *J. Environ. Qual.*, 35, 1764–1778, 2006.
- Holden, J., Gascoign, M., and Bosanko, N. R.: Erosion and natural revegetation associated with surface land drains in upland peatlands, *Earth Surf. Proc. Land.*, 32, 1547–1557, 2007b.
- Holden, J., Shotbolt, L., Bonn, A., Burt, T. P., Chapman, P. J., Dougill, A. J., Fraser, E. D. G., Hubacek, K., Irvine, B., Kirkby, M. J., Reed, M. S., Prell, C., Stagl, S., Stringer, L. C., Turner, A., and Worrall, F.: Environmental change in moorland landscapes, *Earth-Sci. Rev.*, 82, 75–100, 2007a.

- Hooijer, A., Silvius, M., Woesten, H., and Page, S.: Peat-CO₂: Assessment of CO₂ emissions from drained peatlands in SE Asia, Delft Hydraulics report Q3943, 41 pp., 2006.
- Hullo, M. F., Moszer, I., Danchin, A., and Martin-Verstraete, I.: CotA of *Bacillus subtilis* is a copper-dependent laccase, *J. Bacteriol.*, 183, 5426–5430, 2001.
- 5 Humphreys, E. R., Lafleur, P. M., Flanagan, L. B., Hedstrom, N., Syed, K. H., Glenn, A. J., and Granger, R.: Summer carbon dioxide and water vapor fluxes across a range of northern peatlands, *J. Geophys. Res.-Biogeosci.*, 111, doi:10.1029/2005JG000111, 2006.
- IPCC: Climate change, 2007: The physical science basis, Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change, edited by: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L., Cambridge University Press, Cambridge, UK and New York, USA, 996 pp., <http://www.ipcc.ch/ipccreports/ar4-wg1.htm>, 2007.
- 10 Jauhainen, J., Vasander, H., and Silvola, J.: Nutrient concentration in *Sphagna* at increased N-deposition rates and raised atmospheric CO₂ concentrations, *Plant. Ecol.*, 138, 149–160, 1998.
- 15 Joiner, D. W., Lafleur, P. M., McCaughey, J. H., and Bartlett, P. A.: Interannual variability in carbon dioxide exchanges at a boreal wetland in the BOREAS northern study area, *J. Geophys. Res.-Atmos.*, 104, 27 663–27 672, 1999.
- Keller, J. K. and Bridgman, S. D.: Pathways of anaerobic carbon cycling across an ombrotrophic-minerotrophic peatland gradient, *Limnol. Oceanogr.*, 52, 96–107, 2007.
- 20 Kirkby, M. J., Kneale, P. E., Lewis, S. L., and Smith, R. T.: Modelling the form and distribution of peat mires, in: *Hydrology and hydrochemistry of British wetlands*, edited by: Heathwaite, J. M. R., and Heathwaite, A. L., John Wiley, New York, USA, 83–93, 1995.
- Kristjansson, J. K., Schönheit, P., and Thauer, R. K.: Different K_s-values for hydrogen of methanogenic bacteria and sulfate reducing bacteria – an explanation for the apparent inhibition of methanogenesis by sulfate, *Arch. Microbiol.*, 131, 278–282, 1982.
- 25 Kuhry, P.: The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada, *J. Ecol.*, 82, 899–910, 1994.
- Lafleur, P. M., Roulet, N. T., Bubier, J. L., Frolking, S., and Moore, T. R.: Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog, *Global Biogeochem. Cy.*, 17, doi:10.1029/2002GB001983, 2003.
- 30 Laine, A., Wilson, D., Kiely, G., and Byrne, K. A.: Methane flux dynamics in an Irish lowland blanket bog, *Plant Soil*, 299, 181–193, 2007.

