Report

R-21-20

January 2022

A review of sources, transport and losses of methane in the biosphere

Ari T K Ikonen

SVENSK KÄRNBRÄNSLEHANTERING AB

SWEDISH NUCLEAR FUEL
AND WASTE MANAGEMENT CO

Box 3091, SE-169 03 Solna
Phone +46 8 459 84 00
skb.se

ISSN 1402-3091
SKB R-21-20
ID 1607247

January 2022

A review of sources, transport and losses of methane in the biosphere

Ari T K Ikonen, EnviroCase, Ltd.

Keywords: Methane, Carbon-14, Biosphere, Lake, Stream, Mire.

This report concerns a study which was conducted for Svensk Kärnbränslehantering AB (SKB). The conclusions and viewpoints presented in the report are those of the authors. SKB may draw modified conclusions, based on additional literature sources and/or expert opinions.

Abstract

Currently in the long-term safety assessments for repositories of radioactive waste, it is assumed that all C-14 released from a geological repository would be available for biological uptake in the surface environments; that is, in practice, that all methane and organic carbon would be oxidised into carbon dioxide in the soil or sediment. There have been indications in the literature, though, that there is potential for a substantial fraction of the methane to evade the oxidation and thus pass the incorporation by higher organisms. The aims of this review were

1. to collate and summarise literature at hand into descriptions of methane sources, transport and losses in various ecosystems relevant to the Forsmark site, with emphasis on lakes and wetlands that typically exhibit net emission of methane and also are often primary recipients of releases from a repository in safety analyses,
2. to evaluate the possibility to establish an estimate of the minimum fraction of methane fluxes evading the oxidation, and
3. to evaluate implications to the assessments, including identification of possible needs of further studies.

In this report, first general mechanisms of methane production and consumption (oxidation) are described, followed by more in-depth discussion on the methane cycling processes in the different ecosystem types. In the final chapter, a cross-ecosystem summary is presented, as well as coarse estimates of the potential role of the various mechanisms at the Forsmark site, implications for the assessments and recommendations for further work.

Basically, low-molecular-weight organic carbon (LMWOC, for example acetate) and carbon dioxide can be microbially transformed into methane primarily in anoxic parts of the environment. This and possibly repository-originated methane either is transported to the atmosphere or becomes oxidised. Relatively fast transport mechanisms (diffusive, storage-flux, ebullition and plant-mediated transport) are more typical to wet environments, whereas for unsaturated upland soils it has been shown that typically a layer of a few tens of centimetres is sufficient for complete oxidation of methane. However, in the detailed picture, there is a large number of mechanisms that are regulated in varying degree by partly the same and partly separate factors. There is also considerable spatial and temporal variability particularly in the methane transport modes and fluxes, and few field studies yet seem to have encompassed all of these over a longer time period. Therefore, it is difficult to establish a coherent quantitative overall picture for specific environmental conditions. To aid this, further work is proposed to primarily establish a harmonised interaction matrix of the key components, state variables and controlling processes that can then be complemented with more focused process-level information, (partial) quantification and possibly even with numerical modelling.

As an overall conclusion regarding the main issue, the present modelling assumption that all C-14 released from a repository will be transformed into carbon dioxide and enter food chain through plant uptake is pessimistic but not unjustifiably so, since such situations cannot be completely ruled out in any of the recipient environments.

Sammanfattning

För närvarande antas det i de långsiktiga säkerhetsbedömningarna att allt C-14 som frigörs från ett geologiskt förvar för radioaktivt avfall skulle vara tillgängligt för biologiskt upptag i ytekosystemen. Det betyder att allt metan och organiskt kol skulle oxideras till koldioxid i berget, jorden eller sedimentet. Det finns dock studier som visar att en betydande del av metan kan undvika oxidationen och därmed passera till atmosfären. Syftet med denna genomgång är flera.

1. Sammanställa och sammanfatta tillgänglig litteratur (tom år 2017) om metankällor, transport och förluster i olika ekosystem. Tonvikten är på sjöar och våtmarker som ofta uppvisar nettoutsläpp av metan samt är primärt mottagare av utsläpp från ett förvar i säkerhetsanalyser.
2. Utvärdera möjligheten att upprätta en uppskattning av minimifraktionen av metanflöden som undviker oxidationen.
3. Utvärdera konsekvenserna för säkerhetsanalyserna, inklusive identifiering av eventuella behov av ytterligare studier.

I början av rapporten beskrivs generella mekanismer för metanproduktion och konsumtion (oxidation) följt av en diskussion om metans cirkulation i de olika ekosystemen. Därefter en sammanfattning över ekosystemen och uppskattningar av de olika mekanismerna i Forsmark, vilken betydelse det har för säkerhetsanalyserna och några rekommendationer för vidare arbete.

Organisk kol med låg molekylvikt (LMWOC, till exempel acetat) och koldioxid kan omvandlas mikrobiellt till metan främst i anoxiska delar av miljön. Tillsammans med metan från berget transporteras de till ytan och oxideras eller transporteras vidare till atmosfären. Snabba transportmekanismer (diffusion, lagringsflöde, gasbubblor och växtmedierad transport) är mer typiska för våta miljötyper, medan för omättade jord har det visats att ett skikt av några tiotals centimeter är tillräckligt för fullständig oxidation av metan. Mekanismerna för metanoxidation regleras av olika faktorer. Det finns en betydande rumslig och tidsmässig variabilitet, särskilt i metans transportsätt och flöden. Få fältstudier har omfattat alla dessa under en längre tidsperiod, och det är svårt att skapa en sammanhängande kvantitativ helhetsbild för specifika miljöförhållanden. Därför föreslås ytterligare arbete med att i första hand upprätta en interaktionsmatris av nyckelkomponenterna, tillståndsvariabler och kontrollprocesser som sedan kan kompletteras med mer fokuserad processnivåinformation, (partiell) kvantifiering och eventuellt även med numerisk modellering.

En övergripande slutsats att det nuvarande modelleringsantagandet av att all C-14 som frigörs från ett djupförvar förvandlas till koldioxid och tas upp av växter är pessimistisk men inte orimligt, eftersom sådana situationer inte helt kan uteslutas i någon av recipienterna.

Contents

1 Introduction

In this chapter, first the general context of radioactive waste repositories in respect of the methane fluxes and storages in the surface environment is described as the motivation of the present study. Thereafter, the scope and structure of this report is outlined.

1.1 Context of radioactive waste repositories

Radioactive waste is generally considered hazardous and its isolation from the living environment of people, plants and animals for long time periods is highly recommended (e.g. IAEA 1997, ICRP 2013). In Sweden, both low- and intermediate-level radioactive waste and spent nuclear fuel will be disposed of in deep bedrock, at the depths of about 50 and 500 metres, respectively (e.g. SKB 2011, 2015, 2019a). To assess the potential radiological risk to humans and the environment from these geological repositories, safety assessments must be developed and presented. This implies that the release and transfer of radionuclides from the repository into the surface environment are calculated and that the effects in the biosphere are evaluated for an assessment period (e.g. Kautsky et al. 2016) up to one million years, depending on the type of waste, as stipulated by the Swedish regulations (SSM 2009). An example of such an overall safety assessment has been presented by SKB (2015, 2019a) and examples of biosphere assessments by SKB (2014, 2019b) and Kautsky et al. (2013, 2016).

Especially with the low- and intermediate-level waste, C-14 constitutes a considerable part of the potential radiological risk. It is produced in the nuclear fuel and in the components of nuclear reactors, and it is also distributed to an extent elsewhere in the nuclear power plants. In the reactors, C-14 is produced by the same (n, p) reaction that occurs naturally in the atmosphere when N-14, also present as an impurity in reactor fuel and in other power plant systems, is exposed to neutron irradiation. In addition, O-17 may be present, from which the (n, α) reaction can produce C-14. Similarly, small quantities of C-13 within steel and other metal components in reactors can become activated to C-14 which can be released as the metal corrodes within a repository. (Shaw and Atkinson 2014).

C-14 from a geological repository may enter surface ecosystems in different forms. A significant fraction of the C-14 can be expected to be in the form of low-weight organic molecules (LMWOC), such as acetate, or in the form of inorganic carbon (CO_2, H_2CO_3). No methane is expected to be formed in the repository as a high pH environment inhibits microbial degradation of waste packages. (SKB 2015, App I). However, both LMWOC and CO_2 may be transformed to methane in the geosphere or in the biosphere, and methane may be oxidised or incorporated into microbial biomass before it enters the atmosphere. The biochemical transformations of the radioactive carbon entering surface ecosystem will depend on the environmental conditions and the presence of microbial populations.

Uptake of carbon into plant material occurs primarily by photosynthesis utilising the CO_2 in the air. There is also evidence for a contribution of photosynthesis-independent root uptake of soil inorganic carbon regulated by the plant transpiration (Amiro and Ewing 1992; also cited in Shaw and Atkinson 2014, p 7). This may be related to the continuum of transpiration stream within the plant xylem from the lower parts of the plant to the stomatal cavities and further to the canopy atmosphere, resulting in a CO_2 sink in the soil; this may provide a mechanistic link between the root uptake of CO_2 (C-14) and the photosynthesis (Shaw and Atkinson 2014, p 7, referring to personal communication with Sheppard). Generally, the root uptake of carbon has been estimated to be 1–2 % of that fixed by photosynthesis (Amiro and Ewing 1992; also cited in Shaw and Atkinson 2014, p 7). For C-14 released from below-ground, though, the corresponding contribution can be much higher due to the differences of the specific activities in the soil and in the canopy air (possibly considerably higher for the former than for the latter in case of an underground C-14 source; e.g. Limer 2019). The methane [and other organic carbon forms] are not available directly to plants, neither through atmospheric nor root uptake, so they have to be converted to carbon dioxide by microbial metabolism in the soil zone or in the water (Limer et al. 2011). The degree of transformation of the other radiocarbon forms released from the repository into $^{14}CO_2$ is the key for the majority of the C-14 uptake into the plants and further into the food web.

In the current biosphere nuclide transport model of SKB (e.g. SKB 2019b), it is pessimistically assumed that no C-14 escapes as methane. Rather, all C-14 readily released as, or transformed into, methane is assumed to be completely oxidised to carbon dioxide in the soil/sediment and, thus, becomes available for uptake by plants. However, as outlined above, it may be more realistic to assume that a part of the methane will escape the oxidation, and is not taken up by plants, and not contributing to the radiation doses. This would not only reduce the degree of pessimism in the assessments as such, but also allow for more margin for the C-14 inventory to be accepted in the waste. However, assigning a value for the fraction of the methane to always escape the oxidation needs to be on scientifically solid and reliable grounds, which has not been possible so far.

1.2 This report

Regarding the C-14 transport and fate in the surface environment in the context of radioactive waste disposal, international efforts include earlier BIOPROTA collaboration projects (Limer et al. 2012, Mobbs et al. 2014, Smith 2015, Smith and Smith 2014), the IUR task group report (Avila et al. 2006), and the more recent BIOPROTA model comparisons (Limer et al. 2017, Thorne et al. 2018). They all have been looking at the C-14 cycling and dose implications in the broader biosphere system, and these model comparisons have found considerable pessimism in the modelling approaches. Overlapping, but in dialogue, with these international efforts, SKB has developed C-14 modelling for the safety assessments based on a specific activity approach, resulting in gradual improvements in the models (Avila and Kovalets 2016, Avila and Pröhl 2008, Saetre et al. 2013), although they are rather stylised, as necessary for the assessment models. Recently there have also been considerable efforts to develop more elaborate, process-based models for mineral-soil agricultural systems in the context of radioactive waste disposal (e.g. Hoch et al. 2014, Shaw and Thorne 2016). However, most of the process-level information on the C-14 cycling remains on a rather general level or focussed on other applications than radioactive waste disposal.

The aim of this report has been to elaborate the knowledge basis on the processes underlying the methane transformations and transport in, and emissions from, ecosystems relevant to SKB's biosphere assessments – that is, freshwater bodies, wetlands and mires (forested or treeless) – based on the literature readily at hand. This recognises the sheer bulk of potentially relevant literature, not aimed to be digested in full; rather gaining an overall look to focus further developments has been the aim. On the other hand, this focus on the ecosystem types relevant in the assessments results in a degree of repetition and iteration in the report since most of the processes are common to practically all ecosystems. However, to allow the material to be digested ecosystem-by-ecosystem as a handbook, this has been a conscious choice not to separate all the general process-level discussion from the ecosystem-specific descriptions, even if it might had condensed the report. Another set of aims has been 1) to provide further support to evaluate the present assessment assumption that all repository-released methane would become oxidised and available to plants and other biota, 2) to identify in which parts of the surface environment the methane release and its fate could be of importance to the biosphere assessment, and 3) to identify whether further development efforts seem warranted. This latter set of aims is more in the focus towards the end of this report.

It may be questioned whether the generic literature on stable carbon isotopes (C-12, C-13) would be applicable to C-14. This is because, in principle, oxidation of methane to carbon dioxide, or the opposite reduction, are kinetic reactions which exhibit isotopic discrimination (i.e. the reaction rates for isotopic lighter substrates necessarily are faster than those for chemically identical, but isotopically heavier, substances) (Baker and Fritz 1981, Chanton et al. 2005, Gonzales Gil et al. 2008, and Maxfield et al. 2006, all cited in Shaw and Atkinson 2014, pp 12–13). However, based on laboratory studies with the different carbon isotopes for upland agricultural and grassland conditions (i.e. well-drained, oxic conditions), conclusions drawn from studies with stable carbon isotopes can be applied equally when considering the behaviour of C-14 in soils (Hoch et al. 2014, p 29). It needs to be noted, though, that isotope discrimination effects may play a role in some specific circumstances, such as in the diffusion of carbon species across thick peat layers over long time frames. In the present report the discussion relates mostly to the surface layers in which C-13 and C-14 can be expected to behave similarly to each other as indicated by the experiments referred to above.

Since little material readily oriented towards radioactive waste disposal was at hand regarding methane in other than drier upland ecosystems and landfills, the commission in this work was to compile a first-stage review of common literature on the methane production, cycling and oxidation, with a focus on the general patterns and on the ecosystems relevant to SKB's biosphere assessments (including particularly freshwaters and wetlands). The aim was to summarise key characteristics of methane behaviour in these ecosystems for further reference in order to support later biosphere assessments. However, since the basic processes are the same regardless of the ecosystem, this report first addresses the methane cycling in a general level, focusing on the production and oxidation processes. Then, Chapter 3 briefly addresses the topic for upland soils and for landfills, dominated by thick oxic surface layer and high degree of methane oxidation. In Chapters 4–6 further literature is summarised regarding the specifics of methane behaviour in freshwater (lakes, ponds and streams) and mire environments, all of them characterised by extensive anoxic domain and relatively high methane emissions. In Chapter 7, the report is summarised, the outcome is applied to the Forsmark site, and conclusions on the implications of the present work for biosphere assessments are drawn. The biota names used in the report are listed in the appendix by their scientific and vernacular English and Swedish names.

The review work reported here essentially commenced in mid-2017, with the main literature searches conducted in spring 2017. The author is grateful to Peter Saetre (SKB) for managing the contract, guidance, review and extensive material to start with; Ville Kangasniemi (EnviroCase, Ltd.) for technical assistance; David Bastviken (Linköping University) and Olle Hjerne (SKB) for meticulous review; and Lena Sivars Becker (Studsvik Nuclear AB), Claes Becker (Ramboll Sverige AB), Sabine Jordan (Swedish University of Agricultural Sciences), and Anders Löfgren (Ecoanalytica) for the early draft material on methane cycling made available to the project.

2 Methane cycling in general

Methane is the main hydrocarbon present in the atmosphere, with an average concentration of 1.8 ppm in 2012 (and increasing), with seasonal variations of about 0.03 ppm (Dlugokencky et al. 1994, cited in Le Mer and Roger 2001, p 25, Saunois et al. 2016). The atmospheric methane *inventory* has traditionally been attributed mainly (70–80 %) to biological origins from anoxic environments, including submerged soils (Le Mer and Roger 2001). However, most of the addition since the preindustrial era has been related particularly to anthropogenic sources (Saunois et al. 2016). As during this change the methane concentrations have grown by a factor of about 2.5 (Saunois et al. 2016), human-related sources seem to dominate. Methane in the atmosphere is mainly eliminated through oxidation by hydroxyl (OH) radicals and in aerobic soils by microbial oxidation. Rice paddies, peatlands and landfills often exhibit very high potential for methane consumption (oxidation), but in such environments predominated by anaerobiosis, the balance between methane production and oxidation is usually positive, resulting in methane emissions. Of the overall global methane *emissions* 30–40 % are natural (wetlands, oceans, some forest soils, termites, wild ruminants etc.) and 50–70 % are anthropogenic (mainly domesticated ruminants and rice fields). (Le Mer and Roger 2001, Saunois et al. 2016).

