

Towards developing IPCC methane ‘emission factors’ for peatlands (organic soils)

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SUMMARY

- (1) Huge reductions of carbon dioxide (CO₂) and nitrous oxide (N₂O) effluxes can be attained by rewetting drained peatlands, but this will increase methane (CH₄) effluxes.
- (2) The scientific data base for methane effluxes from peatlands is much larger than that for CO₂ or N₂O. Once anoxic conditions are provided, the availability of fresh plant material is the major factor in methane production. Old (recalcitrant) peat plays only a subordinate role in gas efflux.
- (3) The annual mean water level is a surprisingly good indicator for methane effluxes, but at high water levels the cover of aerenchymous shunts (gas conductive plant tissue) becomes a better proxy. Ideally, both water level and cover of aerenchymous shunts should be assessed to arrive at robust estimates of methane effluxes.
- (4) The available data provide sufficient guidance for arriving at moderately accurate (Tier 1) estimates consistent with IPCC methodologies. For more accurate estimation (higher tier approaches), vegetation provides a promising basis for development of more detailed efflux factors. Vegetation is a good proxy for mean water levels and can provide - with extra attention to aerenchymous shunts - a robust proxy for accurate and spatially explicit estimates of methane effluxes over large areas.

KEY WORDS: decomposition; peatland drainage; organic soils; shunt species; rewetting

INTRODUCTION

Drainage of peatlands results in global carbon dioxide (CO₂) and nitrous oxide (N₂O) emissions of more than 2 Gt CO₂-eq. yr⁻¹ (Joosten 2011) - a rate that we should try to reduce substantially in the light of climate change predictions. Many of these effluxes can be avoided by peatland rewetting and restoration (Trumper *et al.* 2009). Rewetting leads to increased methane (CH₄) effluxes, however, and for this reason some people hesitate to support it. But the scientific data base for methane effluxes from peatlands is much larger than those for CO₂ or N₂O (for which IPCC default emission factors are available, see Couwenberg 2009a, 2011) and there are several recent detailed reviews of the subject (Couwenberg *et al.* 2009b, Lai 2009, Saarnio *et al.* 2009).

In this article we consider methane effluxes from peatlands, discuss the mechanisms behind these effluxes, and present tentative ‘emission factors’. These ‘emission factors’ follow IPCC guidance (IPCC 2006) that provides advice on emission estimation methods at three levels of detail. The simplest method (Tier 1) uses default ‘emission

factors’ that are typically provided for broad climate zones and general types of land use. More detail is added at higher tiers, using country specific ‘emission factors’ and other data (Tier 2) or complex spatio-temporal modelling approaches (Tier 3). In this paper we focus on Tier 1 ‘default’ values and suggest ways to arrive at more detailed Tier 2 values.

METHANE DYNAMICS IN PEATLANDS

In peatlands, decomposition of organic matter is incomplete and peat accumulates. Incomplete decomposition, with conservation of peat, is caused by waterlogging with its associated low temperatures, anoxic conditions and small microbial populations. Microbial decomposition does continue under anoxic conditions, but such anaerobic degradation of organic material is slow. It is carried out stepwise by a complex food web of specialised micro-organisms, each producing specific intermediate substrates (Whalen 2005, Lai 2009). The final step in anaerobic decomposition is then performed by methanogenic *Archaea*, i.e. methane-

producing micro-organisms. The amount of methane emitted to the atmosphere depends on the balance between methane production and consumption and the mode of methane transport.

Methane production

Literature reviews (Segers 1998, Whalen 2005, Lai 2009) reveal that:

- most methane release from peat columns is derived from recently fixed (young) carbon;
- methane production decreases when labile substrates are depleted, for example with depth below the water table;
- methane production can be stimulated substantially with addition of intermediate substrates (e.g. acetate); and
- methane production is lowered by two orders of magnitude under oxic conditions.

These observations lead to the conclusion that, once oxygen-deprived conditions are established, the quality and supply of the substrate is the major factor in methane production. Substantial amounts of methane are produced only when labile carbon substrates (e.g. acetate, sugars) are available. Old (recalcitrant) peat plays a subordinate role as a substrate for methane production (Chanton *et al.* 1995, Hornibrook *et al.* 1997, Charman *et al.* 1999). Vegetation composition is a major control on substrate quality (litter quality) and subsequently on rates of methane production (Williams & Yavitt 2011). Limited transport (at low diffusion rates; Chanton 2005) seems to cause an accumulation of methane at increasing depth in peat columns, but this does not indicate high rates of production (Clymo & Bryant 2008, Fritz *et al.* 2011).

Temperature has been found to increase the rate of methane production. The effect of temperature is, however, highly variable (Segers 1998, Whalen 2005). This variable effect is probably due to varying temperature response within the anaerobic food web (Whalen 2005). At temperatures below -5 °C methane production is consistently low. While most methanogenic Archaea grow only within a narrow pH range between 6 and 8, some operate under more acidic conditions as well (Garcia *et al.* 2000, Whalen 2005, Lai 2009). Quantitative assessments of the effect of pH on methanogenesis arrive at inconsistent results (Whalen 2005). *In situ* estimations of the pH effect are complicated because of the auto-correlation between pH and soil chemistry (e.g. Ca²⁺, DOC) (Yavitt *et al.* 2005).