1409

- Li, W. H., Dickinson, R. E., Fu, R., Niu, G. Y., Yang, Z. L., and Canadell, J. G.: Future precipitation changes and their implications for tropical peatlands, *Geophys. Res. Lett.*, 34, doi:10.1029/2006GL028364, 2007.
- Limpens, J. and Berendse, F.: How litter quality affects mass loss and N loss from decomposing *Sphagnum*, *Oikos*, 103, 537–547, 2003.
- 5 Limpens, J., Berendse, F., and Klees, H.: How phosphorus availability affects the impact of nitrogen deposition on *Sphagnum* and vascular plants in bogs, *Ecosystems*, 7, 793–804, 2004.
- Limpens, J., Heijmans, M. M. P. D., and Berendse, F.: Nitrogen in peatlands, in: *Boreal peatland ecosystems*, edited by: Wieder, R. K., and Vitt, D. H., Ecological Studies Series, Springer Verlag, Berlin, 195–230, 2006.
- 10 Lindroth, A., Lund, M., Nilsson, M., Aurela, M., Christensen, T. R., Laurila, T., Rinne, J., Riutta, T., Sagerfors, J., Strom, L., Tuovinen, J. P., and Vesala, T.: Environmental controls on the CO₂ exchange in north European mires, *Tellus B*, 59, 812–825, 2007.
- 15 Lovett, G., Cole, J., and Pace, M.: Is net ecosystem production equal to ecosystem carbon accumulation?, *Ecosystems*, 9, 152–155, 2006.
- McLatchey, G. P., and Reddy, K. R.: Regulation of organic matter decomposition and nutrient release in a wetland soil, *J. Environ. Qual.*, 27, 1268–1274, 1998.
- Mikaloff Fletcher, S. E., Tans, P. P., Bruhwiler, L. M., Miller, J. B., and Heimann, M.: CH₄ sources estimated from atmospheric observations of CH₄ and its C-13/C-12 isotopic ratios: 2. Inverse modeling of CH₄ fluxes from geographical regions, *Global Biogeochem. Cy.*, 18, doi:10.1029/2004GB002224, 2004.
- 20 Mitchell, E. A. D., Buttler, A., Grosvernier, P., Rydin, H., Siegenthaler, A., and Gobat, J. M.: Contrasted effects of increased N and CO₂ supply on two keystone species in peatland restoration and implications for global change, *J. Ecol.*, 90, 529–533, 2002.
- Moore, T. R., Roulet, N. T., and Waddington, J. M.: Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands, *Climatic Change*, 40, 229–245, 1998.
- Moore, P. D.: The future of cool temperate bogs, *Environ. Conserv.*, 29, 3–20, 2002.
- Moore, T. R., Bubier, J. L., Frolking, S. E., Lafleur, P. M., and Roulet, N. T.: Plant biomass and production and CO₂ exchange in an ombrotrophic bog, *J. Ecol.*, 90, 25–36, 2002.
- 30 Nedwell, D. B., and Watson, A.: CH₄ production, oxidation and emission in a UK ombrotrophic peat bog - influence of SO₄²⁻ from acid-rain, *Soil Biol. Biochem.*, 27, 893–903, 1995.
- Neff, J. C. and Hooper, D. U.: Vegetation and climate controls on potential CO₂, DOC and DON