In plants and soils, there are three major methane production mechanisms (acetotrophic, hydrogenotrophic and methylotrophic methanogenesis; Section 2.1), two methane oxidation mechanisms (anaerobic and aerobic methanotrophy; Section 2.2) and three methane transport and release mechanisms aggregating a number of processes (plant-mediated, diffusion, and ebullition; addressed in more detailed in the specific contexts of Chapters 3–6), as illustrated in Figure 2-1. It should also be noted that a part of the methane is incorporated into the biomass of the microbial cells for growth and regeneration (Hanson and Hanson 1996, cited in Chanton et al. 2009, p 654).

Changes in the biogeochemical environment can affect microbial activity directly (e.g. through acting on availability of nutrients and electron acceptors for example through atmospheric deposition or change in oxygenation status with water-table variation) or indirectly through changes in vegetation (e.g. affecting the litter type or root exudates) or soil structure (Limpens et al. 2008).

Primary production provides reduced compounds that are buried as litter or released belowground by vascular roots, creating a redox gradient to the atmosphere (Limpens et al. 2008). Soil respiration refers to the production of carbon dioxide from decomposition of soil organic matter (including leaf litter and woody material) either when microorganisms decompose the compounds in the soil or when plant roots respire (e.g., Hoch et al. 2014). It consists of root, or autotrophic, respiration (root respiration and respiration from root-derived, recent components) and soil organic matter decomposition by heterotrophs (soil microbial respiration); the latter is also closely linked to the function of roots through delivery of easily available carbon compounds (Biasi et al. 2014). Soil microbial respiration is often considered to depend on soil structure, temperature and moisture regimes, community composition of the soil microbes and soil quality, and there may be also secondary constraints in field conditions, such as the soil organic carbon content (e.g., Biasi et al. 2014, p 122, and references therein). Traditional culture-dependent methods to identify microbial communities have proved inadequate to describe the vast microbial diversity; they may miss > 99 % of the organisms and enrich those thriving in cultures but not numerically or functionally important in the environment – however, such problems can be avoided with culture-independent molecular methods introduced over thirty years ago (Juottonen 2008, p 8, and references therein). However, in field work it is often more convenient to rather study the gas fluxes resulting from the microbial activity and other processes, complemented with laboratory studies on the underlying mechanisms.

In unsaturated soil, the degradation of organic matter produces carbon dioxide: $C_6H_{10}O_5 + H_2O + 6O_2 \rightarrow 6CO_2 + 6H_2O$ (the soil organic matter is denoted here to nominally have the chemical formula of $[C_5H_{10}O_5]_n$). This process is limited, at a given temperature, mainly by the availability of oxygen, and can therefore be distributed rather uniformly throughout the unsaturated soil. (Hoch et al. 2014).

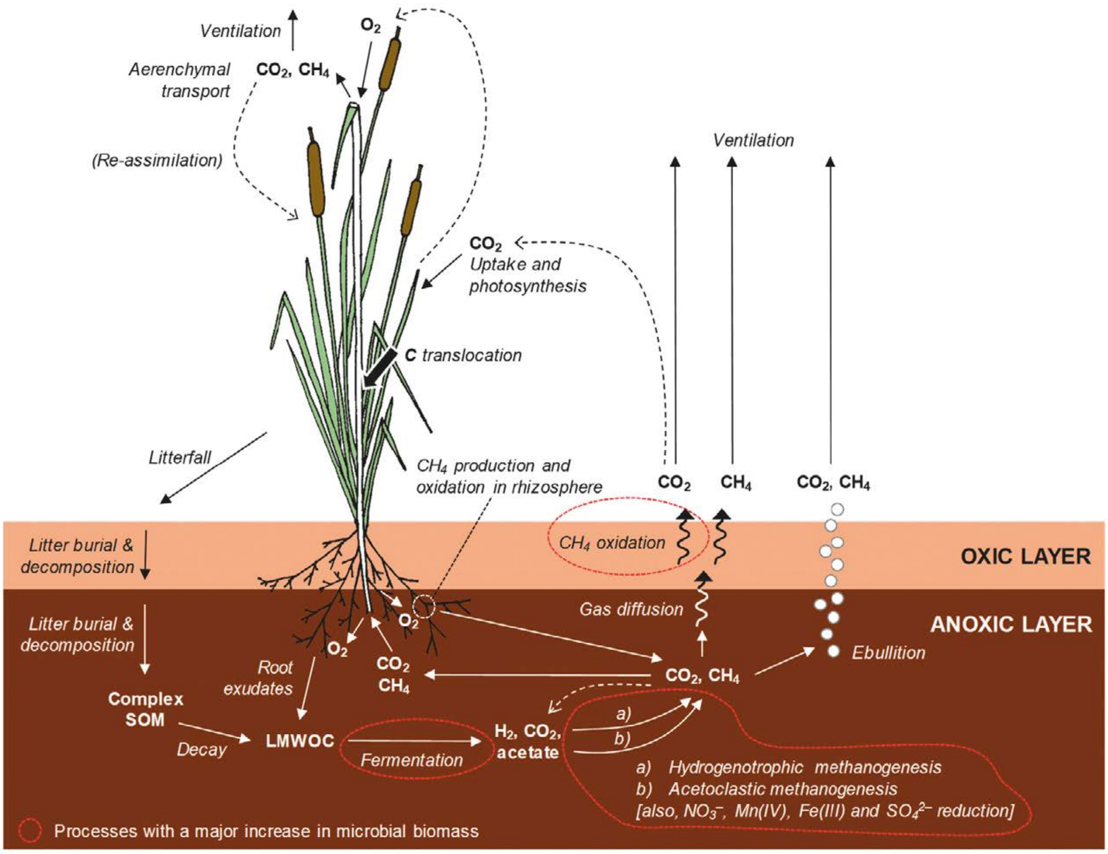

Figure 2-1. *Stylised illustration of carbon transformation and transport pathways in the environment (based on Bastviken 2009, p 784, Bastviken et al. 2004, p 2, Bubier and Moore 1993, p 461; Bubier and Moore 1994 and Conrad 1989, both cited in Charman 2002, p 195; Hanson and Hanson 1996, cited in Shaw and Atkinson 2014, p 12, Hoch et al. 2014, pp 14, 44; Conrad 1999 and Whalen 2005, both cited in Juottonen 2008, pp 4, 5, Le Mer and Roger 2011, p 30; Lieberman and Rosenzweig 2004, cited in Shaw and Thorne 2016, p 16, Limpens et al. 2008, p 1477, Shaw and Atkinson 2014, p 1, Shaw and Thorne 2016, p 15, Xu et al. 2016, p 3740). SOM denotes soil/sediment organic matter and LMWOC low-molecular-weight organic-carbon intermediary products.*

In saturated and anaerobic horizons, the degradation of organic matter will be performed by

- anaerobic respiration, with CO_2 as an end product,
- fermentation, which produces low-molecular-weight organic carbon such as lactic acid and acetate, and
- methanogenesis from simple compounds (Section 2.1), specifically H_2, CO_2 and acetate.

To reduce the organic matter itself into low-molecular-weight organic compounds, and CO_2 into CH_4, a redox potential below −200 mV is required. (Le Mer and Roger 2001, Shaw and Atkinson 2014); however, some recent results seem to challenge this rather traditional view at least for methane production in oxic lake surface waters (Donis et al. 2017 and their references). This final step in the anaerobic degradation occurs after nitrogen, manganese, iron and sulphur have been reduced. Which oxidant is used by the resident microbial community is broadly regulated by differences in the Gibbs free energy of the respective respiration processes (Table 2-1) and the concentrations of electron acceptors and donors (Limpens et al. 2008, p 1476, and references therein).

Table 2-1 Examples of redox reactions used in the microbial degradation of organic carbon (modified from Bastviken 2009). The Gibbs free energy decreases from top to bottom in the table.

Process	Substrates		End products other than CO_2
	e^- donor	e^- acceptor	
Aerobic respiration	OC	O_2	H_2O
Denitrification*	OC	NO_3	N_2
Manganese reduction*	OC	Mn(IV)	Mn(III), Mn(II)
Iron reduction*	OC	Fe(III)	Fe(II)
Fermentation	OC	OC	LMWOC, H_2
Sulphate reduction*	LMWOC	SO_4	S
Methanogenesis	LMWOC	LMWOC	CH_4

* Processes involved in anaerobic respiration.
OC = Organic carbon.
LMWOC = Low-weight organic molecules.

Whereas in forests, grassland and arable or agricultural systems atmospheric methane is typically consumed (i.e. even drawn from the atmosphere to the soil due to the low methane production in these soils), in wetland [or otherwise wetted/flooded] environments the methane production exceeds the consumption and there is a net flux of methane out of the soils (Hoch et al. 2014, Raivonen et al. 2017).

The dominant direct factors controlling both methane production (methanogenesis) and consumption/oxidation (methanotrophy) in most ecosystems include oxygen availability, concentration of dissolved organic carbon (i.e. methanogens' substrate), pH, temperature, moisture, nitrate and other reducers, ferric iron, microbial community structure, active microbial biomass, aeration, and plant root structure. Indirect factors include soil texture and mineralogy, vegetation, air temperature, air exchange (mainly air pressure and wind speed), soil fauna, nitrogen input, irrigation, agricultural practices, sulphate reduction and carbon quality. (Xu et al. 2016, p 3738, and references therein).

In the following sections, the methanogenic and methanotrophic mechanisms are described on a general basis before further reviewing literature on the phenomena in the various ecosystems in the subsequent chapters.

2.1 Methanogenesis

Methane production occurs in anoxic environments or in micro-niches hosting anoxic conditions within otherwise aerated layers (Shaw and Thorne 2016). Such micro-niches include, for example, centres of wet soil crumbs (Shaw and Thorne 2016). Methanogenesis is initiated by the onset of anoxia, but the methanogens (and methanotrophs) can maintain their populations under unfavourable conditions, such as during drainage and drying-up (Le Mer and Roger 2001, p 29, and references therein, Shaw and Thorne 2016).

Methanogens are anaerobic prokaryotes that belong to the domain Archaea and are metabolically unique among the domain and all other organisms due to their ability to obtain energy from selected low-molecular-weight carbon compounds and hydrogen while producing methane. Beyond their shared energy metabolism, methanogens are physiologically and morphologically divergent and can only grow with a limited set of one- or two-carbon compounds and hydrogen. Unable to gain energy from complex compounds, methanogens are dependent on substrate supply from associated anaerobic microbial communities or geological sources. (Juottonen 2008). In addition to lake, river and seabed sediments, marshes and peatlands, geothermal environments and seafloor hydrothermal vents, and various other ecosystems, other biological sources of methane include the gastrointestinal tracts of mammals (principally the rumens of cattle, sheep and goats, but also non-ruminants such as humans and arthropods), decaying vegetation (including wet heartwood of rotting trees), and even living terrestrial plants (Juottonen 2008, p 2; Shaw and Atkinson 2014, p 8, and references in both).

Metabolic pathways

Three types of methanogenic pathways have been identified, differing in their substrates (Deppenmeier 2002, cited in Juottonen 2008, p 1; Whiticar 1999, cited in Shaw and Atkinson 2014, pp 8-9, Whalen 2005):

- *Hydrogenotrophic (autotrophic) methanogens* grow by reducing carbon dioxide with hydrogen ($CO_2 + 8H^+ + 8e^- \rightarrow CH_4 + 2\ H_2O$). Some hydrogenotrophs also use formate ($HCOO^-$), which is the source of both CO_2 and H_2.
- *Acetotrophic (acetoclastic) methanogens* use acetate as a substrate: $^*CH_3COOH \rightarrow {}^*CH_4 + CO_2$, where the asterisk (*) denotes the intact transfer of the methyl group to methane; oxidation of the carbonyl group into CO_2 provides the reducing potential for reduction of the methyl group into CH_4.
- *Methylotrophic methanogens* utilise methylated compounds such as methanol, methylamines, and methyl sulphides, which act as both electron donor and acceptor, or are reduced with H_2.

In general, acetotrophic methanogenesis can be favoured in soil layers with abundant labile organic carbon, and H_2- and CO_2-dependent methanogenesis predominates in the more recalcitrant layers (Hornibrook et al. 1997; see also further discussion for mires in Section 6.2); however, it is also rather clear that temperature affects the various pathways of methanogenesis slightly differently and may favour some over others, depending on the local conditions (e.g. Conrad 1996). In sulphate-rich surface pore waters, acetate can be consumed by sulphate-reducing bacteria. Some authors (Conrad 1999, Shannon and White 1996) indicate that sulphate, nitrate or ferrihydrite inhibit the acetate-dependent methanogenesis and consequently the hydrogenotrophic pathway can be expected to dominate methanogenesis in systems that are rich in non-organic electron acceptors (Avery et al. 2003), although expected to remain at a low level. Selected examples of the contribution of the methanogenesis pathways are summarised in Table 2-2. Methylotrophic methanogenesis is usually considered a minor contributor, but it may be significant in marine systems (Xu et al. 2016 and references therein). However, methane formation from 'non-competitive substrates' (i.e. those less accessible to non-methanogenic bacteria but utilisable by methanogens) such as methanol, methyl amines and organic sulphur compounds (e.g. dimethyl sulphide) may be important in wetland soils (Shaw and Atkinson 2014).

Table 2-2. Selected examples of the relative importance of the methanogenesis pathways, expressed as the fraction of the CH_4 produced by the pathway.

Type of environment	Acetotrophic	Hydrogenotrophic	Reference
In general	2/3	1/3	Ferry 1992 (a review)
Globally	50–90 %	10–43 %	Xu et al. 2016 (a review)
Freshwater systems	About 70 %	Not reported	Avery et al. 2003, Whiticar et al. 1986
Methanogenic environments	> 2/3	< 1/3	Conrad 1999 (a review)
Intermediate fen	50–90 %	10–50 %	Keller and Bridgham 2007
Rich fen	80–98 %	2–20 %	Keller and Bridgham 2007
Peat bog	6–64 %	36–94 %	Keller and Bridgham 2007

Influencing factors

As outlined above, hydrogenotrophic methanogens utilise hydrogen and carbon dioxide directly, or formate that is a precursor of hydrogen and carbon dioxide. For their energy source, acetotrophic methanogens, in turn, use acetate that derives from recently assimilated fresh carbon; for instance, the root exudates of vascular plants are known to be an important substrate for methanogens. A connection between ecosystem productivity and methane emissions has been observed in several wetland studies. However, anoxic decomposition of litter and older peat produces methane as well. (Ström et al. 2003, cited in Peltola et al. 2018, p 939; Susiluoto et al. 2018, p 1203, and references therein).

Methanogen activity is usually at the optimum around neutrality or under slightly alkaline conditions (a minimum pH of 5.6 has been indicated for growth of 68 methanogen species), and it is sensitive to variations in soil pH (Garcia et al. 2000 and Wang et al. 1993, both cited in Le Mer and Roger 2001, p 33). However, methanogens can adapt to acidic environments as methane production and consumption does occur also in peat soils in temperate and sub-arctic areas (pH 3.5–6.3), even though the laboratory-derived optimum pH ranges were at 5.5–7.0 for methanogenesis and at 5.0–6.5 for methanotrophy, methanotrophs being more tolerant to pH variations (Dunfield et al. 1993, cited in Le Mer and Roger 2001, p 33).

Methane production is highly temperature-dependent (e.g. Bastviken et al. 2008, p 11, DelSontro et al. 2016, p S63, and references in both). Regarding the soil or sediment temperature, methanogenesis is at optimum at +30…+40 °C; low temperatures reduce methane production by decreasing the activity of methanogens but also that of other bacteria implied in methanogenic fermentation, the latter being more sensitive to temperature variations. However, significant methane emissions have still been observed in swamp and forest soils in winter (even below +1 °C). (Le Mer and Roger 2001, p 34, and references therein).

Nitrate reducers, ferric iron reducers and sulphate reducers constitute a sequence of competitors of methanogens for acetate and electrons, but a high Fe content of the soils, which allows fast decrease in the redox potential after submersion, favours methanogenesis. Ferric iron can have both a chemical and a biological impact, the former because of its re-oxidation by root oxygen and the latter through increase in carbon oxidation into CO_2. Methane emission are usually lower in sulphate-rich soils than in other soil types. The impact of various heavy metals on methane production is complex and generally seems to be inhibitory. (Le Mer and Roger 2001, p 34, and references therein; also, Conrad 1999, Shannon and White 1996).