Methane consumption

Only part of the methane produced is emitted to the atmosphere. Considerable amounts are consumed by methanotrophic bacteria (Hanson & Hanson 1996,

Segers 1998). The concentration of methane in peat above the water table mostly decreases as methane moves upwards through the peat towards the air (below mmol range; Watson *et al.* 1997, Daulat & Clymo 1998, Hornibrook *et al.* 2009). The re-oxidation of methane is mainly confined to the zone close to the water table, where the supply of neither oxygen nor methane is limited (Segers & Leffelaar 2001b, Askaer *et al.* 2011b). Similarly, methane consumption occurs in the oxygenated zone surrounding plant roots (Figure 1), which is small compared to the entire volume of the rooting zone, allowing for the presence of methane in the direct vicinity of roots (Armstrong *et al.* 1992, Grosse *et al.* 1996, Segers *et al.* 2001). Rates of methane oxidation by methanotrophs (on a volume basis) are typically an order of magnitude larger than the potential for methane production by methanogens (Segers 1998, Kip *et al.* 2012). As a result, methanotrophic bacteria can limit the amount of methane that is released to the atmosphere substantially (Pearce & Clymo 2001, Laanbroek 2009, Fritz *et al.* 2011). However, a thorough reduction of methane release is limited by the thickness of the oxic near-surface layer (Daulat & Clymo 1998, Askaer *et al.* 2011b). Extensive oxygen input by plant roots creating oxic conditions seems uncommon in most peatland types (Armstrong *et al.* 1991, de Mars & Wassen 1999, Ding *et al.* 2005, Fritz *et al.* 2011). Data and insight on the influence of temperature and pH on methanotrophs are still scanty and dependencies uncertain (Whalen 2005). Methane consumption has also been described in the absence of oxygen but at much lower rates than aerobic methane oxidation (Ettwig *et al.* 2010, Smemo & Yavitt 2011).

Methane transport

Methane gas is emitted from the peat column to the atmosphere *via* three main pathways: diffusion, ebullition and plant mediated transport (Figure 1).

Diffusion of methane is slow, and the overall diffusive efflux from peatlands is small compared to the other two pathways (Kiene 1991, Lai 2009). However, methane diffusion plays an important role in providing the methanotrophic community in the oxic near-surface zone with methane from the oxygen-depleted zone below (Whalen 2005).

Ebullition refers to methane released to the atmosphere as bubbles. Methane-containing bubbles commonly occur in water-saturated peat layers because the solubility of methane and nitrogen in water is low (about 0.04 and 0.02 cm³ cm⁻³ respectively). Already formed gas bubbles strip methane and nitrogen from the porewater and when methane production exceeds depletion (transport,

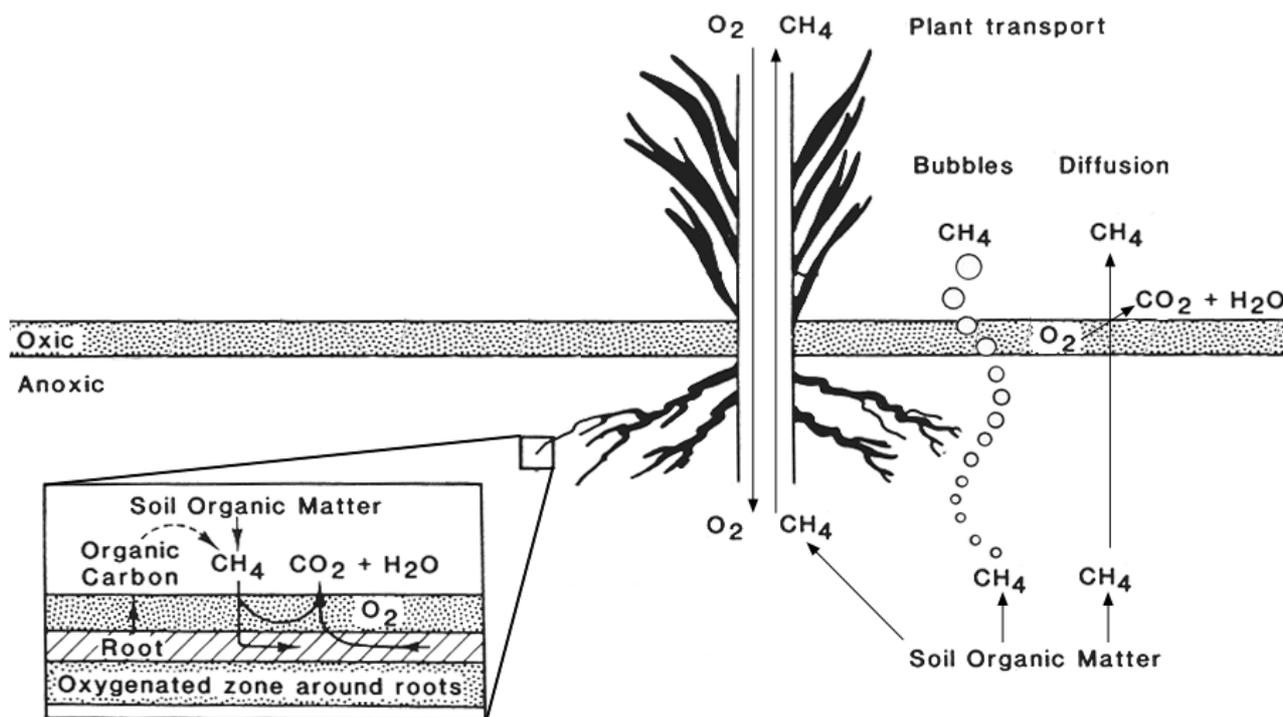


Figure 1. Production, re-oxidation and efflux of CH₄ from a vegetated peatland site (after Kiene 1991, see also Whalen 2005, Lai 2009, Li *et al.* 2009).

oxidation) bubbles grow in size. A built-up of substantial gas volumes is facilitated by the heterogenic and anisotropic nature of peat by which gas bubbles are trapped (Beckwith *et al.* 2003). If bubble pressure exceeds a threshold, which depends on bubble volume and peat compressibility, a sudden release of the trapped methane can occur (Kellner *et al.* 2004, Coulthard *et al.* 2009). This release is often associated with changes in water level (Strack *et al.* 2005), barometric pressure (Kellner *et al.* 2004, Tokida *et al.* 2007b, Comas *et al.* 2008) and temperature (Beckmann *et al.* 2004) as well as mechanical disturbance (Fechner-Levy & Hemond 1996, Goodrich *et al.* 2011). Ebullition events are also observed during spring thaw when methane trapped under ice is released to the atmosphere (Moore & Knowles 1990, Hargreaves *et al.* 2001, Tokida *et al.* 2007a). The rapid transfer of methane bubbles through the oxic near-surface layer means there will be little or no consumption by methanotrophs because methane diffusion towards methanotrophs is slower than transport by bubble movement. As a result, even small and slowly moving bubbles are only partially oxidised (Laing *et al.* 2011).