1410

- production in northern latitude soils, *Glob. Change Biol.*, 8, 872–884, 2002.
- Nilsson, M., Mikkela, C., Sundh, I., Granberg, G., Svensson, B. H., and Ranneby, B.: Methane emission from Swedish mires: National and regional budgets and dependence on mire vegetation, *J. Geophys. Res.-Atmos.*, 106, 20 847–20 860, 2001.
- 5 Page, S. E., Siegert, F., Rieley, J. O., Boehm, H. D. V., Jaya, A., and Limin, S.: The amount of carbon released from peat and forest fires in Indonesia during 1997, *Nature*, 420, 61–65, 2002.
- Päivänen, J.: Main physical properties of peat soils, in: *Peatlands and their utilization in Finland*, edited by: Laine, J., Finnish Peatland Society, Helsinki, 33–36, 1982.
- 10 Pastor, J., Solin, J., Bridgham, S. D., Updegraff, K., Harth, C., Weishampel, P., and Dewey, B.: Global warming and the export of dissolved organic carbon from boreal peatlands, *Oikos*, 100, 380–386, 2003.
- Petrone, R. M., Price, J. S., Waddington, J. M., and von Waldow, H.: Surface moisture and energy exchange from a restored peatland, Quebec, Canada, *J. Hydrol.*, 295, 198–210, 15 2004.
- Pind, A., Freeman, C., and Lock, M. A.: Enzymatic degradation of phenolic materials in peatlands - measurement of phenol oxidase activity, *Plant Soil*, 159, 227–231, 1994.
- Price, J. S.: Blanket bog in Newfoundland. 2. Hydrological processes, *J. Hydrol.*, 135, 103–119, 1992.
- 20 Robroek, B. J. M., Limpens, J., Breeuwer, A., and Schouten, M. G. C.: Effects of water level and temperature on performance of four Sphagnum mosses, *Plant Ecol.*, 190, 97–107, 2007.
- Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R., and Bubier, J.: Contemporary carbon balance and late holocene carbon accumulation in a northern peatland, *Glob. Change Biol.*, 13, 397–411, 2007.
- 25 Rycroft, D. W., Williams, D. J. A., and Ingram, H. A. P.: Transmission of water through peat. 1. Review, *J. Ecol.*, 63, 535–556, 1975.
- Rydin, H. and Barber, K. E.: Long-term and fine-scale coexistence of closely related species, *Folia Geobot.*, 36, 53–61, 2001.
- Rydin, H., Gunnarsson, U., and Sundberg, S.: The role of Sphagnum in peatland development and persistence, in: *Boreal peatland ecosystems*, edited by: Wieder, R. K., and Vitt, D. H., Ecological Studies Series, Springer Verlag, Berlin, 47–65, 2006.
- 30 Rydin, H. and Jeglum, J. K.: *The biology of peatlands*, Oxford University Press, Oxford, 360 pp., 2006.

1411

- Rydin, H.: Population and community ecology of bryophytes, in: *Bryophyte biology* (2nd edition), edited by: Shaw, A. J., and Goffinet, B., Cambridge University Press, Cambridge, in press, 2008.
- Sagerfors, J.: Land-atmosphere exchange of CO₂, water and energy at a boreal minerotrophic mire, Ph.D. thesis, Swedish University of Agricultural Sciences, Umea, Sweden, 70 pp., 5 2007.
- Schiff, S., Aravena, R., Mewhinney, E., Elgood, R., Warner, B., Dillon, P., and Trumbore, S.: Precambrian shield wetlands: Hydrologic control of the sources and export of dissolved organic matter, *Climatic Change*, 40, 167–188, 1998.
- 10 Shannon, R. D. and White, J. R.: 3-year study of controls on methane emissions from 2 Michigan peatlands, *Biogeochemistry*, 27, 35–60, 1994.
- Shindell, D. T., Walter, B. P., and Faluvegi, G.: Impacts of climate change on methane emissions from wetlands, *Geophys. Res. Lett.*, 31, doi:10.1029/2004GL021009, 2004.
- Shurpali, N. J., Verma, S. B., Clement, R. J., and Billesbach, D. P.: Seasonal distribution of methane flux in a Minnesota peatland measured by eddy-correlation, *J. Geophys. Res.-Atmos.*, 98, 20 649–20 655, 1993.
- 15 Shurpali, N. J., Verma, S. B., Kim, J., and Arkebauer, T. J.: Carbon-dioxide exchange in a peatland ecosystem, *J. Geophys. Res.-Atmos.*, 100, 14 319–14 326, 1995.
- Sonnentag, O., Chen, J. M., Roberts, D. A., Talbot, J., Halligan, K. Q., and Govind, A.: Mapping tree and shrub leaf area indices in an ombrotrophic peatland through multiple endmember spectral unmixing, *Remote Sens. Environ.*, 109, 342–360, 2007.
- Sorensen, K. W.: Indonesian peat swamp forests and their role as a carbon sink, *Chemosphere*, 27, 1065–1082, 1993.
- Sottocornola, M. and Kiely, G.: An Atlantic blanket bog is a modest CO₂ sink, *Geophys. Res. Lett.*, 32, doi:10.1029/2005GL024731, 2005.
- 25 Strack, M., Waddington, J. M., Rochefort, L., and Tuittila, E. S.: Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown, *J. Geophys. Res.-Biogeosci.*, 111, doi:10.1029/2005JG000145, 2006.
- Suyker, A. E., Verma, S. B., Clement, R. J., and Billesbach, D. P.: Methane flux in a boreal fen: Season-long measurement by eddy correlation, *J. Geophys. Res.-Atmos.*, 101, 28 637–28 647, 1996.
- 30 Thomas, K. L., Benstead, J., Davies, K. L., and Lloyd, D.: Role of wetland plants in the diurnal control of CH₄ and CO₂ fluxes in peat, *Soil Biol. Biochem.*, 28, 17–23, 1996.