It is also to be noted that methane produced in the soil profile or under water is not immediately transported into the atmosphere, but over a range from minutes to days, or even up to a season if the surface is frozen. The migration time depends, for example, on temperature, moisture conditions or water pressure, soil texture and emissivity of plant roots. These processes consist of plant-mediated diffusive and advective transport, aqueous and gaseous diffusion, and ebullition. (Xu et al. 2016). These migration types are further addressed in Chapters 3–6.

2.2 Methanotrophy

Methane is consumed in aerobic soils by biogenic oxidation to CO_2 (methanotrophy), which involves a diverse group of bacteria (methanotrophs) that metabolise methane as their sole source of carbon and energy; as strict aerobes, these microbes occupy different ecological niches to the methanogens (Le Mer and Roger 2001, Chanton et al. 2009, Shaw and Atkinson 2014, Shaw and Thorne 2016). However, also more limited anaerobic oxidation by other types of microbes, which use sulphate and various other compounds as a terminal electron acceptor, has been documented in marine sediments and deeper environments (Alperin and Reeburg 1984 and Murase and Kimura 1994, both cited in Le Mer and Roger 2001, p 28, Capone and Kiene 1988, Shaw and Atkinson 2014, Shaw and Thorne 2016) and more recently also for freshwater lakes, rivers, wetlands and marine systems (e.g., Bogard et al. 2014 and Grossart et al. 2011, both cited in DelSontro et al. 2016, p 2, Shen et al. 2015; also, Raivonen et al. 2017, p 4667, and references therein). In soils, the anaerobic methane oxidation seems to have only a minor contribution (Xu et al. 2016, p 3737, and references therein).

Although found everywhere in soils, methanotrophs are concentrated above the anaerobic regions where methane is produced, as well as in the rhizosphere of aerenchymal wetland plants providing microscale aerobic conditions in otherwise anaerobic domain (Chanton et al. 2009, p 654, and references therein; Bosse and Frenzel 1997, Gilbert and Frenzel 1995, and King et al. 1990, all three cited in Le Mer and Roger 2001, pp 28–29). Methanotrophs are common throughout forest soils where they are thought to consume methane directly from the atmosphere (Chanton et al. 2009), but likely rely mostly on the methane supply from the deeper soil layers. This is supported also by that the highest methanotrophic activities are observed near to methanogenic environments, particularly at the interface of anaerobic and aerobic horizons especially in soils subject to periodic anaerobiosis (Le Mer and Roger 2001, Shaw and Thorne 2016; also Conrad 1996, Saari et al. 2004 and Yavitt et al. 1990, all three cited in Shaw and Thorne 2016, p 26). There is evidence that the methanotrophs still remain largely unknown, especially regarding those operating at ranges of methane concentrations below those at which cultured methanotrophs thrive (Juottonen 2008, Shaw and Thorne 2016, Tsitko et al. 2014). Methanotrophs have been observed to be inhibited by nitrate and be sensitive to acetylene in the soil (Megraw and Knowles 1987, p 57, and also references therein).

Metabolic pathways

Methane is oxidised to carbon dioxide by a series of two-electron oxidation steps via methanol, formaldehyde and formate (Anthony 1982, cited in Megraw and Knowles 1987, p 59), and the carbon is assimilated into the microbial biomass either at the level of formaldehyde or as a combination of formaldehyde and carbon dioxide (Megraw and Knowles 1987). However, methane oxidation is not simply a first-order process due to being catalysed by enzymes and some energy is used to produce biomass in the process (Chanton et al. 2009, Shaw and Thorne 2016). Methanotrophic activity is related to soil water content; it increases to a value close to field capacity and then decreases when water content increases towards saturation (Czepiel et al. 1995 and Le Mer et al. 1996, both cited in Le Mer and Roger 2001, p 33) and limits the oxygen availability. The reaction is catalysed by enzymes, such as the particulate methane monooxygenase, pMMO (e.g. Shaw and Thorne 2016).

Described genera of aerobic methanotrophs are by convention grouped into categories, differing in phylogenetic affiliation (*Gammaproteobacteria* vs. *Alphaproteobacteria*) and in several biochemical properties (e.g. Shaw and Thorne 2016): Type I methanotrophs include the genera *Methylobacter* and *Methylomonas* that use the ribulose monophosphate (RuMP) pathway, whereas Type II includes *Methylosinus* and *Methylocystis* using the serine pathway. Both groups of organisms are methylotrophs, that is, organisms that can oxidise C_1 compounds. A third group of methanotrophs, Type X, includes *Methylococcus*, which uses both the RuMP and serine pathways of the Type I and Type II groups. Formaldehyde is used in the synthesis of multi-carbon compounds within microbial biomass via either the RuMP or serine pathways. However, it needs to be noted that also other taxa have been found and reported largely during and after this review. There is also increasing evidence of anoxic methanotrophy in sediments and water columns that is not covered by this conventional categorisation.

Kinetics and influential factors

Methane oxidation is suggested to be based on two distinct populations of methanotrophs in soils, one operating at high (enhanced, i.e. >40 ppm$_v$) methane concentrations with low affinity for methane, the other operating at low (ambient, i.e. 1–2 ppm$_v$, or <12 ppm) concentrations with high affinity (Le Mer and Roger 2001, Shaw and Atkinson 2014). Methanotrophy of high affinity is typically measured in the well-drained oxic upland soils as contrast to wetland soils, with higher values for the upland areas typically observed in forest soils and lower in cultivated soils (Le Mer and Roger 2001). The higher methanotrophic activity of forest soils has been attributed to a stimulation by a significant methanogenic activity of the litter (Keller et al. 1983, Seiler and Conrad 1987, and Steudler et al. 1989, all cited in Le Mer and Roger 2001, p 31). Low-affinity methanotrophy has been observed either *in situ* in methanogenic environments or in soil samples incubated in a methane-enriched atmosphere (Le Mer and Roger 2001).

Methane oxidation has been shown to follow Michaelis–Menten kinetics, that is, the rate of the process depends on the flux of methane entering the oxidation zone (Shaw and Thorne 2016, and many others) since each of the four steps in the methane oxidation process is enzyme-mediated. For the type of kinetics, the overall oxidation rate (*v*) can be expressed as:

$$v = V_m \frac{[CH_4]}{[CH_4] + K_m} \tag{2-1}$$

in which K_m, the Michaelis constant, is the methane concentration giving rise to half the maximal rate of reaction (i.e. reflecting the affinity), and V_m is that maximal rate. The lower the K_m, the lower the methane concentration at which oxidation can occur at an appreciable rate. If also oxygen availability is a limiting factor, the kinetic equation takes the form of a double Monod expression:

$$v = V_m \frac{[CH_4]}{[CH_4]+K_{m,CH_4}} \frac{[O_2]}{[O_2]+K_{m,O_2}} \tag{2-2}$$

where the former K_m parameter refers to the half-saturation constant for methane and the latter for that for oxygen.

For soils pre-incubated in higher methane concentrations, adaptation of the microbial community leads to a change in the Michaelis–Menten parameter values and also to a lower sensitivity: the methane oxidation rates after such pre-incubation at low to moderate methane concentrations are higher than for soils without pre-incubation, and also at high methane concentrations the oxidation rates continue to increase, rather than saturating (Shaw and Thorne 2016). The capacity of bacteria to oxidise methane at ambient concentrations, which can be low, is limited by the K_m value (Conrad 1996, cited in Shaw and Thorne 2016, p 8). As the methane concentration decreases below the K_m value, a threshold may be reached below which oxidation ceases (Shaw and Thorne 2016).

At very low methane concentrations, the rate of methane consumption should vary in a linear manner with the methane concentration; this follows from the Michaelis–Menten equation since, at very low concentrations, the efficiency of methane oxidation can be expressed as a ratio due to Equation 2-1 reducing into $v = V_m/K_m$ (Shaw and Thorne 2016). Indeed, based on field and laboratory studies on cultivated soils by Hoch et al. (2014, p 47), oxidation of methane can be described as a first-order reaction, although it is acknowledged that other experimental data indicate Michaelis–Menten kinetics (Hoch et al. 2014, p 52) – this may be explained by that there is a threshold value above which the Michaelis–Menten kinetics takes place (Shaw and Thorne 2016), implying that in high-affinity (low-concentration) conditions first-order kinetics would take place and in low-affinity (high-concentration) processes the more complex kinetics would apply. In mineral and organic soils in a Sitka spruce plantation, methane oxidation rates followed Michaelis–Menten kinetics at 1.8–300 ppm_v, with increased rates below 50 ppm_v, indicating activity of high-affinity methanotrophs (Bull et al. 2000 cited in Shaw and Atkinson 2014, p 11). Methane oxidation showed typical Michaelis–Menten kinetics also in air-dried cultivated Humisol (i.e. 'organic muck soil') surface samples collected at a farm in Québec, Canada (Megraw and Knowles 1987).

The methane oxidation rates depend on substrate CH_4 and O_2 concentrations and methanotroph populations (i.e. the oxidation rates increase with pre-incubation). Elevated CH_4 levels increased oxidation rates, and pre-incubation of about 6 days (and addition of NH_4Cl) was sufficient to elevate rates by an additional 4–5 times (Megraw and Knowles 1987). Thus, the methane-oxidising characteristics of soil will depend on the release rate (i.e. essentially the CH_4 concentration in the solution) and the length of the release (hours/days/week). Continuous artificial supply of methane into the basal layers of oxic zone can also lead to stimulation of methanotrophic activity to exaggerated levels (Steven et al. 2006, cited in Shaw and Thorne 2016, p 1), which may be unreflective of the oxidation rates achievable under ambient conditions (Shaw and Thorne 2016).

Similarly to other (bio)chemical processes, also methanotrophy is affected also by the ambient temperature. Particularly in field conditions this is not always straightforward, though, due to the large numbers of controls acting simultaneously. For example, in a study, methanotrophy in soil cores from temperate forest did not show large variation between −1 and +30 °C, but in another forest study methanotrophy was affected between −5 and +10 °C but not between +10 and +20 °C. (Le Mer and Roger 2001, p 34, and references therein).

Similarly to methanogens addressed above, also methanotrophs are expected to usually be active around neutrality or under slightly alkaline conditions, and rather sensitive to variations in soil pH (Garcia et al. 2000 and Wang et al. 1993, both cited in Le Mer and Roger 2001, p 33). Newer methods have evidenced acidophilic methanotrophs, non-cultivable on classical media, in peat soils at pH < 4.7 (McDonald et al. 1996, cited in Le Mer and Roger 2001, p 33). Indeed, more of such evidence has more recently been obtained, for example, from a few fens and bogs in Finland (Juottonen 2008, Tsitko et al. 2014).

Methanol, formaldehyde and formic acid form during the oxidation process as intermediate metabolites, but according to a review there is no evidence from earlier literature that the production and subsequent use of these intermediates are rate-controlling steps in the process, or that the metabolites can be transported a significant distance from their point of production to their point of utilisation (Shaw and Thorne 2016). However, a recent interpretation of tracer experiments in agricultural soils in Nottingham (Hoch et al. 2016) indicates evidence for a significant delay between the oxidation of methane and the subsequent production of CO_2 (Shaw and Thorne 2016). A lag between methanogenesis and methane emission, due to the oxidation process, has been observed also elsewhere, and this has been pointed out to affect the spatial variability (hotspots), but especially the seasonality ('hot moments') of the methane efflux (Xu et al. 2016).

3 Upland soils and landfills

Some three quarters of the land area in the Forsmark site is covered by forests, dominated by Scots pine and Norway spruce. Most of the many, typically smaller, wetlands that pattern the landscape are coniferous forest swamps or open mires, and the less mature wetlands consist of nutrient-rich fens due to the high calcareous content of the regolith. Agricultural land (cropland/arable land and grassland) only covers a minor part of the land area of Forsmark. (Löfgren 2010; SKB 2014, p 49, and references therein). However, for the radiation dose implications of the release scenarios for the repositories, the agricultural areas are usually the most important in the upland terrain (e.g. SKB 2014, 2019b). Peatlands drained for agriculture are discussed more in the wetlands chapter (Section 6.6), although in the long term they can be expected to develop in respect of the methane production and oxidation towards conditions similar to the upland fields.

Upland (i.e. well-drained, oxic) soils are a net sink for atmospheric methane. Since Bender and Conrad's (1993) study, numerous measurements have been published that quantify methane flux from the atmosphere into [upland] soils – this 'consumption' of atmospheric methane by oxic soils provides evidence of net oxidation of methane within the soil (Shaw and Thorne 2016). Methane in the soil gas is drawn down from the free atmosphere, if methanotrophic consumption in the aerobic soil exceeds methanogenic supply from the anaerobic soil below; if the supply from the anaerobic soil exceeds the methanotrophic consumption in the aerobic layer then the soil provides a net source of methane that diffuses out of the soil into the free atmosphere (Shaw and Thorne 2016). However, the methanotrophic activities are very low in comparison to wetland soils and aquatic sediments; on average, forest soils are the most active, followed by grassland and cultivated soils, but the ranges overlap (Bender and Conrad 1995, Le Mer and Roger 2001, Shaw and Thorne 2016). In some cases, though, the methane oxidation rate can be 130-fold lower in an arable soil than in an adjacent forest soil (Jensen and Olsen 1998, cited in Limer et al. 2011, p 39). The efficacy of methane oxidation in an oxic region of the soil is controlled by the residence time of methane in that region; hence the degree of oxidation is likely to be inversely related to the rate of diffusion through such layers (Shaw and Thorne 2016). The usual observations of maximum methanotrophy occurring in the lower layers of oxic soils (Bender and Conrad 1994, cited in Le Mer and Roger 2001, p 28) may be a result of this.

A key parameter in quantifying the influx or efflux of gases in soils is the diffusion coefficient (Shaw and Atkinson 2014, pp 20–27). However, Flechard et al. (2007, cited in Shaw and Atkinson 2014, p 24) found that diffusion of CO_2 is the dominant transport mechanism at night, but that 'wind-induced pressure pumping' during the daytime could reduce CO_2 storage in the soil gas space on a diurnal basis. Kayler et al. (2010, cited in Shaw and Atkinson 2014, p 24), on the other hand, observed little or no influence of advective gas transport in measurements of CO_2 in forest soils and concluded that gas diffusion is the dominant transport mechanism within the soil. In any case, since the air content in soil is controlled by fluctuations in the soil moisture, also the gas movement by diffusion in soils is highly dependent on the moisture conditions (Shaw and Atkinson 2014). In addition, the oxidative activity of methanotrophic bacteria declines at low soil moisture due to desiccation stress (von Fischer et al. 2009), and soil nitrogen levels reduce methane uptake rates (Hütsch et al. 1994, Mosier et al. 1998), due to inhibition of the methane mono-oxygenase enzyme (Dunfield and Knowles 1995). However, it is also recognised that there are controversial results on the effect of nitrogen compounds on methanotrophy, likely to be explained by the differences in the microbial communities in a particular setting (Bodelier 2011).

As a rule of thumb (Limer et al. 2011), for soils with methane concentrations close to atmospheric levels, around 10 % of the methane supplied from subsurface is oxidised, as also suggested by the review of Le Mer and Roger (2001). However, if the flux of methane is large, this may stimulate methanotrophic bacterial populations, and lead to much higher oxidation rates (greater than 80 %), as has been observed in rice fields and grasslands (Limer et al. 2011) as well as under certain conditions in landfills (also, cf. Sections 2.2 and 3.2). This illustrates the high dependency of the situation from the particular system and conditions (as well as the difficulty of presenting any meaningful single estimate of the fraction of the subsurface methane becoming oxidised). In the following sections, observations more specific to upland agricultural and forest soils, as well as to landfills, are summarised and discussed to shed further light on the topic.

3.1 Methane in upland agricultural and forest soils

Jang et al. (2006) reviewed and summarised literature and derived a mean methane oxidation rate of 1.54 mg CH_4 m^{-2} d^{-1} for forest soils in 11 countries. They also observed a significant inhibitory effect of inorganic nitrogen on methane oxidation, whereas natural variation in temperature and pH appeared to have little or no effect on the methane oxidation rates (Jang et al. 2006). In some forest soils, it has been observed that the highest rates of both methanogenesis and methanotrophy are located in the organic layers close to the surface (Le Mer and Roger 2001; Saari et al. 2004 and Yavitt et al. 1990, both two cited in Shaw and Thorne 2016, p 26), even though several studies have shown that consumption of atmospheric methane occurs between the surface soil and the subsoil (Conrad 1996, cited in Shaw and Thorne 2016, p 26). This seems counterintuitive, because the majority of microbial activity is located at the soil surface, which is where oxidation of other trace gases (e.g. hydrogen to water) is known to occur (Shaw and Thorne 2016). Fluctuations in soil moisture and higher ammonium concentrations towards the soil surface have been suggested as possible reasons for reduced methane oxidation in this region of the soil profile (Czepiel et al. 1995 and Schnell and King 1996, cited in Shaw and Thorne 2016, p 26).