Diffuse ebullition can be measured using the eddy covariance technique or even closed chambers of sufficient size and measurement frequency (Goodrich *et al.* 2011; Box 1). The localised extent

and episodic nature of *large* ebullition events, however, make them difficult to detect or assess quantitatively by closed chamber measurements (Glaser *et al.* 2004, Comas *et al.* 2007, Denmead 2008). Eddy covariance techniques may also not be suitable for measuring large ebullition events because these events are too localised and short-lived (Tokida *et al.* 2007b). Instead, Glaser *et al.* (2004) use surface deformations to estimate a total CH₄ efflux of 136 g m⁻² from three large degassing events during a summer drought. This value exceeds the remaining annual fluxes by an order of magnitude. The role of these large ebullition events in rewetted peat sites needs further research and quantification.

Many wetland plants possess aerenchymous tissue (Figure 2) that allows oxygen to reach the root zone: an adaptation to rooting in waterlogged soils. This oxygen allows oxidation of methane in the root zone (Chanton *et al.* 1992, Fritz *et al.* 2011), but at the same time methane moves out into the atmosphere through the aerenchyma, bypassing the zone of aerobic methane oxidation (Figure 1; see also Whalen 2005 and Chanton 2005). Plant species displaying this bypass, or shunt, are referred to as 'chimney' or 'shunt species'. This 'shunt flow' occurs both as diffusive flux and as much more effective pressure-driven internal gas flow from younger leaves through the aerenchyma down to the

Box 1. CLOSED CHAMBER MEASUREMENTS AND EBULLITION

Due to their erratic nature, ebullition events may not be sufficiently represented in the closed chamber flux measurements we used in our assessment. However, where and when there are a large number of (small) ebullition events (> 500 per day; Goodrich *et al.* 2011) the probability of incorporating at least part of the ebullitive efflux is increased, even at low measurement intervals. The use of chambers may also produce an increase in ebullition frequency caused by higher temperatures and mechanical stress on the peat matrix. We therefore argue that ebullition is at least partly incorporated in the closed chamber methane flux studies cited here. Eddy-covariance methods are likely to capture a large part of ebullition events (Grant & Roulet 2002, but see Tokida *et al.* 2007b). In a study comparing methane budgets based on eddy-covariance and chamber fluxes Forbrich *et al.* (2011) found little difference between the two methods, suggesting that chamber based methane budgets may be biased by only a relatively small proportion as a result of erratic ebullition events.