1412

- Thornton, P. E., Lamarque, J. F., Rosenbloom, N. A., and Mahowald, N. M.: Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability, *Global Biogeochem. Cy.*, 21, doi:10.1029/2006GB002868, 2007.
- 5 Turunen, J., Tomppo, E., Tolonen, K., and Reinikainen, A.: Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions, *Holocene*, 12, 69–80, 2002.
- Vile, M. A., Bridgham, S. D., Wieder, R. K., and Novak, M.: Atmospheric sulfur deposition alters pathways of gaseous carbon production in peatlands, *Global Biogeochem. Cy.*, 17, doi:10.1029/2002GB001966, 2003.
- 10 Waddington, J. M. and Roulet, N. T.: Groundwater flow and dissolved carbon movement in a boreal peatland, *J. Hydrol.*, 191, 122–138, 1997.
- Wallage, Z. E., Holden, J., and McDonald, A. T.: Drain blocking: An effective treatment for reducing dissolved organic carbon loss and water discolouration in a drained peatland, *Sci. Total Environ.*, 367, 811–821, 2006.
- 15 Walter, B. P., Heimann, M., and Matthews, E.: Modeling modern methane emissions from natural wetlands 1. Model description and results, *J. Geophys. Res.-Atmos.*, 106, 34 189–34 206, 2001a.
- Walter, B. P., Heimann, M., and Matthews, E.: Modeling modern methane emissions from natural wetlands 2. Interannual variations 1982–1993, *J. Geophys. Res.-Atmos.*, 106, 34 207–34 219, 2001b.
- 20 Weltzin, J. F., Harth, C., Bridgham, S. D., Pastor, J., and Vonderharr, M.: Production and microtopography of bog bryophytes: Response to warming and water-table manipulations, *Oecologia*, 128, 557–565, 2001.
- Wieder, R. K., Canadell, J., Limpens, J., Moore, T., Roulet, N., and Schaepman-Strub, G.: Peatlands and the carbon cycle: From local processes to global implications, *EOS*, 88, 295, 2007.
- 25 Wieder, R. K., Scott, K. D., Vile, M. A., Kamminga, K., and Vitt, D. H.: Burning bogs and changing climate: Will peatland carbon sinks become sources?, *First International Symposium on Carbon in Peatlands*, 15–18 April, 2007, Wageningen, The Netherlands, Wageningen, NL, 41, 2007.
- 30 Wiedermann, M. M., Nordin, A., Gunnarsson, U., Nilsson, M. B., and Ericson, L.: Global change shifts vegetation and plant-parasite interactions in a boreal mire, *Ecology*, 88, 454–464, 2007.