Traditionally, there has been a view that the methane oxidation potential of upland soils is reduced by cultivation, especially by ammonium fertiliser application; nitrogen fertilisation that leads directly or indirectly to an increase in ammonium content of the soil has an inhibitory effect on methane oxidation, through competition at the level of the methane mono-oxygenase towards nitrification and the toxicity of NO_2 produced (Le Mer and Roger 2001, pp 38–39, and references therein). However, this view has also been contradicted by some observations, which may be explained by the observation of relatively common nitrogen limitation of methanotrophy also in upland soils (Bodelier 2011; Bodelier and Laanbroek 2004, cited by Bodelier 2011, p 381). Cultivation practices that destroy aerated micro-niches suitable for methanotrophs also reduce atmospheric methane oxidation. Methods identified as less detrimental for the methane oxidising potential are using organic and/or nitrate-based fertilisers and direct seeding with no ploughing. (Le Mer and Roger 2001, pp 38–39, and references therein). Similarly, urea application on forest soils for fertilisation is known to decrease methanotrophy by five to twenty times, avoidable by fertilisation with a $(NH_4)_2SO_4$ solution instead (Le Mer and Roger 2001, p 41, and references therein).

Del Grosso et al. (2000) examined methane oxidation rates under field conditions in native and cropped grassland soils from a large number of sites in Colorado and Nebraska. They found that methane uptake rates peaked at intermediate soil water content, and that cultivation decreased the methane oxidation rates, as compared to similar non-ploughed and fertilized soil. However, this reduction was primarily observed in coarse soils with high gas diffusivity (up to 75 % reduction from that in sandy loam). Le Mer and Roger (2001) reported a very broad range of methane oxidation rates from thirteen cultivated soils (0–87 mg CH_4 m^{-2} d^{-1}) with a median rate of 0.55 mg CH_4 m^{-2} d^{-1} and also concluded that methane oxidation potential of upland soils is reduced by cultivation. Thorne and MacKenzie (2005) noted that the methane oxidation potential is low or undetectable in disturbed soils. This may be partly explained by the ploughing that breaks up soil aggregates and pore surfaces, and thereby diminishes the activity of the methanotrophs, possibly for a long time (Regina et al. 2007).

In their field experiment in a spring wheat area in Nottingham, UK, Hoch et al. (2014) observed that a methane pulse injected into the subsoil at the depth of 50 cm had largely exited the soil profile by 24 hours, and that after 7 days the profile of methane concentrations in the soil had returned to almost the same as before the injection (the injection was sufficiently large in the amount to momentarily reverse the typical concentration profile in the soil). Also, a difference of 22–23 hours between the peaks of isotopic signatures for CH_4 and CO_2 was observed, suggesting a kinetic delay between the oxidation of the methane and the eventual production of CO_2, possibly related to the four-stage enzyme-catalysed biochemical process (Chapter 2). From the field and related laboratory experiments combined, it was concluded that there was consistent evidence for rapid diffusion of stable and radioactive methane from the sub-surface to the free atmosphere. However, the presence of vegetation affects the soil pore architecture and moisture content, and hence also the rate of diffusion. In the case of pulse injection, typically there is a pre-injection balance between oxidation and diffusion, which turns immediately after the injection into a diffusion-dominated system (because of the large gradients in the methane concentration), and about an hour after the injection the system becomes dominated by the methane oxidation due to the sufficiently low gradients. (Hoch et al. 2014).

Another interesting outcome of the Nottingham field and laboratory experiments was that there seems to be a characteristic length scale of the order of few tens of centimetres in which the injected methane gets oxidised between the water table and the atmosphere (Hoch et al. 2014). Provided that the water table is at a depth of more than a few times this length scale, the conversion of methane to carbon dioxide will be essentially complete, regardless of the particular rates of the diffusion and the oxidation. A value of 26 cm was derived for the characteristic length based on typical model inputs for the conditions with the Nottingham experiments. (Hoch et al. 2014, pp 31, 52, 59, 67).

Based on a simple analytical model applying Michaelis–Menten kinetics (cf. Section 2.2) for concentrations of methane above a threshold, Shaw and Thorne (2016) derived an estimate of 50–100 % of the methane flux entering the soil from below being oxidised in upland cultivated or arable soils, with the possible exception of very high fluxes and absence of an incubation effect of the microbial community adapting to the high methane concentrations. For a situation in which the threshold above which the Michaelis–Menten kinetics takes place is much less than the ambient atmospheric methane concentration (a typical situation), they derived a corresponding estimate of 90 % of repository-derived methane getting oxidised (Shaw and Thorne 2016, pp 6, 26).

Upland soils may become methane sources when temporarily submerged. In poorly drained soils around Canadian forests, methane consumption was negatively correlated with soil water content, and similar negative correlation was found also in Massachusetts forests, where at low water content (22–60 %) methanotrophy was observed to be inversely correlated to ammonium concentrations. In Norwegian forests, a small increase in the water content over the field capacity markedly reduced methanotrophy. In temporarily submerged Danish soils, methane emission and consumption had their highest rates during the drying-up of the soil, probably because of increased methane diffusion and oxygenation of the soil. (Le Mer and Roger 2001, p 33, and references therein).

In submerged (mineral) soils, texture is involved in the establishment of the anaerobiosis needed for methanogenesis, in the transfer and trapping of methane produced in the reduced soil, and through affecting the depth of the oxidised layer hosting methanotrophs. Soils rich in swelling clays are usually more favourable for methanogenesis than sandy soils, silty soils or soils rich in kaolinite, where density increases after submersion, slowing down the change in pH and redox potential. High clay content can also favour trapping of methane bubbles in soils and thus inhibit ebullition. Methane production also seems to be partly stimulated by a buffering effect of carbonates. However, some particular clay types protect the soil organic matter from mineralisation, which in turn delays methanogenesis (Neue and Roger 1994, Neue et al. 1990, Oades 1988, and Sass et al. 1994, all cited in Le Mer and Roger 2001, p 34).

3.2 Methane in landfills

In landfills, methane and other volatile hydrocarbons are produced by decomposition of the waste. Bacteria near the landfill surface consume these substances to harness the energy from enzyme-catalysed chemical reactions to fuel their respiration. As mentioned already above, a part of the methane is incorporated into the biomass of the microbial cells for growth and regeneration (Hanson and Hanson 1996, cited in Chanton et al. 2009, p 654). The typically thick and porous engineered soil layers above landfills provide an environment in which methane oxidation can be extremely high (Whalen et al. 1990, cited in Shaw and Thorne 2016, p 15). Most of the oxidation is likely to occur in the upper 30 cm of the landfill cover (De Visscher et al. 1999, cited in Chanton et al. 2009, p 658).

In the first journal report on methanotrophy in landfill cover soils (Whalen et al. 1990, cited in Chanton et al. 2009, p 654), methane oxidation rates (45 g CH_4 m^{-2} d^{-1}) higher than observed in any soil earlier were found, estimated to correspond to a consumption of approximately 50 % of the methane produced in the landfill. Half a decade later considerably higher rates (156 g CH_4 m^{-2} d^{-1}) were observed in a coarse sandy landfill soil permeated with methane for six months (Kightley et al. 1995, cited in Chanton et al. 2009, p 654). After a decade of further results, the current default for the methane oxidation in landfill cover soils was set to 0–10 % (IPCC 2006 and USEPA 2004, both cited in Chanton et al. 2009, p 655), although leaving room for a higher value if clearly documented, referenced and supported by relevant data (IPCC 2006, cited in Chanton et al. 2009, p 655).

Shedding more light on the matter, Chanton et al. (2009) compiled literature data on the methane oxidation rates and on the fraction of methane oxidised when passing the cover soil. Based on their compilation of 47 data entries, the mean fraction of the methane flux through the cover soil that becomes oxidised ranges 22–55 % (in terms of rates, 52–102 g CH_4 m^{-2} d^{-1}, although not all data entries provided data for both the fractions and the rates). This oxidation fraction (or rate) varies with the type of the cover soil. As a maximum value over the dataset, a 100 % oxidation fraction was provided for an organic, compost-derived, landfill cover material in a repacked column. For a group of studies conducted over an annual cycle, they reported correspondingly oxidised fractions of 11–89 %. Another grouping of data extracted from their review is presented for the different landfill cover materials in Table 3-1. Whilst the general temperature dependence of biochemical processes under the denaturation limit of the enzymes was confirmed (an increase in the oxidation rate by about a factor of 33 from 5.5 °C to 36 °C), the mean of oxidised fraction derived from whole-year studies alone was close to the mean derived from the entire dataset; however, the five whole-year studies conducted in northern Europe gave an average oxidised fraction of 54 %, exhibiting an inverse temperature-dependence that may illustrate involvement of other environmental factors or differences in the methodology (Chanton et al. 2009). It was also noted that column experiments, in general, result in higher oxidation rates than field studies. This was attributed possibly being due to the columns being prone to methane bypassing the oxidation along cracks and fissures in the experimental setup (Chanton et al. 2009), which seemingly was then erroneously accounted for a higher oxidation even if the actual oxidation must then have been lower due to the evasion paths.

Table 3-1. Methane oxidation rates and fractions of methane oxidised in landfill cover materials, extracted from the literature review of Chanton et al. (2009).

Soil/material type	Oxidation rate (mol m^{-2} d^{-1})		Fraction oxidised (-)		Fraction oxidised (field studies alone)
	Average	Standard error	Average	Standard error	Average
Organic	9.39	2.33	0.40	0.09	0.34
Clayey	3.88	2.18	0.22	0.05	0.18
Sandy	6.43	2.77	0.55	0.09	0.53
Composite/other	3.72	1.21	0.30	0.05	0.28

In the review summarised above, no trend was found in the data between the fraction oxidised and the cover thickness. This was attributed to the oxidation being confined to the aerobic surface zone, fed with oxygen diffusing from the atmosphere. That is, the cover thickness does not affect the oxygen penetration, but a thicker cover may attenuate the methane flux pushing oxygen out of the soil via advection (Chanton et al. 2009). However, a thicker cover will result in increased retention of the methane that yields in lower emission rates and a higher fraction of the methane being oxidised (Stern et al. 2007, cited in Chanton et al. 2009, p 658). It was also observed that the organic materials had the lowest oxidation rate (but a reasonably high fraction of the methane oxidised) due to such covers limiting the gas transmissivity of the underlying clay lining by their moisture holding capacity preserving the hydration of the clay (Chanton et al. 2009). Such phenomenon is also called ‘blockage’ (Stern et al. 2007, cited in Chanton et al. 2009, p 658). Also, the oxidised fraction is an inverse function of the emission rate (Stern et al. 2007, cited in Chanton et al. 2009, p 661): at lower emission rates the methanotrophs can oxidise up to 95–100 % of methane delivered to them (Huber-Humer et al. 2008, Humer and Lechner 1999, 2001, Kjeldsen et al. 1997, and Powelson et al. 2006, 2007, all cited in Chanton et al. 2009, p 661), but as the emission rate increases the methanotrophs become overwhelmed with the methane and the oxidised fraction decreases (Powelson et al. 2006, 2007, cited in Chanton et al. 2009, p 661).

4 Lakes

In this chapter, methane sources, transformations, transport and emissions from freshwater lakes are discussed in further detail, based on the general description of key processes in Chapter 2.

4.1 General characteristics

Lakes lie in basins (i.e. depressions) of the landscape formed in Fennoscandia typically by past glacial activity. For a lake to survive as a permanent water body, the precipitation and inflow must at least equal losses by evapotranspiration, outflow and seepage through the bottom. Most lakes have a natural outflow in the form of a river or stream, but endorheic lakes lose water solely by evaporation or underground seepage, or both. (Wetzel 2001). With the water exchange, suspended solids, macro- and micronutrients and other compounds visit the lake or become temporally or permanently trapped in the sediment. Once in the lake, substances can also be taken up by aquatic organisms and transported through the food web. (Brönmark and Hansson 2005). For the habitats of the biota, typically pelagic (open-water) and littoral (shoreline) areas are identified in the lateral direction, in addition to the benthic habitat relating to the bottom sediment, and in the vertical depth distinction is usually made between the photic ('well-lit') and aphotic ('dark') zone according to the penetration depth of the sunlight (Figure 4-1).

A thermocline (also known as the thermal layer, or the metalimnion, in lakes) is a thin but distinct layer in a deep enough water body, in which temperature changes more rapidly with depth than it does in the layers above or below. In the summer, the warm, less dense water (epilimnion) lies on top of the colder, denser water (hypolimnion) below the thermocline (cf. also Figure 4-2 further below), and little mixing of the warmer and the colder water occurs especially under calm weather conditions. Due to the small mixing and continued oxygen consumption, the hypolimnion may turn oxygen-poor or even anoxic. The depth of the epilimnion depends on the lake morphometry, water clarity and exposure to winds. (Brönmark and Hansson 2005).

In the autumn, the solar energy input decreases, but the heat loss from epilimnion by evapotranspiration continues to be relatively high. As a result, the temperature difference, and thus also the density difference, across the thermocline decreases. Autumn weather is typically windy, and eventually, when the density differences between the strata are small enough, this will cause the whole water column to re-circulate (the autumn turnover). Correspondingly in winter, when the temperature of the lake water has cooled down to about 4 °C and the water density is at its maximum, an inverse stratification with the epilimnion having the lowest temperature (reaching the freezing point, water becoming then also less dense again) will establish if the wind-induced water movements remain small enough, and possibly an ice cover forms, sealing the lake from further wind energy input. In the spring the ice cover breaks, and solar energy warms up the surface water that reaches again the maximum density and sinks to the bottom (the spring turnover). (Brönmark and Hansson 2005).

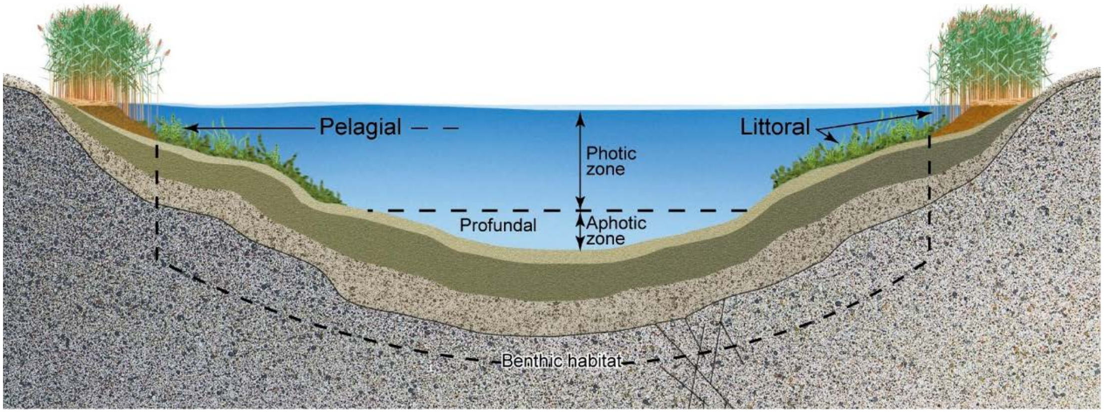

Figure 4-1. Basic concepts in description of functional parts, and habitats, of a lake (reproduced from Andersson 2010, p 171; also, cf. Figure 4-2).

Lakes in the Forsmark area are small (< 0.75 km²) and shallow (0.4–2 m deep) oligotrophic hard-water lakes, with a high pH and high concentrations of calcium and bicarbonate. This lake type is common along the coast of northern Uppland region where Forsmark is situated, but rare in the rest of Sweden. Relatively clear water and shallow depths of the lakes permits photosynthesis in the entire benthic zone and the lake bottoms are covered by dense stands of macroalgae of the genus *Chara*. Many lakes also have a thick microbial mat consisting of cyanobacteria, diatoms and heterotrophic bacteria. The high biomass of benthic macro- and microalgae gives rise to high primary production, whereas the pelagic primary production is relatively low. All lakes are surrounded by reed belts, which are extensive especially around the smaller lakes. Modelling of carbon dynamics in limnic ecosystems shows that, contrary to typical Swedish lakes, primary production exceeds respiration in many lakes in the Forsmark area. Much of the recently primary-produced carbon within a lake/pond is circulated within the microbial food web and transferred back to abiotic pools or sequestered in sediments. In the larger lakes, there is a relatively large deposition in sediments, which can be a permanent sink for radionuclides and other contaminants. In smaller lakes and ponds, the amounts of carbon involved in the primary production and deposited in sediments within a lake/pond are small compared with the amounts of carbon transported into the system from the surrounding catchment area. There are several small and shallow (< 0.5 m) ponds in the area. (Andersson 2010, Saetre et al. 2013, p 44, SKB 2014, pp 47–48, and references therein).