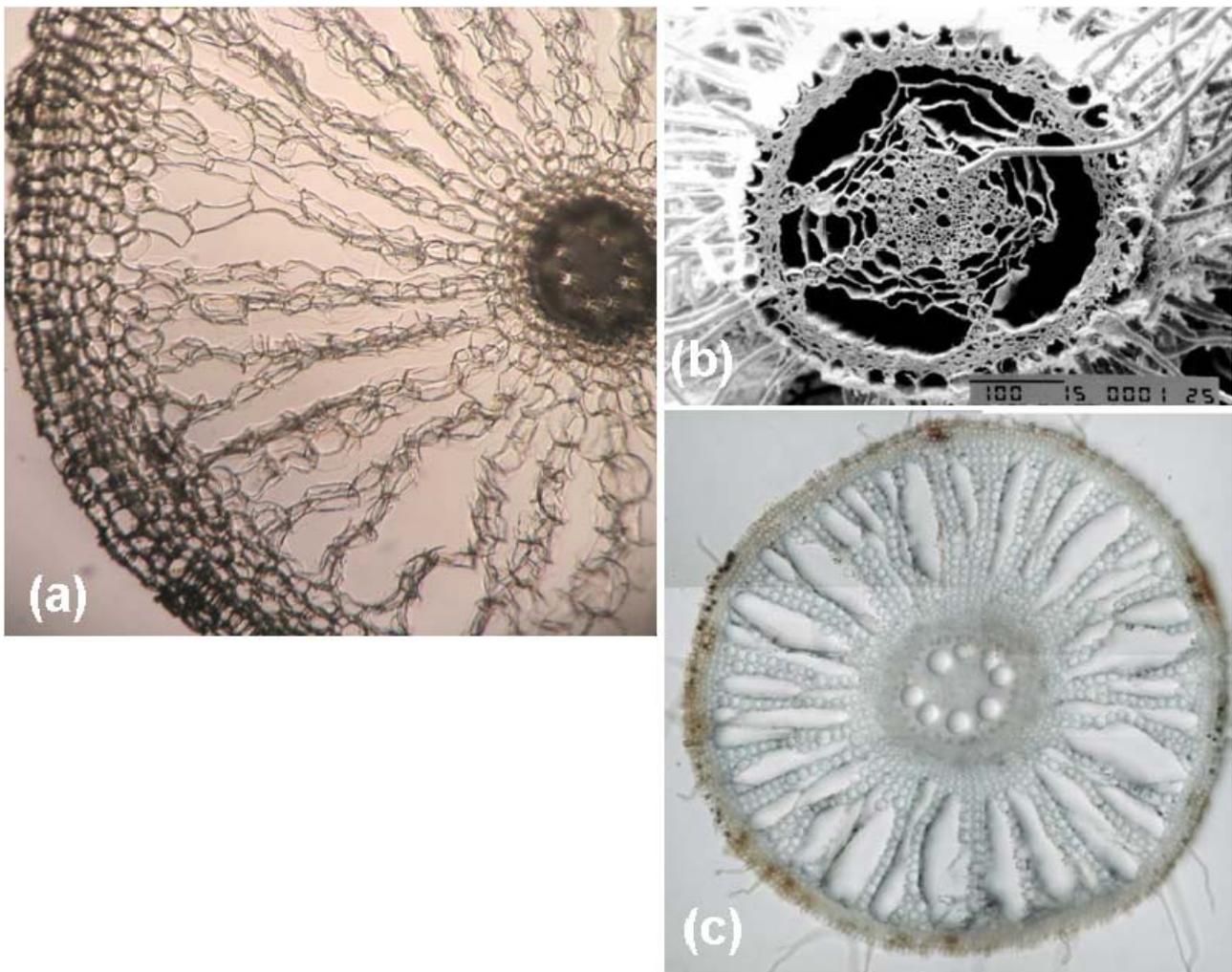


Figure 2. Cross-sections of wetland plant roots showing coarse aerenchyma. (a): *Astelia pumila*, photo courtesy of Annette Teltewskaya (Greifswald University); (b): *Carex limosa*, photo courtesy of Eric Visser (Nijmegen University); (c): *Juncus effusus*, photo courtesy of Eric Visser.

rhizomes and then back out to the atmosphere through the older leaves (Armstrong *et al.* 1992, Brix *et al.* 1992, Konnerup *et al.* 2011).

The contribution of shunt species to overall methane effluxes can be assessed using various experimental set-ups and has been estimated to account for 25–97 % of effluxes (see Whalen 2005 for a review). Plants acting as shunts in methane efflux include, for example, species of *Nymphaea*, *Nuphar*, *Calla*, *Peltandra*, *Sagittaria*, *Cladium*, *Glyceria*, *Phalaris*, *Scirpus*, *Eleocharis*, *Equisetum*, *Eriophorum*, *Carex*, *Scheuchzeria*, *Phragmites* and *Typha* (Sebacher *et al.* 1985, Chanton *et al.* 1992, Schimel 1995, Shannon *et al.* 1996, Frenzel & Rudolph 1998, Verville *et al.* 1998, Yavitt & Knapp 1998, Grünfeld & Brix 1999, Frenzel & Karofeld 2000, Greenup *et al.* 2000, Arkebauer *et al.* 2001, Armstrong & Armstrong 2011, Askaer *et al.* 2011a). Wetland species that are less common in northern peatlands also substantially stimulate gas exchange between wet soils and the atmosphere (Sorrel *et al.* 2000, Konnerup *et al.* 2011). In addition, methane efflux through pneumatophores and prop roots (Purvaja *et al.* 2004, Kreuzwieser *et al.* 2003, Pulliam 1992), as well as through the bark aerenchyma of alder trees (*Alnus* spp.), has been observed; albeit only as slower diffusive flux (Rusch & Rennenberg 1998).

Rates of gas movement through aerenchymous tissue of plants are several orders of magnitude higher than diffusion rates of gases in wet soils. In addition to facilitated transport, plants increase the gas concentration gradient between soil and atmosphere by creating short-cuts to zones of high methane production potential and high methane concentrations (Saarnio *et al.* 1997, Popp *et al.* 2000, Strack *et al.* 2006, Hornibrook *et al.* 2009). In contrast, the oxic near-surface peat is depleted in methane and, thus, hardly contributes to methane efflux (Daulat & Clymo 1998, Hornibrook *et al.* 2009). By facilitating rapid transport, shunts furthermore dampen the build-up of gases in the rooting zone, as suggested by field and mesocosm studies (Frenzel & Rudolph 1998, Van der Nat & Middelburg 1998, Christensen *et al.* 2003, Beckmann *et al.* 2004), thus lowering fluxes from ebullition events (Chanton 2005). Rapid transport also stimulates methane production, however, which is otherwise suppressed by accumulation of products from methanogenesis (Beer & Blodau 2007). Quantification of the net transport effect by plants is complicated by the side-effects of plants on methane production (carbon input) and methane consumption (oxygen input), respectively. A dominance of methane consumption *via* root-derived oxygen seems unusual in peatlands (Askaer *et al.* 2011b,

Fritz *et al.* 2011). The majority of studies find a net surplus effect of shunt species on methane effluxes (Joabsson *et al.* 1999, Kutzbach *et al.* 2004, Ding *et al.* 2005, Laine *et al.* 2007, Dorodnikov *et al.* 2011). The relative effectiveness of different plant species in transporting methane through their aerenchyma remains poorly studied.

TOWARDS ESTIMATING ANNUAL METHANE EFFLUXES

Whereas instantaneous methane effluxes frequently show high variability in time and space (Whalen 2005), fluctuations are damped out over larger areas and time intervals. To derive estimates of annual methane fluxes from peatlands and identify possible proxies, we collated annual flux measurements from boreal and temperate peatlands from published sources together with available associated site parameters (Couwenberg 2009b). Measuring methane effluxes (particularly when using closed chambers) is much more straightforward and much less cumbersome than measuring carbon dioxide effluxes and the data processed to produce Figures 3 and 4 are not exhaustive. Yet, making actual measurements to assess fluxes over large areas is impractical and proxies are needed (Joosten & Couwenberg 2009).