1413

- Worrall, F., Reed, M., Warburton, J., and Burt, T.: Carbon budget for a British upland peat catchment, *Sci. Total Environ.*, 312, 133–146, 2003.
- Worrall, F., Armstrong, A., and Holden, J.: Short-term impact of peat drain-blocking on water colour, dissolved organic carbon concentration, and water table depth, *J. Hydrol.*, 337, 315–325, 2007.
- 5 Yallop, A. R., Thacker, J. I., Thomas, G., Stephens, M., Clutterbuck, B., Brewer, T., and Sannier, C. A. D.: The extent and intensity of management burning in the English uplands, *J. Appl. Ecol.*, 43, 1138–1148, 2006.

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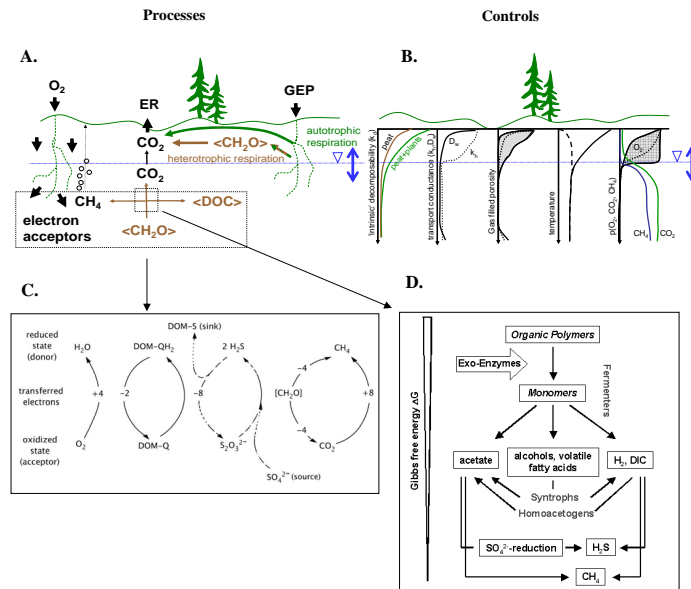


Fig. 1. Schematic of small-scale biogeochemical processes (**A.** ER: Ecosystem Respiration, GEP: Gross Ecosystem Production, CH_2O : organic matter) and distribution of controls involved in belowground carbon cycling in peatlands (**B.** constants: k_d : decomposition; k_h : hydraulic conductivity, D_w : Diffusion). Uncertainties exist for example regarding (I) the spatiotemporal distribution of gas filled porosity and associated oxygen concentrations and transport rates, (II) the magnitude and temporal variability of autotrophic root respiration, (III) the nature, generation and the recycling of the electron acceptors resulting in reduced methane production in peat soils (**C.**) and (IV) the regulation and impact of exo-enzymatic activity on decomposition (**D.**).

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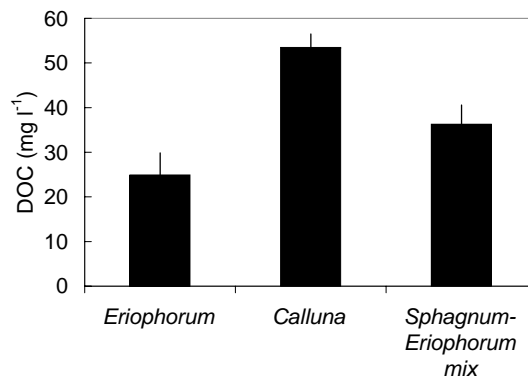


Fig. 2. DOC concentrations in stream water from UK blanket peatland catchments (mean \pm SE) dominated by particular vegetation types. No burning occurred on the catchments used to derive data in the figure. Collection of the data was performed by A. Armstrong and was funded by Yorkshire Water.

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Fig. 3. A natural peatland pipe showing **(A)** the outlet on a stream bank (with compass for scale) and **(B)** the internal features of the pipe channel which is 27 cm tall.