4.2 Methane cycling in lakes in general

Methane is a major product of carbon metabolism in lakes. It has been suggested that the anaerobic processes account for as much as 20–60 % of the overall mineralisation in freshwater environments, and that methanogenesis corresponds to 30–80 % of the anaerobic contribution in waters and sediments. This yields methanogenesis accounting for 10–50 % of the overall carbon mineralisation (Bastviken et al. 2008, p 1, and references therein). Similarly, several studies indicate that 20–59 % of the total contribution of sestonic carbon to sediments is converted to methane (Wetzel 2001, cited in Bastviken et al. 2008, p 1). As much as 30–99 % of the methane produced in lakes can be oxidised (Bastviken et al. 2008, p 1, and references therein). Water-column methane oxidation also affects aquatic organisms indirectly by the associated oxygen consumption, contributing to the oxygen depletion of isolated water layers (Rudd and Taylor 1980, cited in Bastviken et al. 2008, pp 1, 2), but also since the microbial biomass is a source of energy and carbon to the higher trophic levels in the food web (see below).

Once produced in the sediments, methane can be lost through the emission from the lake surface to the air and by methane oxidation mostly at the metalimnion and within the epilimnion (Bastviken et al. 2004; also, cf. Figure 4-2) – unless the produced methane has already been oxidised in the sediment (see below). Methane production in profundal sediments can result in methane accumulation in anoxic hypolimnion and subsequent rapid release to the atmosphere upon lake circulation. As described further in the subsequent sections, a methane budget of a lake consists of production in and release from the sediment at different depths (including the direct plant-mediated gas transport from the sediment to the air), water column transport and methane oxidation, methane storage in the water column, emissions to the atmosphere by diffusion and ebullition ('bubbling'), and contribution to the carbon uptake in pelagic food webs (Bastviken et al. 2008), as well as of possible inputs from upstream areas and losses with discharges downstream. Through the oxidation, the methane flux from sediments to the deeper anoxic water layers could make a large share of the dissolved inorganic carbon (DIC) in the hypolimnion (Houser et al. 2003, cited in Bastviken et al. 2008, pp 11, 12). Despite of the low methane concentrations in surface waters, the shallow, epilimnetic sediments can be a major source of the methane emitted to the atmosphere; these areas account for most of the ebullition and plant-mediated flux to the atmosphere, and the related sediment-to-water diffusive flux can compare with or exceed that of the profundal zone (Bastviken et al. 2008, p 2, and references therein). Also, in temperate and boreal lakes, changes in temperature will affect methane production in shallow sediments much more than in deeper sediments (Bastviken et al. 2008).

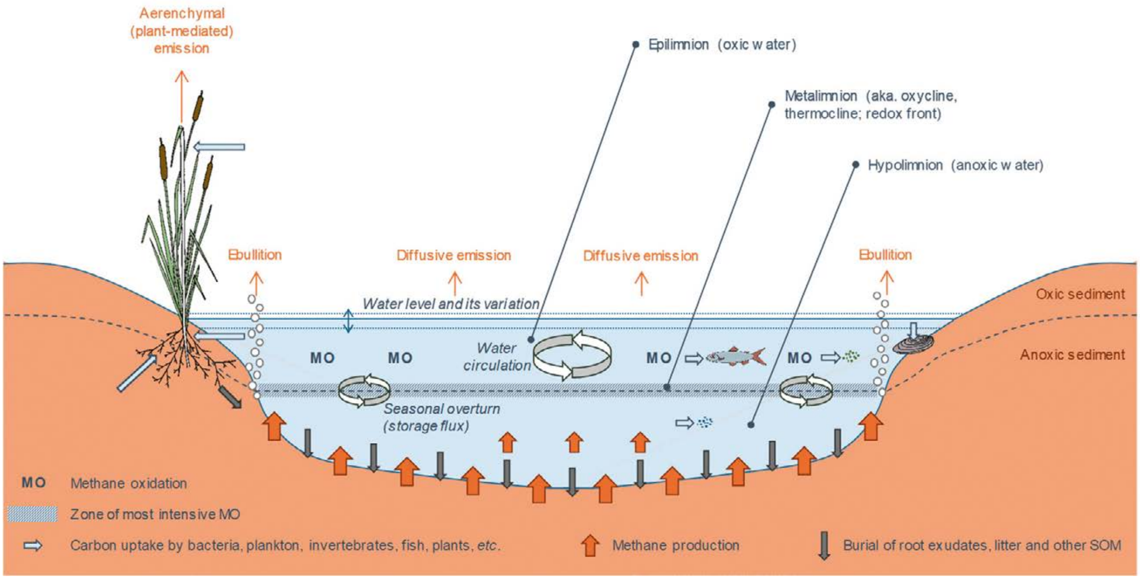

Figure 4-2. *Schematic presentation of methane pathways in a stratified lake (modified from Bastviken et al. 2004, p 2, particularly incorporating features from the similar illustration of wetlands by Charman 2002, p 95).*

Typically, methane concentrations are very small in the mixed surface layer of a lake, and increase more or less steadily with depth in the anoxic bottom water (e.g., Bastviken et al. 2008). At least in relatively small and humic lakes, the concentrations in the bottom water close to the sediment tend to have their maximum in late winter (seemingly due to accumulation of bottom-water storage during stratification and ice cover), those in the surface water to be the largest both in late winter and in late summer (seemingly coinciding with low transfer to the atmosphere and high supply rate, respectively), and the vertical concentration gradient to be steepest in late winter (Juutinen et al. 2009). The correlation between the concentrations in the surface and in the bottom water may be weak in general either due to homogeneity or dominance of other concentration patterns but, naturally, a stronger (negative) correlation typically occurs during the stratification periods (Juutinen et al. 2009). Generally, the surface-water concentrations may be more related to the morphological characteristics of the lake while the bottom-water concentrations are more controlled by the net production of methane (Juutinen et al. 2009).

In three stratified lakes in Wisconsin, US, Bastviken et al. (2008) found the dissolved methane flux from the sediment to the water to be highest from sediments overlain by anoxic water and very low in intermediate water depths, characterised by oxic surface sediments and strong temperature gradients likely implying very slow diffusion and thereby high fraction of methane oxidised. However, it was also found that the relative contributions of the ebullition, diffusive flux and storage flux can differ substantially between lakes, although the proportion of the ebullition or storage fluxes to the total flux tends to increase with the total areal flux (Bastviken et al. 2004). In their other study consisting of measurements for 24 lakes in Sweden and the US, and of literature data for another 49 lakes, Bastviken et al. (2004) observed that the methane concentration in surface waters was positively related to the fraction of the lake volume that is anoxic, and negatively to the DOC concentration and the lake area.

4.3 Methane production and oxidation in lakes

As outlined in Section 2.1, the production of methane is a microbial process also in freshwater lake sediments, and it is mainly regulated by the presence of anoxia, temperature, and the amount and quality of substrates (Juutinen et al. 2009, p 210, and references therein). A large proportion of methane produced in the sediment can be consumed at the sediment surface or in the water column by methanotrophs, a process that also contributes to oxygen deficiency (Juutinen et al. 2009, p 210, and references therein). Although methane production is generally believed to occur in anaerobic environments (i.e. in lakes in anoxic sediments), recent data suggest that methane production may also occur in oxygenated waters (Alperin and Reeburg 1984 and Murase and Kimura 1994, both cited in Le Mer and Roger 2001, p 28; Bogard et al. 2014 and Grossart et al. 2011, both cited in DelSontro et al. 2016, p 2) and this production can possibly explain as much as 33–44 % of methane accumulation in oxygenated waters (Grossart et al. 2011). In some, usually marine, aquatic sediments, methane is typically produced beneath the zone of sulphate reduction due to the process competing with or the sulphate inhibiting methanogenesis (Capone and Kiene 1988, Shaw and Atkinson 2014, Shen et al. 2015).

In freshwater environments, the principal precursors of CH_4 are acetate and H_2. Acetate is considered to account for two thirds of the produced CH_4 (Juottonen 2008, Segers 1998, and references in both). Of acetate, methanogens turn 60–85 % into methane and 15–40 % into CO_2 (Kuivila et al. 1989, Lovley and Klug 1982). Further, Lovley and Klug (1982) found that other carbon compounds such as propionate and lactate were metabolised into acetate, as well as CO_2 and CH_4. In their study the acetate turnover rates were 4–5 times higher in top 4 cm of the sediments compared to the sediments 4–10 cm below sediment surface. However, the turnover ratio of acetate into about 80 % methane remained stable independent of the sediment depth (0–10 cm) (Lovley and Klug 1982).

Methane can enter aerobic sediment or the water column from the anoxic sediment layer through diffusive export. Once methane enters aerobic layers, a large proportion is oxidized by methanotrophs (Frenzel et al. 1990, Bastviken 2009). They can be found in the highest density on the periphery of the methane producing zone, i.e. in the oxic sediment adjacent to the anoxic layer. The highest rate of methane oxidation will occur in this region (Conrad 2009, Segers 1998). This pattern was seen also in a study of three lakes in Wisconsin, US, where the highest methane oxidation rates were observed in the zone with the steepest methane and oxygen gradients (i.e. at the change from the anoxic to oxic conditions), whereas in the deep anoxic layers the oxidation did not significantly differ from zero and in the surface layers intermediate rates were found (Bastviken et al. 2008).

Whereas methane production is highly temperature-dependent (Bastviken et al. 2008, p 11, DelSontro et al. 2016, p S63, and references in both), and also dependent on organic content and nutrient ratios, methane oxidisation is primarily controlled by the levels of methane (and oxygen) (Bastviken et al. 2008; Sundh et al. 2005, cited in Bastviken et al. 2008, p 9, Thanh Duc et al. 2010). Indeed, CH_4 oxidation rates are coupled to the methane production rates (cf. Sections 2.1 and 2.2) and, as a result, a large but variable fraction of the CH_4 escaping anaerobic lake sediments may be oxidized before reaching the air–water interface, depending on water column depth and stability (i.e., well-mixed vs. stratified) (DelSontro et al. 2016, p S63, and references therein). Another consequence of the coupling is that with rising temperatures the methane production will increase, making more methane available for the methanotrophs to utilise, and this further yields in enhanced CH_4 oxidation.

The level of methane oxidation varies seasonally within lakes. A general range for the proportion of the methane produced in lakes that is oxidised lies at 30–99 % (Bastviken et al. 2008, p 1, and references therein). Averaged over the year, Utsumi et al. (1998) described that 74 % of dissolved methane was oxidized, with the highest (absolute) oxidation rates occurring in late summer and early fall. Fallon et al. (1980) estimated for two separate lakes in North America that 45 % and 11 % of the methane produced during the stratified period was oxidised. In three lakes in Wisconsin, US, 51–80 % of the methane produced in deep sediments was oxidised in the water column, but most of the methane released from shallow sediment escaped oxidation and reached the atmosphere (Bastviken et al. 2008). These shallow (epilimnetic) sediments accounted for 100 % of methane emissions during summer stratification, and 14–76 % for the period of the release of the methane stored in deep water layers during lake circulation (Bastviken et al. 2008).

4.4 Methane transport in and emission from lakes

Although many studies indicate that a large proportion of the produced methane is oxidised in lakes, inland waters (lakes, reservoirs and rivers) are considered to be a significant source in global methane budgets (e.g. St. Louis et al. 2000, Bastviken et al. 2004, 2011, Saunois et al. 2016). Bastviken et al. (2004) found indications that methane emissions may be related to variables such as lake area, water depth, concentrations of total phosphorus, dissolved organic carbon and methane, the anoxic fraction of the lake volume, and possibly temperature. This can be interpreted to indicate that the methane dynamics are affected by lake morphometry, productivity and the allochthonous load of organic carbon, as well as the interaction between morphometry, metabolism and water mixing reflected in the ratio of the anoxic volume to the oxic one (Bastviken et al. 2004). Further, Yvon-Durocher et al. (2014) showed that both the emission of CH_4 and the ratio of CH_4 to CO_2 emissions increased markedly with seasonal increases in temperature.

Estimating emissions from lakes is challenging, since there are five emission pathways which may be regulated differently (Bastviken et al. 2004; DelSontro et al. 2016, p S62, and references therein): ebullition flux, flux through aquatic vegetation, diffusive sediment-to-water flux, storage flux and water-to-air gas transfer flux. The relative contribution of these emission pathways tends to differ substantially between lakes (e.g. Bastviken et al. 2004). These are addressed in more detail in the sub-sections to follow.

4.4.1 Ebullition

Ebullition has been shown to be quantitatively the most important factor for emission of CH_4 from lakes (Bastviken et al. 2004). The difference between studies can probably to a large extent be explained by the fact that ebullition has been proved to be very variable among and within lakes and that ebullition is more difficult to measure than the other emission components; particularly, ebullition is well-known to be episodic and linked to air pressure changes (Bastviken et al. 2004; DelSontro et al. 2016, p S63, Natchimuthu et al. 2016, pp S13–S14, and the several references in both, Peltola et al. 2018).

The rapid emission of methane in ebullition events allows the methane to practically bypass the oxic zone and the oxidation (Rosenberry et al. 2006, cited in Peltola et al. 2018, p 937). Hence the ebullition flux component should be related primarily to the net methane production rate in the sediments (i.e., the gross methane production rate minus potential methane oxidation) and the hydrostatic pressure (related to the water depth) which has to be overcome for the bubbles to leave the sediment (Bastviken et al. 2004; Fendinger et al. 1992 and Mattson and Likens 1990, both cited in Bastviken et al. 2004, p 1). Based on the ideal gas law and Henry's law, the gas-phase bubble volume can be modified by hydrostatic and/or atmospheric pressure, temperature, or pore water concentration changes (Fechner-Levy and Hemond 1996, cited in Peltola et al. 2018, p 938). Therefore, considering also the bubble volume threshold of gaining sufficient buoyancy to exceed the retention forces trapping the bubble, an ebullition event may be triggered by decreasing atmospheric pressure, changes in hydrostatic pressure (due to either climatic barometric fluctuations or change in water level), increasing sediment (or peat; cf. Section 6.4) temperature, wind-induced disturbance of the sediments, or increase in the pore-water methane concentration (DelSontro et al. 2016, p S63, Peltola et al. 2018, pp 937–938, Raivonen et al. 2017, pp 4667–4668, and references in all three; also, Bastviken et al. 2004). Bubbles in sediments under a shallow water column have less hydrostatic pressure to overcome before release to the atmosphere. Thus, changes in air pressure will have a proportionally greater impact on shallow sediments, resulting in the contribution of ebullition to total methane emissions to decline steeply with the water depth (Bastviken et al. 2004; DelSontro et al. 2016, p S63, and references therein).

As yet another factor, other gases increase the gas pressure, and soil particles and impurities lower the energy barrier for gas nucleation (Raivonen et al. 2017, p 4667). The bubbles consist largely of methane, the rest being nitrogen, oxygen and carbon dioxide, which suggests that the bubbles originate from conditions with relatively high methane concentrations in the pore water (Peltola et al. 2018, pp 937–938, Raivonen et al. 2017, p 4667, and references in both). In a study in temperate and boreal regions of Québec, Canada, the methane concentration in the bubbles was on average 57.6 % in ponds and 31 % in lakes, with ranges of 1.3–97 % and < 1–93 %, respectively (DelSontro et al. 2016).