In order to estimate methane effluxes on a large scale, easily assessable environmental variables are required to encompass much of the variation between sites. While pH, C/N quotient, temperature and atmospheric pressure certainly affect production, consumption and transport of methane, dependencies and dynamics are complex and simple rules cannot be derived for the field situation. Moreover, many published studies fail to report the variables listed above. On the other hand, water level and the presence/absence of shunt species are easily established for large areas (Joosten & Couwenberg 2009, Couwenberg *et al.* 2011) and provide robust indicators for methane effluxes (Figures 3, 4).

Methanogenic and methanotrophic microorganisms in the peat are well adapted to adverse conditions and microbial communities remain abundant at a particular depth below the surface despite water level fluctuations changing the supply of oxygen and methane (Kettunen *et al.* 1999, Knorr & Blodau 2009, Kip *et al.* 2012). When the water level rises, the thickness of the methane production zone increases whereas the thickness of the methane oxidation zone decreases, and *vice versa* (Whalen 2005, Lai 2009). The overall result of the water level dependency and stress resistance of the

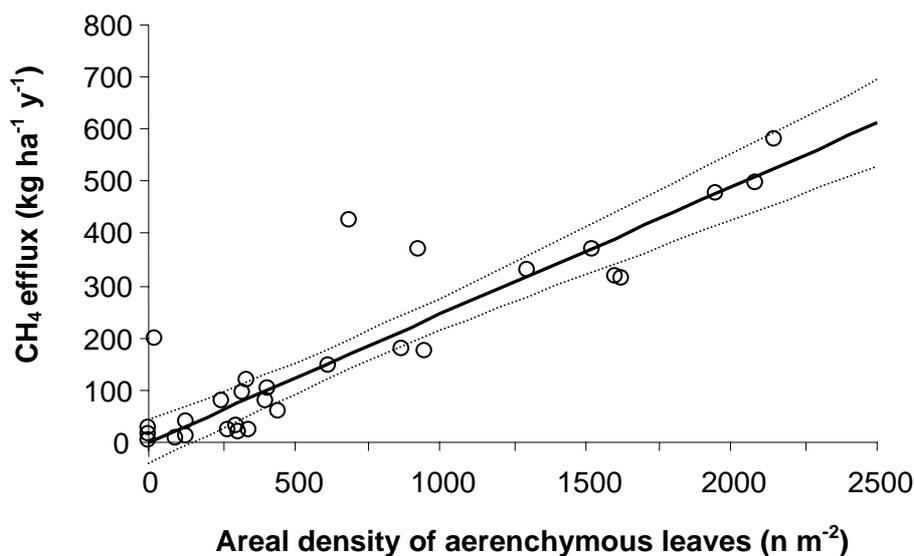


Figure 3. Annual methane effluxes from the Kendlmühlfilze (Germany) - a disturbed bog site under restoration - in relation to density of aerenchymous leaves of *Eriophorum vaginatum* and *Scheuchzeria palustris* that act as shunts (or short cuts) for methane efflux from the anoxic zone directly to the atmosphere. Mean annual water level is above -20 cm at all measurement sites. Linear regression: $y = 0.24 \times x$ [$n = 29$; $R^2 = 0.91$, $p < 0.01$] (after Drösler 2005).

microbial community is that the annual mean water level is a surprisingly good proxy for methane effluxes (Figures 3, 4). Significant methane effluxes occur only at mean annual water levels above -20 cm, and this rule applies to boreal as well as to temperate peatlands and to bogs and fens alike (Figure 4). There is ample evidence that a 20 cm thick layer of (semi-)oxic peat is sufficient to oxidise the bulk of methane produced in the peat column before entering the atmosphere (Daulat & Clymo 1998, Frenzel & Karofeld 2000, Hornibrook *et al.* 2009).

Water levels above the peat surface often result in reduced methane effluxes because of enhanced methane consumption in the oxygenated water column (Figure 4, Bubier 1995) and lower cover of shunt species. The movement of surface water may also limit the downward transport of labile carbon and thus reduce substrate availability for methane production in anoxic peat layers. Peatland habitats that are frequently flooded show typically much lower biomass production than their drier counterparts (Belyea & Clymo 2001, Strack *et al.* 2006).

The amount of methane that can be emitted to the atmosphere depends on the balance between its production and consumption and, as already explained, this balance is determined by the water level. However, at high water levels, the ability to bypass the high methane oxidation potential in the

oxic near-surface layer seems to assume substantial importance and the cover of aerenchymous shunts becomes a better proxy for effluxes than the mean annual water level (Figure 3). Higher water levels and consequently higher near-surface methane concentrations increase the transport effect of shunt species. Common shunt species (e.g. *Carex*, *Phragmites*, *Eriophorum*, *Scheuchzeria*) concentrate their root biomass in the upper 20–30 cm of surface peat (Frenzel & Karofeld 2000, van der Nat & Middelburg 1998, Popp *et al.* 2000, Strack *et al.* 2006, Murphy *et al.* 2009). Thus, both water level and cover of aerenchymous shunts may allow an even more robust assessment of methane effluxes (Drösler 2005).

Monitoring peatland water levels over large areas by direct measurements (and extrapolations) is expensive, time-consuming and probably inaccurate. For example, common water level gauges fail to correct for volume changes of the near-surface peat (Mooratmung, often of the same order of magnitude as water level fluctuations) (Fritz *et al.* 2008 and literature therein). On the other hand, vegetation can be used as a good proxy for water level and can be mapped using remote sensing (Joosten & Couwenberg 2009, Couwenberg *et al.* 2011). Vegetation mapping can also focus on the presence of aerenchymous shunts, thereby providing a robust basis for accurately estimating methane effluxes over large areas.