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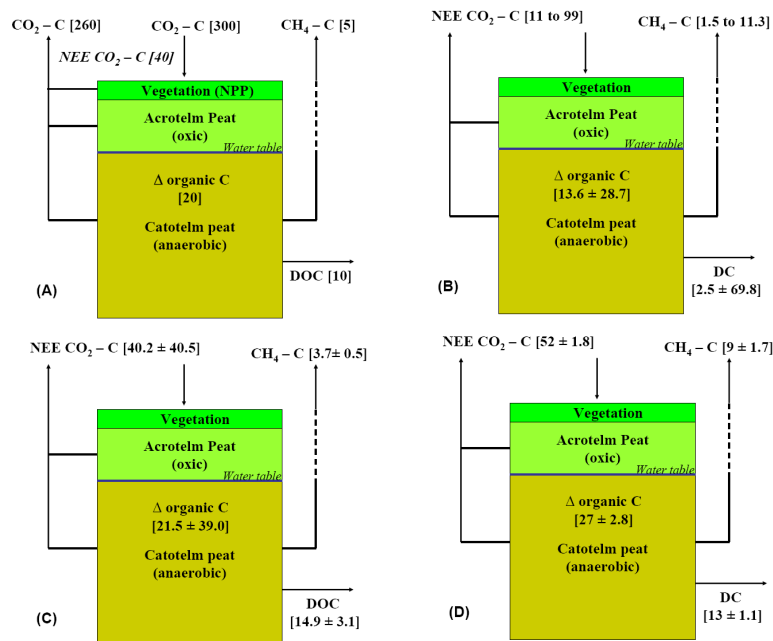


Fig. 4. Four carbon balances for northern peatlands reported in the literature. **(A)**: Deduced C balance by Gorham (1995); **(B)** Average C balance of UK peatlands compiled by Worrall et al. (2003); **(C)** Six-year average C balance for the Mer Bleue, raised shrub bog. Southern Canada compiled from measurements of all components (Roulet et al., 2006); **(D)** Two-year average C balance for Degerö Stormyr, northern Sweden compiled from direct measurements of all components (Sagerfors, 2007).

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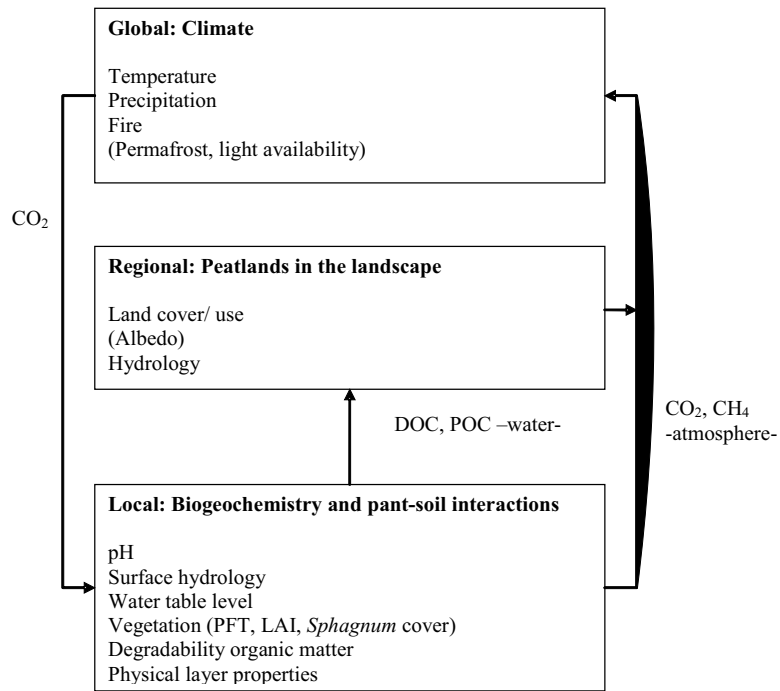


Fig. 5. Conceptual overview of the key biogeochemical and biophysical drivers of the peatland carbon balance at different spatial scales. Drivers and feedbacks within brackets are not discussed in this paper. PFT=Plant functional type, LAI=Leaf area index.