In the study of ten shallow ponds and three lakes in temperate and boreal regions of Québec, Canada, mentioned just above, it was also concluded that the temperature dependency of methane diffusion and ebullition is strongly modulated by system trophic status (particularly total phosphorus). This suggests that organic substrate limitation reduces the effect of temperature on methane fluxes in oligotrophic systems (DelSontro et al. 2016). Also, both diffusion and ebullition correlated positively with chlorophyll *a*, which suggests that higher fluxes would be found in more productive systems (DelSontro et al. 2016). Observations from lakes in Sweden included higher ebullition fluxes coinciding with rapidly decreasing air pressure and lake mixing in autumn, which was considered to be in line with other studies (Natchimuthu et al. 2016, p S24, and references therein). In another study, both the lake-total and per-area ebullition rates were found to relate with the total phosphorus concentration, likely reflecting a positive effect of nutrient load and lake productivity on methane production (Bastviken et al. 2004). Very high ebullition rates have been observed in Siberian thaw lakes (Walter et al. 2006, cited in Bastviken et al. 2008, p 11), resulting from thermokarst erosion along lake margins supplying previously frozen labile organic material to lake sediments (Bastviken et al. 2008). Enhanced ebullition has been observed also close to a reed belt, likely associated with turbulence created by waves, indicating that plants may also influence other than the aerenchymal fluxes discussed in another section below (Natchimuthu et al. 2016; also, Wang et al. 2006, cited in Natchimuthu et al. 2016, p S20).

Only a few studies have measured diffusion and ebullition simultaneously, and these report a range of generally 30–95 % for the contribution by ebullition to total methane emissions (Bastviken et al. 2004; Repo et al. 2007, cited in DelSontro et al. 2016, p S63; in addition to other studies summarised below). In a study from the UK concerning a small hypertrophic lake where loss of methane by ebullition was compared to diffusive processes, it was shown that more methane was lost by ebullition (96 %) compared to diffusive processes (Casper et al. 2000). In three lakes in southwest Sweden monitored over two annual cycles, the contribution of ebullition to the total open-water methane fluxes (i.e. non-littoral areas) varied 56–79 %, which was found to be in the range of 10 to >90 % found earlier at boreal and temperate latitudes (Natchimuthu et al. 2016, p S18, and references therein). In ten shallow ponds and three lakes in Québec, for which some results were summarised already above, the ebullition flux contributed about 56 % to the total open-water flux (i.e. sum of diffusion and ebullition) in ponds and 18–22 % in lakes in respect of the whole lake area, although occurring only in waters less than three metres deep (DelSontro et al. 2016). This was found comparable with results from beaver ponds in Manitoba (52 %) and Ontario (65 %) (Dove et al. 1999 and Weyhenmeyer 1999, both cited in DelSontro et al. 2016, p S71). In Lake Vesijärvi, southern Finland, the ebullition flux was 30–56 mg CH_4 m^{-2} h^{-1} at the peak season (July), falling within the corresponding range of the plant-mediated flux (15–80 mg CH_4 m^{-2} h^{-1}) (Käki et al. 2001).

In their measurements in 11 small lakes in Wisconsin, US, Bastviken et al. (2004) observed that the ebullition flux was highly variable within and between the lakes, and non-linearly correlated to water depth, with ebullition occurring in 25–80 % of the measurement chambers in locations where the depth was four metres or less, and only in 10 % of the chambers on deeper waters (Table 4-1; Bastviken et al. 2004, pp 4, 6). This occurred primarily from sediments overlain with the most mixed surface water (Bastviken et al. 2008). A strong depth-dependence has been observed also elsewhere, although the depth at which ebullition ceases varies (Casper et al. 2000 and Mattson and Likens 1990, both cited in Bastviken et al. 2004, p 8; Wik et al. 2013, cited in DelSontro et al. 2016, p S71). For a subset of three of these lakes in Wisconsin, 52–74 % of the total methane fluxes from shallow (epilimnetic) sediments occurred through ebullition (Bastviken et al. 2008). In a lake in southwest Sweden, Erssjön, the ebullition flux was found to have a pattern that the mean flux in shallow depth zones (<0.5 and 0.5–1 m) was 1.5- and 1.4-fold higher, respectively, than the whole lake average (Natchimuthu et al. 2016). This emphasises the importance of the shallow zones contributing about 42 % and 33 % of the whole ebullition and diffusion amounts from the lake, respectively (Natchimuthu et al. 2016). In three lakes in Québec, the observed depth-dependency of ebullition may be due to a number of single factors or a combination of them, such as lower production rates due to colder sediment temperatures or less available substrate as well as higher saturation concentrations in colder sediments at larger depths that, along with increasing hydrostatic pressure, could result in less bubble formation and release (DelSontro et al. 2016). The observed depth-dependence has been related also earlier to the connection between ebullition and air pressure (Casper et al. 2000 and Mattson and Likens 1990, both cited in Bastviken et al. 2004, p 10; Fendinger et al. 1992).

Table 4-1. Approximate incidence of observations of ebullition (i.e. fraction of the floating chambers receiving ebullition flux identified based on magnitude and variability) at different water depths in 11 lakes in Wisconsin, US (derived from Bastviken et al. 2004, p 7).

Depth interval	Incidence
0–0.5 m	65 %
0.5–1 m	88 %
1–2 m	63 %
2–4 m	29 %
4–8 m	12 %
> 8 m	5 %

4.4.2 Plant-mediated gas transport (aerenchymal transport)

In general, plants affect methane cycling in diverse ways, including provision of gas transport routes mainly through aerenchyma (see below) and providing oxygen, root exudates and plant litter in the organic carbon pool (e.g. Schütz et al. 1991, cited in Käki et al. 2001, p 260). Littoral zones with aquatic emergent macrophytes have been identified important to the overall methane emissions from lakes (e.g. Juutinen et al. 2003, cited in Bastviken et al. 2008, p 11).

Plant-mediated transport of methane is associated with the adaptation of wetland and aquatic species to living in oxygen-depleted sediments (Juutinen et al. 2004). These emergent aquatic plants (macrophytes) photosynthesise and, thus, produce oxygen in their above-water parts, and transport oxygen to their roots and rhizomes located mostly in the generally anoxic sediment (Brönmark and Hansson 2005). Gases move through the plants by diffusion along a concentration gradient or are transported by convective (bulk) flow (Chanton et al. 1992 and Dacey and Klug 1979, both cited in Juutinen et al. 2004, p 1; Schütz et al. 1991, cited in Käki et al. 2001, p 260). These processes occur in 'tunnels' (lacunae) leading from the stomata in the leaves through the stem and down the roots partly by diffusion but mostly by convection (Figure 4-3; Brönmark and Hansson 2005, Juutinen et al. 2004). The diffusion is due to the gradient of the oxygen concentration decreasing from the air to the respiring submerged parts, and the convection is caused by the temperature and humidity being higher inside the plant, particularly inside the young leaves, than in the outside air, allowing dead and cracked culms and leaves to act as 'vents' evacuating respiration products (and other gases) from the root system (Figure 4-3; Brönmark and Hansson 2005, Juutinen et al. 2004). Hence, in sandy, often wind-exposed areas such emergent macrophytes will grow in deeper water than in sheltered areas with muddy, low-oxygen bottoms (Weisner 1987, cited in Brönmark and Hansson 2005, p 57). Generally, this kind of vegetation primarily grows at water depths less than 1.5 m (Kalff 2002, cited in Bastviken et al. 2004, p 9) and cover 1–15 % of the lake surface for most lakes (Carpenter 1983, cited in Bastviken et al. 2004, p 9). Such plant species include water lily (*Nuphar* spp.), common reed (*Phragmites australis*), *Typha* spp, *Nymphaea* spp., *Nelumbo* spp., *Eleocharis* spp. and *Potamogeton* spp., although considerable differences in the convective transport efficiency have been observed across them (Brönmark and Hansson 2005; Juutinen et al. 2004, pp 1–2, and references therein).

Plant-mediated fluxes change seasonally and may peak in late summer, and at times the plant-mediated flux may be the dominating methane emission pathway (96 %) from for example rice paddies (Schütz et al. 1989). Many reed stands show low resistances to convective gas-flow during summer, but increases in the resistance are measured later in the growing season (Grünfeld and Brix 1999 and Kohl et al. 1996, cited in Käki et al. 2001, p 260). In stands of cattail in a lake littoral > 50 %, and in mature reed stands > 90 %, of the methane transport can be plant-mediated (Sebacher et al. 1985 and Van Der Nat and Middelburg 1998, cited in Käki et al. 2001, p 260). However, the relative contribution of plant-mediated flux in comparison to the other flux components (i.e. ebullition, diffusion and storage fluxes) decreases with increasing lake size (Bastviken et al. 2004). This is explained by that the proportion of lake area covered by emergent plants generally declines with increasing lake size. It has been estimated that methane emissions from areas with *Phragmites* spp. and *Typha* spp. account for as much as 10 % of total methane emissions from wetlands in Sweden (Kasimir-Klemedtsson et al. 2001).

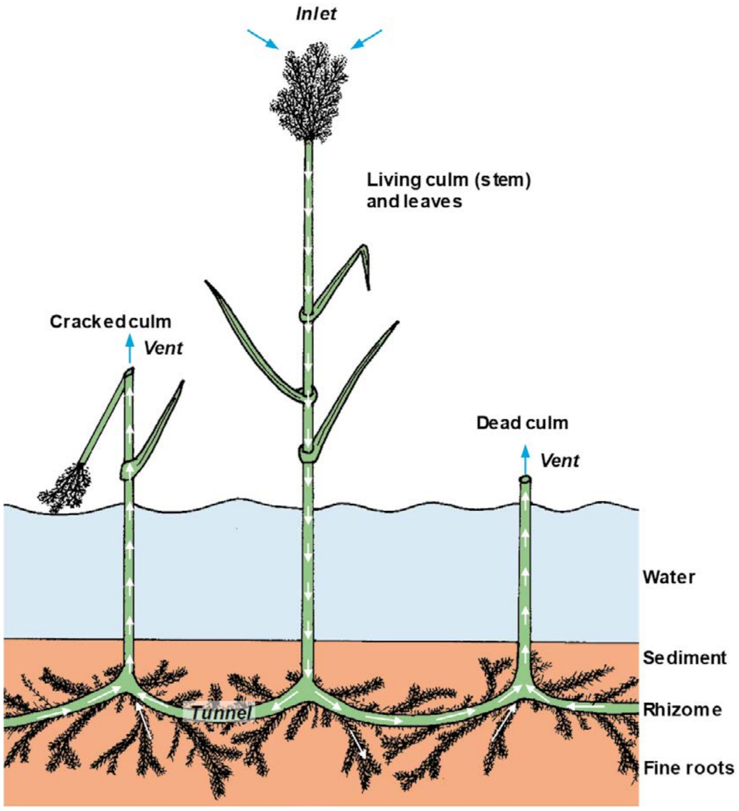

Figure 4-3. *Stem, root and culm system of common reed functioning together as 'inlets', 'tunnels' and 'vents' for the convective oxygen transport and evacuation of root respiration products (modified from Brönmark and Hansson 2005, p 56, and Juutinen et al. 2004, p 2). However, in* ***Typha*** *spp. and Nymphaeaceae the gas circulation occurs within an individual plant only (Juutinen et al. 2004, p 9, and references therein). Some proportions have been exaggerated for clarity of the presentation.*

In certain wetland plants such as the common reed, the convective ventilation seems to be driven mostly by solar irradiance, and at the end of the season and in the outermost parts of the stand also by relative humidity and air temperature (Brönmark and Hansson 2005, p 57; Juutinen et al. 2004, p 2; as well as references in both of these), thus, possibly also related to the transpiration. This also supplies the photosynthesising parts with additional CO_2 by recirculating the root respiration products (Brönmark and Hansson 2005). However, the relationship is not linear, since the methane efflux depends also from the methane production in the rhizosphere and the storage in the plant; the limiting 'gate parameter' is the diffusion rate of methane into the root aerenchyma, which results in vigorous increase in the methane efflux after dawn, but in the daily maximum efflux occurring earlier than that in the irradiance (Juutinen et al. 2004, p 8, and references therein). Thus, it has traditionally been considered that the convective flow exhibits strong diurnal dynamics (Chanton et al. 1992 and Dacey and Klug 1979, both cited in Juutinen et al. 2004, p 1). However, a recent study (Milberg et al. 2017) published after the initial literature search for the current review seems to challenge this view.

Among some wetland species, like *Carex* spp., ventilation of the roots is based on diffusion only, and the diurnal variation in methane fluxes is associated with changes in temperature, oxygen supply, or availability of photosynthates regulating the production and oxidation of methane (Juutinen et al. 2004, p 2, and references therein). Regarding the diffusive transport within the plant, highly anoxic sediments, such as mud, demand more oxygen than sandy sediments, due to the larger difference in the oxygen concentration between the root system and the substrate, and a longer transport distance between the air and the roots decreasing the amount of diffusively transported oxygen in the sediment (Brönmark and Hansson 2005, p 57).

Due to these mechanisms, the convective flow occurs during daylight, while the diffusive ventilation mainly occurs at night (Juutinen et al. 2004). This results in that the methane efflux through, for example water lily and common reed, at midday can be considerably higher than at night, whereas the methane efflux through species not facilitating the convective transportation seems to peak in the afternoon, evening or at night (Juutinen et al. 2004, p 2, and references therein). Even in otherwise convection-dominated stands, a large methane storage in the sediment not exhausted during the daytime may enable also a strong 'residual' diffusive flux in the evening and at night (Juutinen et al. 2004). There may also be ebullition (see Section 4.4.1) associated (Käki et al. 2001, cited in Juutinen et al. 2004, p 7). However, the plant-mediated methane flux is ultimately regulated by the methane production and oxidation in the sediments, and vegetation characteristics (Bastviken et al. 2004) such as the leaf area that relates to the root mass available to facilitate the gas transport (Peltola et al. 2018, p 939).

The diel pattern in methane emission in reed largely results from the changes in the internal convective flow (Grünfeld and Brix 1999 and Kohl et al. 1996, both cited in Käki et al. 2001, p 260). In cattail (*T. latifolia* as well as *T. angustifolia*), humidity-induced diffusion is the dominant mechanism, and light influences its efficiency, likely linked with the light-induced stomatal movements (Bendix et al. 1994, cited in Käki et al. 2001, p 260). In a study of common reed and cattail stands at lakeshore in southern Finland, neither of the species closed stomata at night, but still showed diel patterns in lacunal methane concentrations (Käki et al. 2001). There was also some diel patterns observed in the plant-mediated fluxes for some vegetation types, but the situation was more obscure in some other situations; generally, the diel differences seem to increase with the progress of the growing season (Table 4-2; Käki et al. 2001). A relationship with the irradiance was also observed when the difference between the day- and night-time fluxes was significant (Käki et al. 2001). These results were found reasonably similar with reed stands in central Europe, northcentral Nebraska, US, and elsewhere, as well as with stands of *Typha* spp. even in sub-tropical conditions (Käki et al. 2001, pp 269–270, and references therein). Also stands of *Equisetum fluviatile* have been studied for variations in the methane efflux, but no diel patterns were found (Hyvönen et al. 1998, cited in Käki et al. 2001, p 260), which indicates that the species is not employing pressurised ventilation in the gas exchange (Käki et al. 2001).

Table 4-2. Plant-mediated methane effluxes (mg m^{-2} d^{-1}) observed in Lake Vesijärvi, southern Finland (compiled from the text and graphs in Käki et al. 2001).

Plant stand	Month	Efflux (Day)	Efflux (Night)
Common reed, inner (i.e. drier) zone	May	~ 24	19–22
	June	48–170	24–170
	July	170–360	70–190
	August	120–1440 (2064*)	240–260 (79*)
	September	120–310	~70
Common reed, outer zone	May	0	0
	June	70–1300	~ 24
	July	360–1800	190–1900
	August	240–625	0–960
	September	0–1400	0
Mixed common reed and cattail	May	24–50	24–50
	June	70–120	50–190
	July	95–340	24–600
	August	95–430	70–120
	September	70–220	~ 50

* indicates values mentioned in the text that likely refer to more momentary fluxes.