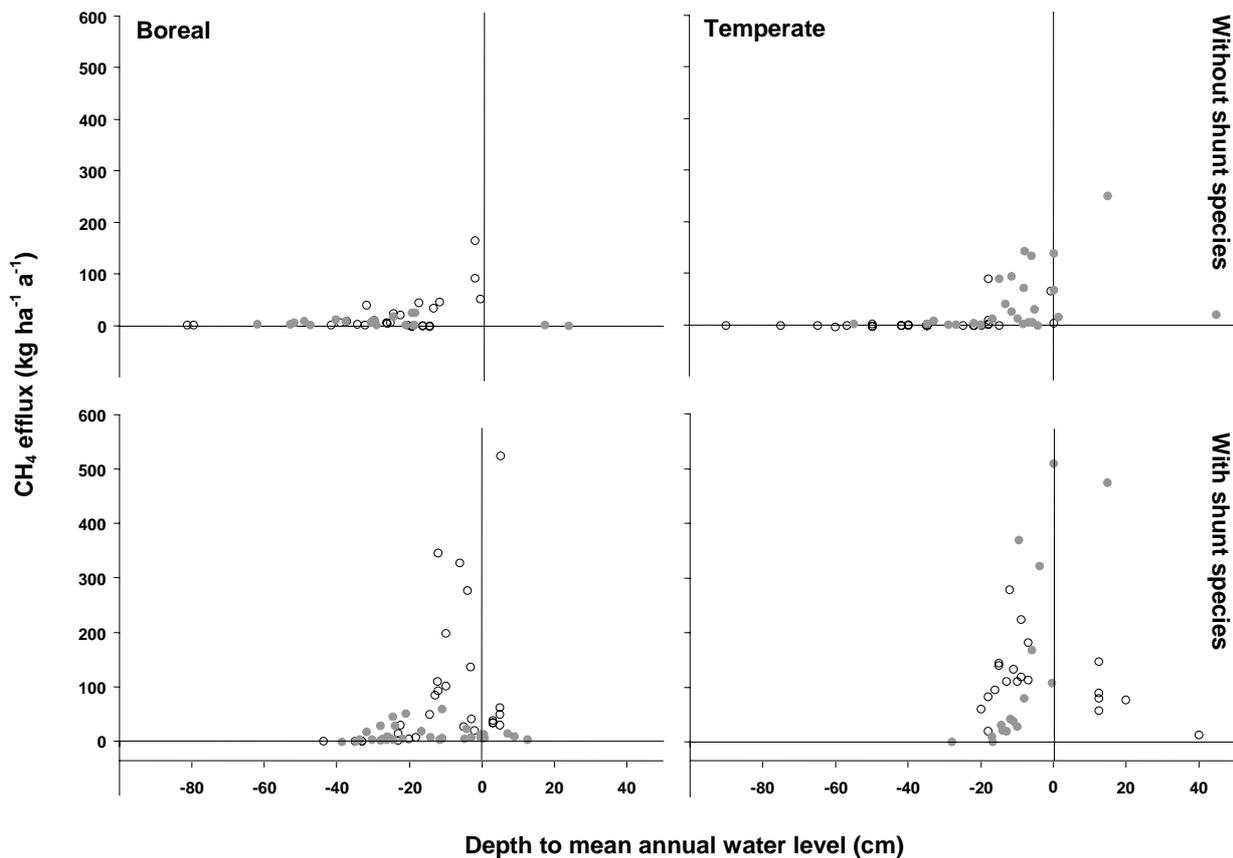


Figure 4. Annual methane effluxes from boreal (left) and temperate (right) raised bogs (●) and fens (○) in relation to water level and absence (top) or presence (bottom) of shunt species. Data from Bubier *et al.* (1993), Shannon & White (1994), Nykänen *et al.* (1995), Augustin *et al.* (1996a), Augustin *et al.* (1996b), Laine *et al.* (1996), Alm *et al.* (1997), Müller *et al.* (1997), Van den Pol-Van Dasselaar *et al.* (1997), Augustin & Merbach (1998), Flessa *et al.* (1998), Van den Pol-Van Dasselaar *et al.* (1999), Tuittila *et al.* (2000), Waddington & Roulet (2000), Whiting & Chanton (2001), Wickland *et al.* (2001), Wild *et al.* (2001), Gauci & Dise (2002), Augustin (2003), Jacobs *et al.* (2003), Sommer *et al.* (2003), Van den Bos (2003), Maljanen *et al.* (2004), Von Arnold (2004), Drösler (2005), Von Arnold *et al.* (2005a), Von Arnold *et al.* (2005b), Von Arnold *et al.* (2005c), Bortoluzzi *et al.* (2006), Van Huissteden *et al.* (2006), Hendriks *et al.* (2007), Jungkunst & Fiedler (2007), Scottish Executive (2007), Augustin & Chojnicki (2008), Tauchnitz *et al.* (2008).

There are few data on annual methane effluxes for (sub)tropical peatlands, but flux measurements from south-east Asia are low (Figure 5) relative to those from temperate and boreal Europe, perhaps due to the recalcitrance of tropical woody peats (Couwenberg *et al.* 2010). On the other hand, effluxes from rice paddies on tropical peat are high (Couwenberg *et al.* 2010, Couwenberg 2011).

JUSTIFICATION OF PARAMETERS

Statistical analysis of the available data (Box 2) supports the notion that water level exerts the strongest control on methane efflux. The mean annual water level serves as a good proxy for

methane release in boreal and temperate peatlands, explaining 34 % of variance in the collated data. However, simple water level classes (< -20 cm and > -20 cm) are just as reliable as a proxy. At water levels below -20 cm (dry to semi-dry peatlands) amount and variation of methane release are small due to the dominance of oxidation processes close to the peat surface. For water levels above -20 cm the uncertainty of quantitative estimates is much larger. If additional factors such as climate zone, presence of shunts and peatland type are taken into account uncertainty is reduced significantly. These factors serve as a (coarse) proxy for relevant variables such as temperature, methane transport, productivity, carbon (litter) quality and carbon supply by decomposition.