Juutinen et al. (2004) measured diurnal variability in methane fluxes for several boreal lakeshore communities consisting of common reed and wetland sedges, grasses and herbs in eastern central Finland (for the numerical data, see below). With the common reed, the methane fluxes were typically at maximum around noon, and in general the efflux rate measured between 08.00–16.00 hours local time should be multiplied with 0.68 (or, 0.54–0.98 varying with the measurement plot) for a more realistic estimate of the daily release. With sedge, grass and herb stands (including *Calamagrostis canescens*, *Calla palustris*, *Carex* spp., *Eriophorum angustifolium*, *Potentilla palustris*) more typical to the temporarily flooded littoral zone than relatively deeper waters, the diurnal variation was found generally small with the daily maximum often occurring during evening or night, even though three-fold diurnal differences could occasionally be observed. Interestingly for the convective transport, cutting the reed culms 5 cm above the water surface within the measurement plots, as well as 5 cm below the water surface in a one-metre radius around the plots, did not attenuate the diurnal methane flux dynamics. However, the treatment resulted in increased means and standard deviations of the flux. Instead, the methane efflux was attenuated only when the culms in the measurement plots were cut below the water surface. (Juutinen et al. 2004). The night-time fluxes being 29–85 % of mean daytime fluxes in the summer (Juutinen et al. 2004; also see Table 4-3) was found to cover the range of results from Nebraskan and Danish studies with common reed (Grünfeld and Brix 1999 and Kim et al. 1998, cited in Juutinen et al. 2004, p 7). However, in the study in Finland summarised above, the diurnal pattern was found only occasionally in several campaigns in boreal lake littoral belts of common reed and *Typha latifolia*, and the former so only starting in August (Käki et al. 2001, cited in Juutinen et al. 2004, p 7). The observed seasonal increase in the methane efflux with increasing aboveground biomass indicates that the vegetation has a positive effect on methane efflux (Juutinen et al. 2004; King et al. 2002 and Torn and Chapin 1993, both two cited in Juutinen et al. 2004, p 7). The cease of the largest diurnal variability in the methane efflux in the autumn (Juutinen et al. 2004) and its reappearance in spring (Arkebauer et al. 2001 and Kim et al. 1998, both cited in Juutinen et al. 2004, p 7), seem to confirm the role of convective transport of methane. However, these also coincide with higher organic matter supply for methanogenesis in the warmer season (Juutinen et al. 2004) and with higher benthic primary production (e.g. algal mat) as well as oxygen release in the daytime (King 1990, cited in Juutinen et al. 2004, p 9). Also, a site with a very high methane release behaved differently, possibly due to the high methane production from the litter accumulated at this measurement plot located at the inner reed stand margin (Juutinen et al. 2004; Juutinen et al. 2003 and Kankaala et al. 2004, both two cited in Juutinen et al. 2004, p 7).

It needs to be noted, however, that the studies summarised above tend to report short-term measurements only. In a recent study (Milberg et al. 2017), published after the initial literature search for the current review, different diel patterns were found when the measurements were repeated on multiple days. As indicated also in the case of the studies referred to above, it seems that the role and variability of the plant-mediated transport is rather strongly coupled with the other transport mechanisms and their variability over the different timescales.

Table 4-3. Plant-mediated methane effluxes (mg m^{-2} d^{-1}) observed in lakeshores in east–central Finland (compiled from Juutinen et al. 2004).

Plant stand	Measurement period	Efflux
Common reed, overall	24 hours	316 (mean) 266 (median) 212 (standard deviation)
Common reed, inner (i.e. drier) margin	12 hours *	0–6160
Common reed, middle	12 hours, day 12 hours, night	193–963 0–578
Common reed, outer margin	12 hours *	0–385
Calla palustris and *Comarum palustre*	12 hours *	0–385
C. palustris, *C. palustre* and *Carex aquatilis*	12 hours *	0–770
Calamagrostis canescens	12 hours *	0–3850

* indicates that the same range of efflux was observed whether the 12-hours period was over the day or over the night.

Even though the aerenchymal transport was not monitored in the study, one isolated hotspot with higher fluxes was found in a lake in Sweden, Erssjön, in the depth category >2 m, where a chamber was close to a group of macrophytes rooted in the sediments (Natchimuthu et al. 2016). In this spot, consistently high fluxes were measured, totalling up to threefold higher than the whole-lake mean estimates (ranging 1.3–35 mg m^{-2} d^{-1} whereas the emission from this location ranged 1.4–102 mg m^{-2} d^{-1}). Possibly, these hotspot fluxes resulted from local sediment accumulation leading to enhanced gas production or interactions between plant roots and the sediment (perhaps by ebullition around roots triggered by plant movement from waves, or local plant induced hydrodynamics favouring methane production and release). (Natchimuthu et al. 2016). In another study, enhanced ebullition close to a reed belt was noted which was likely associated with turbulence created by waves, indicating that plants may also influence local patterns of open-water fluxes (Wang et al. 2006, cited in Natchimuthu et al. 2016, p S20).

In a Swedish emission inventory, a regional estimate of long-term methane emissions from epilittoral reedbeds yielded a mean rate of 200 mg m^{-2} d^{-1}. This was based on seasonal measurements that ranged 140–310 mg m^{-2} d^{-1}. It was also found that the averaging was sensitive to the length of the vegetation period. (Kasimir-Klemedtsson et al. 2001).

4.4.3 Diffusive fluxes from sediment to water

As outlined at a general level in Section 4.2 above, methane eventually escapes the sediment and enters the water column as a result of diffusive export, and as soon as the methane reaches oxic sediment or water, a large proportion is likely oxidised by methane-oxidising bacteria (Bastviken et al. 2002, 2004, 2008, DelSontro et al. 2016). The rest of the methane in the water column rises to the upper mixed layer and becomes emitted by the water-to-air flux (see Section 4.4.5) (Bastviken et al. 2004).

The diffusion fluxes from the sediment to the water are affected by the oxygen concentrations in the close-by water (Bastviken et al. 2008) that is also reflected by the steeper concentration gradient of methane not oxidised. The sediment-to-water diffusion fluxes are also affected by turbulence and bottom shear stress (Bussmann 2005, Cole and Caraco 1998, Cole and Pace 1998, Murase et al. 2005, and Sakai et al. 2002, all cited in Bastviken et al. 2008, p 9). Oxic bottom water and, thus, oxic surface sediment indicate potential for substantial methane oxidation already at the surface sediment and at the sediment–water interface, although a rapid turbulence-enhanced flux from the sediment allows less time for methane oxidation to act at the interface (Bastviken et al. 2008). Such promoting role of wind exposure in the sediment fluxes may indicate that at high-wind events also the overall methane efflux from the lake water to the air is enhanced by increased piston velocity (see Section 4.4.5) (Bastviken et al. 2008). Correspondingly, also the fluxes from epilimnetic sediments may increase due to the increased turbulence, which in turn provides a delayed effect of high methane concentrations being transported from the epilimnetic sediments into the water column at large, which further allows continued efflux (Bastviken et al. 2008).

4.4.4 Storage flux

For stratified lakes, there can be a build-up of methane in the anoxic layer (hypolimnion; cf. Figure 4-2), resulting in methane storage in the water column. This storage will be emitted rapidly by diffusion during periods of lake turnover, for example, during spring after ice melt and autumn when surface cooling breaks down summer stratification (Michmerhuizen et al. 1996 and Riera et al. 1999, both cited in Bastviken et al. 2004, p 2; Natchimuthu et al. 2016, p S13, and references therein). Such 'storage flux' component is likely a function of methane production rates, the volume of the anoxic water layer, and the losses by methane oxidation and diffusion to upper layers (Bastviken et al. 2004). Indeed, lakes without anoxic water layers have shown low storage of methane (Bastviken et al. 2004). The methane concentrations under the ice may increase during the winter, for example, due to the dissolution of methane from bubbles trapped under the ice in the surface water, or they may remain relatively low if the O_2 status allows for methane oxidation during the season. The former case results in a large vernal storage flux, whereas in the latter case the contribution remains minor (Natchimuthu et al. 2016).

In a study of 207 lakes throughout Finland (Juutinen et al. 2009), methane storages were larger during the assumed stratification periods than during the subsequent periods of mixing or soon after them, in 58 % and 75 % of the lakes in spring and autumn, respectively. The methane storage reached it seasonal maximum during late winter in 40 % of the lakes, and during late summer in 36 % of the lakes. However, the storage peaked during spring or autumn in some of the lakes, a result possibly affected by the sampling having occurred prior to the turnover. Accumulation of substantial methane storage during summer was common. (Juutinen et al. 2009).

It has been shown in another field study of 24 lakes in Sweden and the US that in comparison to other flux components, such as ebullision and diffusion, storage component can contribute up to 45 % of the total methane emission in the smallest lakes, but this contribution diminishes with increasing lake size (Bastviken et al. 2004). In some of the 207 lakes in Finland addressed above, the storage flux was found to be up to 91 % of the total open-water efflux from the lake (Juutinen et al. 2009).

In the lakes with a larger storage prior to the assumed turnover, out of the 207 study lakes in Finland, the median percentage of the storage that was lost to the atmosphere during the assumed turnover event was 88 % in the spring and 63 % in the autumn (Juutinen et al. 2009).

A positive relation of the storage flux and the total phosphorus concentration in the lake water has been observed (Bastviken et al. 2004). It is possibly related to a higher production of methane and a larger relative volume being anoxic in more productive lakes, counterbalanced by the observed negative relation with the concentration of dissolved organic carbon (DOC) (Bastviken et al. 2004). The lakes rich in DOC tend also to be smaller and consequently have also a smaller volume to store the methane (Bastviken et al. 2004). In the 207-lake study, the methane concentrations were significantly greater in the late winter in lakes developing anoxic conditions under the ice and having high total phosphorus levels than in lakes with oxic bottom water low in phosphorus; similar pattern was observed also for the whole annual cycles (Juutinen et al. 2009). Also, large storage fluxes were found in small eutrophic lakes, whereas clear-water lakes had the smallest fluxes among the small lakes (Juutinen et al. 2009). In a regression analysis, the springtime storage flux was found to be related to the maximum depth of the lake, the autumn storage flux to the area, maximum depth and nutrient status of the lake, and the sum of the storage fluxes to the lake area and nutrient status (Juutinen et al. 2009).

Bastviken et al. (2004) performed a study based on measurements for the abovementioned 24 lakes in Sweden and the US and they showed that there is a positive relation of methane concentrations in the oxygenated surface water to the anoxic volume fraction of the lake, a negative one to the dissolved organic carbon (DOC) concentration and lake area, and no significant relation to total phosphorus or chlorophyll *a*. This positive relation may indicate that a substantial proportion of the methane in the surface water originates from methane that is stored in anoxic parts of the water column below the mixed surface layer (Bastviken et al. 2004). However, there are also other potential explanations (see Section 4.4.5). In the same study, the storage flux *per lake* was significantly related to the lake area and to total phosphorus and DOC concentrations, and the storage flux *per area* was best predicted by the anoxic volume fraction of the lake, but could also be predicted from surface methane concentration and the total phosphorus, or the surface methane concentration and the DOC (Bastviken et al. 2004). For oligotrophic lakes in Sweden and in comparable conditions, it may be reasonable to assume no methane accumulation in the water column under the ice, though, despite of the mixing both in the spring and fall (Bastviken et al. 2004).

In three lakes in Wisconsin, US, Bastviken et al. (2008) could identify water layers between which negligible methane transport occurred. In two of the lakes sampled down to 11 and 18 m (mean depths 3.7 and 5.7 m, respectively), surface (above 2.5 m), middle (2.5–5 m) and deep (below 5 m) layers could be identified, and in the third lake (sampled down to 7.5 m; mean depth 3.7 m) the middle layer was either absent or thinner than the depth resolution in the measurements and the surface layer was only about one metre thick (Bastviken et al. 2008, p 4). The deep layers were mostly anoxic and hosted high methane concentrations, whereas the surface and middle layers were oxic with the methane concentration minima occurring and the strongest temperature gradients in the middle layer and only the surface layer was affected by diurnal temperature-driven advective mixing (Bastviken et al. 2008).

4.4.5 Fluxes from surface water to air

This flux component depends on the difference in the methane concentration between the water and the atmosphere, and on the physical rate of exchange between the air and water, usually expressed as a 'piston velocity' (Stumm and Morgan 1996, cited in Bastviken et al. 2004, p 1), called also the 'gas transfer velocity' (cf. Chapter 5). The piston velocity is the result of turbulence and therefore depends on the wind speed, whereas the methane concentration in the surface water is a function of methane production, methane oxidation, rates and pattern of methane fluxes within the lake, and the piston velocity affecting the loss rate (Bastviken et al. 2004). The piston velocities, and consequently also the diffusive effluxes, are spatially heterogeneous within lakes (Schilder et al. 2013, cited in Natchimuthu et al. 2016, p S13).

In a study of 207 lakes in Finland, shallow lakes typically had higher total open-water effluxes (19–48 mmol m^{-2} y^{-1}) than the larger lakes (2–8 mmol m^{-2} y^{-1}), due to the shallow lakes having high methane concentrations in the surface water. However, ebullition or plant-mediated efflux were not included in the study. The highest lake-type median value was found for eutrophic lakes. The more or less continuous diffusive water-to-air flux dominated the methane release in most of the lakes, and in half of the lakes the momentary storage flux was less than 5 % of the diffusive one. In a regression analysis, both the diffusive water-to-air flux alone and the sum of this flux and storage fluxes were found to be related to lake area and depth, and to nutrient status. (Juutinen et al. 2009).

The annual total diffusive flux from the water to the air among 24 lakes in Sweden and the US was well predicted by the lake area, and the annual areal flux (i.e. the flux per area) was best predicted by the methane storage per area, indicating that the source of the surface-water methane escaping to the air is from the deeper water layers. For the total flux, the decline in surface-water methane concentration is compensated for by the fetch, and thus the piston velocity, increasing with the lake size. (Bastviken et al. 2004). The positive relation of methane concentrations in the oxygenated surface water to the anoxic volume fraction of the lake observed by Bastviken et al. (2004) may also be explained, in addition to the storage flux, by that piston velocities may be lower in small lakes leading to a lower mixing and then to a larger retention of methane in the water column as the export to the atmosphere is smaller (Bastviken et al. 2004). The negative relation observed between methane concentration in the surface water and lake area can be explained by larger lakes having higher piston velocity resulting in a greater diffusive emission by larger lakes having larger volumes and also longer residence times to allow a more extensive oxidation (Bastviken et al. 2004).

In three small lakes in southwestern Sweden, the surface-water methane concentrations (0.05–64 µM) were always supersaturated with respect to the ambient atmospheric levels throughout the two ice-free seasons monitored, with the highest concentrations likely related to water passing through a shallow area rich in organic matter and low in oxygen (Natchimuthu et al. 2016) that may indicate an effect of enhanced methanogenesis in such conditions.

4.5 Methane utilisation by lake biota

Aquatic food webs are traditionally considered to be rather directly supported by the organic matter from phytoplankton, macrophytes or imported from the surrounding land (allochthonous sources) (Cole et al. 2011 and Pace et al. 2004, cited in Sanseverino et al. 2012, p 1, Wetzel 2001). However, as discussed already above, it has been shown that the methanotrophic bacteria are able to utilise methane for energy purposes to fuel their growth. Methanogenesis accounts for a large proportion of the total organic matter degradation in freshwater lakes (20–56 %; Bastviken 2009), and the methane carbon is incorporated into microbial biomass, which can be further grazed by aquatic organisms. This provides an energy source adding to the 'traditional' ones (Bastviken et al. 2003, Kankaala et al. 2006, and Taipale et al. 2007, all three cited in Bastviken et al. 2008, p 11, Grey 2016; Bastviken et al. 2003, Jones and Grey 2011 and Jones et al. 2008, all three cited in Sanseverino et al. 2012, p 1, Sanseverino et al. 2012, Taipale et al. 2009).

Based on a study of three lakes in Wisconsin, US, the methanotrophic source has been estimated to be about 4–6 % of the net primary production, similar to the pelagic bacterial production. However, most of the methanotrophic production was in the deeper water, likely making a considerable portion of the supply to organisms feeding deeper in the water column (Bastviken et al. 2008).

In addition, it has been shown experimentally and in field studies that carbon from the methanotrophs can be transferred to invertebrate animals and fish (Deines et al. 2007, Sanseverino et al. 2012, Bastviken 2009). Sanseverino et al. (2012) showed by combining analyses of $\delta^{13}C$ and fatty acid composition in fish, benthic macroinvertebrates, zooplankton, and the dominating aquatic macrophyte that methane derived carbon from methanotrophs can be transferred through food webs all the way to fish in a shallow tropical lake in Pantanal, Brazil. The data presented by Sanseverino et al. (2012) demonstrate that CH_4 can be a significant carbon source not only for the microbial food web and invertebrates (in this specific study, 22 % of carbon in zooplankton and 16 % in aquatic insects) but also for higher trophic levels (1–13 % for various fish). The Pantanal floodplain is characterized by conditions that altogether favour production and emissions of CH_4, such as high primary productivity, shallow depth of inundation, and high temperature (Bastviken et al. 2010). Similar indications have been presented also elsewhere for invertebrates and fish (Sanseverino et al. 2012, p 1, and the numerous references therein), although low $\delta^{13}C$ values can result also from other sources of ^{13}C-depleted carbon, warranting further support, such as detection of methanotroph-specific fatty acids transferred in the food web (Sanseverino et al. 2012, p 1, and references therein).