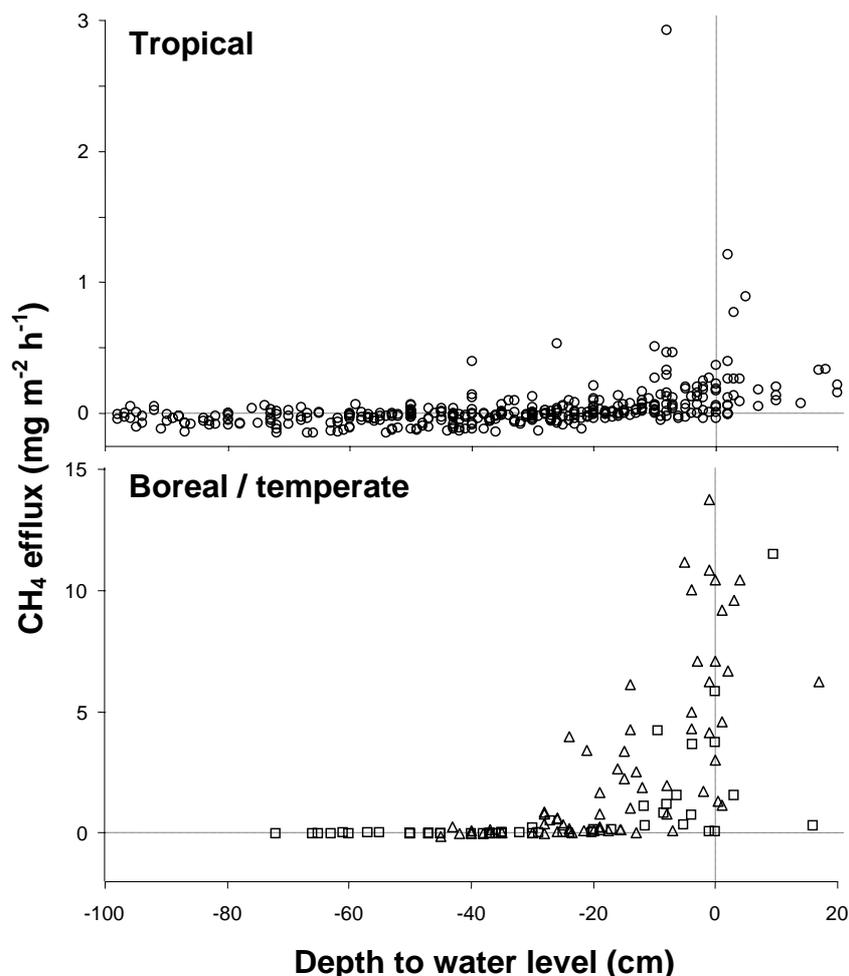


Figure 5. Top: hourly methane fluxes from tropical peat soil in relation to water level. Negative values denote net uptake from the atmosphere by the soil. Bottom: same for (Δ) boreal and (\square) temperate sites. From Couwenberg *et al.* (2010). Note the five-fold difference in scale. Note also that the units are different from those in Figure 4.

Temperature is taken into account indirectly by separating boreal and temperate peatlands (Tables 1 and 2). Applying temperature (e.g. mean annual or mean growing season) as a direct proxy seems troublesome. Firstly, the temperature dependency of single processes of the methane cycle is still very uncertain (Segers 1998, Van Hulzen *et al.* 1999, Whalen 2005, Parmentier *et al.* 2011). Although a number of studies showed methane effluxes to increase with (seasonally) higher soil temperature (Saarnio *et al.* 1997, Daulat & Clymo 1998, Beckmann *et al.* 2004, Forbrich *et al.* 2011, Moore *et al.* 2011), the quantitative effect of temperature is highly variable between studies. Secondly, we expect a strong interaction with water level depth, which determines the zone of methane production. Seasonal warming at greater depths is small compared to warming of oxic near-surface peat. To account for this interaction long-term data on timing

and extent of water level fluctuations would be needed. Thirdly, part of the observed increase also coincides with seasonal increase in aboveground and belowground biomass as well as the total surface area of shunts (Laine *et al.* 2007). Although the currently available literature enables methane efflux data to be classified only according to presence and absence (rather than percentage cover) of aerenchymous shunts, distinct efflux classes can nevertheless be derived (Figure 4, Table 2).

For a Tier 1 approach, a simple division between 'dry' and 'wet' peatlands set at mean annual water level -20 cm (Table 1) may suffice. A more sophisticated approach might distinguish between climate zones and between bog (generally low productivity and acidic) and fen (often greater productivity and more nutrient- and base-rich) peat (cf. Joosten & Clarke 2002), with lower methane production and efflux expected for bog peat (Lai

Box 2. STATISTICAL ANALYSIS OF FACTORS DETERMINING METHANE EMISSIONS

Applying multiple linear regression models using ‘R’ statistical software (R Development Core Team 2010), we tested whether log-transformed methane effluxes were dependent on factors such as mean annual water level, presence of shunt species, climate zone and peatland type (bog or fen). Water level proved to be a strong control on methane effluxes: variations in mean annual water level (continuous scale) explained 34 % of methane efflux variations ($R^2=0.34$; d.f. 1, 188; $F=99.66$, $p < 0.0001$). After dividing the water level into two classes (< -20 cm and > -20 cm, respectively) this dependency remained unchanged ($R^2=0.34$; d.f. 1, 188; $F=98.29$, $p < 0.0001$). Thus, water level classes have the same explanatory power as continuous water levels (34 %).

Incorporating climate zone next to water level class resulted in a simple model (Table 1) of four efflux classes, explaining 42 % of variance ($R^2=0.42$; d.f. 3, 186; $F=46.01$, $p < 0.0001$). We found a strong interaction between water level class and climate zone (d.f. 1; $F=22.57$, $p < 0.0001$), indicating that high water levels will have smaller stimulating effects on methane release in boreal than in temperate peatlands. Expanding this regression model with the presence of shunt species (Table 2) increases its explanatory power ($R^2=0.48$; d.f. 5, 184; $F=36$, $p < 0.0001$) without adding much complexity (six efflux classes explaining 48 % of variance). The presence of shunt species is significant only at high water levels (d.f. 1; $F=23.99$, $p < 0.0001$). Including peatland type (bog or fen) as additional factor resulted in a rather complicated regression model ($R^2=0.54$; d.f. 12, 177; $F=20.08$, $p < 0.0001$) with 13 classes explaining 54 % of variance. As a compromise between complexity and explained variance, we tested a model in which peatland type (bog or fen) was differentiated only for wet boreal peatlands with shunts (Table 2). This model of seven efflux classes explains 51 % of variance ($R^2=0.51$; d.f. 9, 180; $F=22.51$, $p < 0.0001$).

Table 1. Efflux factors for methane from peatlands following a simplified Tier 1 approach. ‘Dry’ means a mean annual water level below -20 cm; ‘Wet’ means a mean annual water level above -20 cm.

	Mean and [range] ($\text{kg ha}^{-1} \text{ a}^{-1}$)	
	Dry	Wet
Boreal	8.6 [-1.1 – 51]	56 [-1.7 – 525]
Temperate	0.2 [-4.0 – 9.0]	122 [-0.2 – 763]

Table 2. Efflux factors of methane from peatlands categorised by climate, peatland type and vegetation. ‘Dry’ means a mean annual water level below -20 cm; ‘Wet’ means a mean annual water level above -20 cm.

		Mean [range] ($\text{kg ha}^{-1} \text{ a}^{-1}$)		
		Dry	Wet	
			Without shunts	With shunts
Boreal	Bogs	8.6 [-1.1 – 51]	24 [-1.7 – 164]	12 [3.1 – 59]
	Fens			123 [6.6 – 525]
Temperate		0.2 [-4.0 – 9.0]	50 [-0.2 – 250]	170 [0 – 763]

2009). This distinction is indeed found in boreal peatlands, and is most apparent from a comparison of bogs and fens with aerenchymous shunts (Figure 4, Table 2). On the other hand, temperate bogs and fens cannot be differentiated on the basis of available data (Figure 4). Table 2 presents methane efflux factors at a more detailed level, also taking into account the presence/absence of shunt species. Comparable data for tropical peatlands are still limited, but current knowledge suggests that methane effluxes from peat swamps in Southeast Asia, representing the largest area of tropical peatland, will be comparatively small (Figure 5, Couwenberg *et al.* 2010).

APPLYING PROXIES

The distinction between dry peatlands (mean annual water level below -20 cm) and wet peatlands (mean annual water level above -20 cm) can be made based on remote sensing and vegetation-water indication schemes (Couwenberg *et al.* 2011). The co-existence of dry and wet habitats (e.g. hummock and hollow microtopography; see Couwenberg & Joosten 2005 and literature therein) imposes difficulties when estimating 'one' mean annual water level for an entire peatland (landscape). The non-linear relationship between methane efflux and water level (Figure 4) requires a weighted representation of dry and wet habitats (Couwenberg *et al.* 2011). Applying a mean water level over an entire area may underestimate effluxes, which was also indicated by model studies (Segers & Leffelaar 2001a, Segers & Leffelaar 2001b, Segers *et al.* 2001, Baird *et al.* 2009).

Existing peatland classification schemes, existing vegetation maps and expert judgement on the proportions of wet and dry habitats will be sufficient for a Tier 1 approach in most cases, with the added advantage that it incorporates peatland type (fen or bog). Rapid advances in remote sensing allow for vegetation mapping that differentiates between dry and wet habitats for a large range of scales and species assemblages (Harris 2008, Anderson *et al.* 2010). This mapping should ideally form a basis for more accurate methane emission estimates by providing spatially detailed information about water levels and cover of aerenchymous shunts. Future efforts to improve estimates of methane effluxes should link methane efflux data to functional landscape units based on high resolution remote sensing.

In general, then, existing data and insights provide sufficient guidance for arriving at Tier 1 methane 'emission factors' consistent with IPCC

methodologies. For higher tier approaches, development of more detailed efflux factors on the basis of vegetation looks promising. Vegetation is a strong indicator for mean water levels and can provide - with extra attention to aerenchymous shunts - a robust proxy for accurate and spatially explicit estimates of methane effluxes over large areas. Although we identified additional factors governing the methane cycle in peatlands (labile carbon input, temperature, pH, availability of oxygen and alternative electron acceptors, biomass production, nutrient availability), none of these factors can be studied or mapped with the necessary detail at landscape scale.

Temporal aspects of carbon dynamics after rewetting need further study. Rewetting of previously drained peat soils may lead to increased methane effluxes initially, due to vegetation killed by flooding becoming a substrate for methanogens. Excessive methane effluxes that even surpass the CO₂ emissions in the drained situation before rewetting have been observed in a particularly enriched site in north-east Germany, where lateral input of easily degradable matter further stimulates methanogenesis (Augustin & Chojnicki 2008, Hahn-Schöffl *et al.* 2011). This situation must be considered atypical, however, and commonly there will be a clear climate benefit from rewetting drained peatlands (Couwenberg *et al.* 2011) and, especially, cutover peatlands (Tuittila *et al.* 2000, Wilson *et al.* 2008).

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