In the study of Sanseverino et al. (2012), two groups of fish were identified in respect of the $\delta^{13}C$ signal: one typically feeding at the oxic–anoxic interface where also the methanotroph abundance is likely to be the highest, and the other typically pelagic or living close to aquatic plants and presenting tendency to a higher degree of herbivory. However, traces of methanotroph-specific fatty acids were found also in plants, possibly due to residual biofilms on the samples or presence of methanotrophs inside living tissues of submerges aquatic plants (Sanseverino et al. 2012, p 3). The results of Sanseverino et al. (2012) also suggest that the transfer of methanotroph-derived carbon may be favoured by predominance of Type I methanotrophs over Type II. Such situations are often met also in temperate and boreal lakes, flood-pulsed wetlands and other environments characterised by low temperatures, low methane and high oxygen concentrations (Amaral and Knowles 1995, Chowdhury and Dick 2011, and Sundh et al. 2005, all cited in Sanseverino et al. 2012, p 5).

It is to be noted that further information on the methane utilisation by freshwater biota has been compiled in a BIOPROTA project that ran parallel to the one reported here. Since overlap was aimed to be avoided between these projects, the reader is advised to see also chapter 4 of Thorne et al. (2018) for complementary information. In addition, also Grey (2016) drew an overall picture of the topic independently.

4.6 Whole-lake methane budgets and interactions

Regarding whole-lake views on the CO_2 and CH_4 budgets, especially small lakes have been in focus of research since they have been shown to have high emissions in arctic, boreal and temperate climates and to be high in number in the boreal and Arctic regions (Juutinen et al. 2009, p 209, and references therein). The higher methane emissions per area from small and shallow lakes than that from deeper and larger ones can be linked to rich substrate supply from the littoral zone and less time for methane oxidation when passing the relatively short well-mixed water column (Natchimuthu et al. 2016, p S18, and references therein). Poor oxygen saturation and high nutrient status predict high methane concentration in the bottom water, related to high methane production rate and hindered methane oxidation (Huttunen et al. 2003 and Rudd and Hamilton 1978, both cited in Juutinen et al. 2009, p 219), as do the often strong stratification and oxygen consumption rates in humic lakes (Bastviken et al. 2004 and Kankaala et al. 2007, both cited in Juutinen et al. 2009, p 219). In shallow lakes, epilimnion and productive littoral sediments constitute a large part of the total area and, thus, a major contribution to the gas production and release into the water – on the other hand, shallow lakes also have lower gas efflux to the air from their open-water areas due to typically being more sheltered from the wind (Juutinen et al. 2009). Generally, high micro- and macrophyte production rate, small water volume, and high organic carbon content all promote the formation of anoxic hypolimnion and are related to increased concentrations and fluxes of methane (Juutinen et al. 2009). As already discussed in more detail in sections above, most of the methane produced in freshwater environments is typically oxidised by methanotrophic bacteria before it can reach the lake surface and be emitted to the atmosphere, and in turn, the biomass of these bacteria can supply zooplankton, macroinvertebrates and fish with energy and carbon (Bastviken et al. 2008, Sanseverino et al. 2012). However, based on the literature reviewed, it seems that even the small lakes are individuals in respect of the methane emissions and particularly their partitioning into the various transport paths, and, thus, drawing any quantitative conclusions in particular is challenging. Some further remarks can, nevertheless, be made as follows.

Ultimately, aquatic CH_4 emissions are driven by the methanogenesis, occurring mostly in anoxic sediments and controlled by redox conditions, organic matter supply and temperature. The temperature dependence of methane diffusion and ebullition is strongly modulated by system trophic status, indicating that the methane [production and thus also] effluxes are limited by the availability of the organic substrate in oligotrophic systems. Cross-system and seasonal changes in primary production and external carbon loading may strongly influence CH_4 production by stimulating anaerobic conditions and/or influencing the supply of organic matter. (DelSontro et al. 2016). Methane fluxes from lakes can vary over timescales in response to seasons, temperature, lake mixing events, atmospheric pressure variations, shifting winds, rainfall events, and diel cycles; in addition, spatial variability can occur both within lakes, for example, in terms of water depth or distance to stream inlets, and between lakes due to the variability in the lake characteristics (Natchimuthu et al. 2016).

The absence of a direct relationship between surface methane fluxes and temperature in lakes, thus, suggests that other factors intervene to either limit CH_4 production independently from temperature otherwise controlling the methanogenesis, or to decouple the methane production and emission. For the decoupling, methane oxidation in the water column is a key modulating factor, and this impact is likely stronger in lakes than in ponds because of their deeper and generally oxic water columns (DelSontro et al. 2016, p S73, and also the references therein). Even in large lakes, though, significant contributions from epilimnetic sediments (i.e. those above the metalimnion) may result in higher surface-water methane concentrations along the shore than in the central lake (Larmola et al. 2004 and Schmidt and Conrad 1993, cited in Bastviken et al. 2008, p 9; Natchimuthu et al. 2016, p S13, and references therein). Proportionally large contributions to the surface-water methane from epilimnetic sediments may occur also in the central-lake epilimnion due to rapid horizontal mixing (Bastviken et al. 2008). Also otherwise, due to this lateral mixing, methane in the surface water likely originates from other sediments than only those right below (Bastviken et al. 2008, Juutinen et al. 2009). Sometimes also horizontal concentration gradients can be observed, though, due to the methane inputs from littoral sediments, adjacent peatlands or incoming river, stream or spring waters (Bastviken et al. 2008, Larmola et al. 2004, Murase et al. 2005, Repo et al. 2007, and Schmidt and Conrad 1993, all cited in Juutinen et al. 2009, p 220; also, Natchimuthu et al. 2016, p S13, and references therein).

In many small lakes in Finland, methane storage during summer is comparable to that during the ice-covered season (Juutinen et al. 2009), and the storage can make significant part of the annual methane release particularly in the humic lakes (Kankaala et al. 2007, cited in Juutinen et al. 2009, p 219). However, ebullition may dominate the methane flux in many nutrient-rich and shallow lakes, and the vegetated and very shallow littoral areas may have much higher methane emissions than those from the pelagic zone (Bastviken et al. 2004, Bergström et al. 2007, Huttunen et al. 2003, Juutinen et al. 2003, Smith and Lewis 1992 and Walter et al. 2007, all cited in Juutinen et al. 2009, p 221).

The negative relationship between the methane concentration in the surface water layer and the lake area observed in some lakes may reflect a higher gas transfer velocity ('piston velocity') in larger lakes or, due to the larger volume and longer residence time, more extensive methane oxidation in the surface layer. The positive relationship to the anoxic volume fraction may indicate that a substantial proportion of the methane in the surface water comes from the storage flux, or that the efflux to the air is smaller in lakes with a high anoxic volume because of the low piston velocity characteristic to poorly mixed lakes. The input of the storage flux is often considered to be highly constrained by both methane oxidation and restricted diffusion across the thermocline. (Bastviken et al. 2003, cited in Bastviken et al. 2004, p 8). The negative relationship between the methane concentration and the DOC concentration may relate to the lakes rich in DOC generally developing a stable and shallow stratification, which then also results in a small volume of the mixed layer and consequently rapid loss of the surface-layer methane (Bastviken et al. 2004).

In a study on 207 lakes smaller than 100 km^2 all around Finland, it was found that 1) the methane concentration in the surface water is related to the depth or area of the lake and tends to be the highest in shallow lakes, 2) the methane concentrations and effluxes to the air are highest in nutrient-rich calcareous lakes, 3) the methane concentration in hypolimnion is correlated negatively with oxygen and positively with nitrogen concentration, and 4) the sum of the storage and diffusion fluxes is the highest in shallow, nutrient-rich, humic lakes (Juutinen et al. 2009). The observed negative correlation between area-to-depth ratio and methane concentration suggests that wind-driven water mixing can keep bottom water low in methane during the open-water season (Juutinen et al. 2009). Methane accumulation is likely also when there is a risk of oxygen deficiency, for example in deep, nutrient-rich and very humic lakes having strong stratification (Bastviken et al. 2004, Huttunen et al. 2002, Kankaala et al. 2007, and Riera et al. 1999, all cited in Juutinen et al. 2009, p 219).

Bastviken et al. (2008) studied methane budgets in three different lake habitats in Wisconsin, USA, and showed that most of the methane produced in deep sediments was oxidised (51–80 %) during the summer stratification. The remaining methane was preferably stored, and only a minute fraction of it was emitted from the deep sediments. However, the opposite relationship was found for shallow sediments (22–40 % oxidation) where the major proportion of methane was emitted to the atmosphere

(60–77 %). Emissions from the epilimnetic sediments made up 100 % of total lake emission during summer stratification, whereas during the autumn circulation they accounted for 14–76 % of the total during lake circulation (Bastviken et al. 2008). A study in Lake Rotsee, Switzerland, yielded in similar estimates, that is, 75 % of produced methane was oxidized within the lake and 25 % was emitted from the lake (Schubert et al. 2012).

5 Streams

Streams and rivers are, in a larger scale, unidirectional and linear (long and relatively narrow), and they form a divided and limitedly coupled network with the upstream reaches influencing more or less the reaches downstream. The stream channel and bed are usually morphologically unstable due to the shear of water and deposit of materials from the bank and suspended in the water. However, there is also reasonably continuous transport of dissolved and particulate matter from surrounding land areas downstream, and opposite flood-event return of matter from the stream on the banks particularly in the lower reaches. Characteristically, the different sub-systems within the stream or river are nested at several spatiotemporal intra-stream scales interacting with each other. (Giller and Malmqvist 1998).

The streams in the Forsmark area are small and many stream stretches are dry during summer. However, some streams close to the coastline carry water for most of the year and function as passages for migrating spawning fish. The vegetation abundance in the streams is heterogeneously distributed, varying between 0 and 100 % coverage of the streambed, but with frequent, and sometimes longer, parts with intense growth (75–100 % coverage). (Andersson 2010; SKB 2014, p 48, and references therein).

Streams, particularly headwaters, and their immediate surroundings are physio-graphically complex and spatially variable, often consisting of a 'step-stair continuum' of small waterfalls, riffles and pools. In contrast to less flowing lentic waters (e.g. lakes and ponds), turbulence is induced by streambed roughness, fluctuations in discharge, variable stream gradient, channel flow constriction and tortuous flow paths, among other factors. The incised nature of many stream channels tends to shelter them from the impact of wind on water surfaces. (Billett and Harvey 2013; also, Wallin et al. 2011, cited in Billett and Harvey 2013, p 166). Unlike in headwater streams, gas exchange and the parameters associated with direct measurements or indirect estimates of CH_4 and CO_2 effluxes are relatively well constrained in estuaries, lakes and large river systems. This is because large open water surfaces, in contrast to small streams, are relatively homogeneous and in many cases variables such as wind speed or models based on water surface turbulence can be used with confidence to predict the gas exchange. (Billett and Harvey 2013, p 166, and references therein). Apparently due to the turbulent conditions, only less than 2 % (Zaiss et al. 1982, cited in Le Mer and Roger 2001, p 31) of the methane produced in river sediments is estimated to be oxidised in the water column.

Peatland headwater streams in the UK were found consistently supersaturated with respect to gaseous carbon and are known to degas CH_4, as well as CO_2, directly to the atmosphere (Billett and Harvey 2013, p 165, and references therein). There were also strong spatial changes in the supersaturation degree along the drainage system, with degassing hotspots characterised by rapid downstream changes in the concentrations, frequently linked to more turbulent areas of the stream network or to upwelling zones (Billett and Harvey 2013, p 166, and references therein). Due to the common supersaturation and increased carbon input from the catchment, effluxes of both CH_4 and CO_2 from streamflow are likely high in the connection of high rainfall, associated also with turbulent flow (Billett et al. 2010, cited in Billett and Harvey 2013, p 165).

A two-year monitoring campaign of methane and carbon dioxide releases from streams in the mainly forested Skogaryd Research Catchment in southwest Sweden revealed disproportionately large emissions during high-discharge events from steep-slope reaches (including waterfalls) in general (Natchimuthu et al. 2017). The variability in both the methane and carbon dioxide emissions were related to the gas transfer velocities that were also usually higher than those in lakes due to the turbulence generated by the flowing water. However, the methane emissions were depending stronger from the methane concentration in the water in streams than in lakes. Spatial variability in the emissions can be explained, for example, by stream channel morphology, slope, flow velocity and inputs from the catchment and groundwater. Considerable temporal variability occurs with changes in the discharge, highlighted at snowmelt and rainstorm events. Photosynthesis and mineralisation processes play a role, as well, varying both in time and space. The gas concentrations represent a net balance between the emission rates off the stream and the input from terrestrial and aquatic sources upstream and along the stream network. (Natchimuthu et al. 2017, p 31, and references therein).

The gas transfer velocities (*k*, or ‘piston velocities’) depend on the diffusivity of the gas and the temperature influencing the viscosity of the water (both reflected in the Schmidt number). For comparison across temperatures and gases, gas transfer velocity normalised to a situation where the Schmidt number for CO_2 at 20 °C has the value of 600 (denoted with k_{600}) (Natchimuthu et al. 2017, p 2, and references therein). In the Skogaryd study mentioned above, k_{600} values of 0.2–560 m/d were estimated based on CO_2 measurements, and were in a multiple linear regression model strongly related to stream velocity and slope, the former further depending on both stream discharge and slope. As the gas transfer velocity is a proxy to the physical forces acting at the turbulent water–air interface, the pattern exhibited by this parameter is the same both for CO_2 and CH_4, even if the numerical values differ (based on this, the normalisation to k_{600} has been introduced to generalise the otherwise case-dependent data). The k_{600} values were very high for steep sections including small water falls, while the mean value excluding the high-turbulent reaches was only 6.5 m/d and the value modelled for the whole stream network 21.3 m/d. (Natchimuthu et al. 2017). Several models have been published to predict k_{600}, but they seem to substantially underestimate the high values possibly due to lack of data for the more turbulent conditions (Natchimuthu et al. 2017, p 6, and references therein).

In the stream water of the Skogaryd catchment, the methane concentrations were on average 1.7 µM with a standard deviation of 3.5 µM and range of 0.01–46 µM – that is, roughly 2–11000 times supersaturated relative to atmospheric levels. The methane emissions, then, had a mean of 8.8 mmol m^{-2} d^{-1}, with a range of 0.009–930 mmol m^{-2} d^{-1} covering both spatial and temporal variability. A large temporal variability was observed in the emissions of both methane and carbon dioxide. The ebullition flux was not representatively measured, so these methane emissions may be underestimates. (Natchimuthu et al. 2017). These methane concentrations were reasonably consistent with literature data ranging 0.002–49 µM as were also the methane emissions (0–60 mmol m^{-2} d^{-1}) especially when taking the differences in the study areas into account (Natchimuthu et al. 2017, p 7, and references therein).

In headwater streams draining peatlands in the UK (Billett and Harvey 2013), gas transfer coefficients (the gas transfer velocity divided by the average water depth) for both CH_4 and CO_2 were found to be positively related to discharge (although for the latter less so). They both also correlated negatively to the reach-length travel time, even though the respective efflux rates showed high variability in time and space. The median methane efflux rate was 0.22 µg C m^{-2} s^{-1} and the median methane concentration in the stream water was 8.1-fold supersaturated in respect of the air. However, in 37 % of the observations, methane fluxes from the air into the water were measured (as opposed to the more common effluxes from the water to the air), but this was very location-specific and may be explained by the local variability in the balance of methane production, consumption and storage dynamics (Billett and Harvey 2013).

6 Wetlands

English terminology related to mires, peatlands and in general wetlands tends to vary with the context (e.g. Joosten et al. 2017a, Päivänen and Hånell 2012). According to a reasonably well accepted set of definitions (Joosten and Clarke 2002, cited in Päivänen and Hånell 2012, p 17), a wetland is an area that is inundated or saturated by water relatively often and for long times enough to support vegetation adapted for living in saturated soil conditions and this includes both peatlands and mineral-soil sites. A peatland, then, is "an area with or without vegetation with a naturally accumulated peat layer at the surface", peat meaning "sedentarily accumulated material of at least 30 % (dry mass) of dead organic material". A mire is "a peatland where peat is currently being formed", whereas the Finnish term 'suo' refers, in this classification, to a wetland with or without peat-forming vegetation. (Joosten and Clarke 2002, cited in Päivänen and Hånell 2012, p 17). It is to be noted that the Swedish term 'myr' refers to treeless or sparsely forested mire, and 'torvmark' and 'våt fastmark' comprise the peatlands with a thicker or thinner peat layer, respectively, among a few other potentially applicable terms (Päivänen and Hånell 2012, pp 15–16). According to definition used in the national wetlands inventory (Gunnarsson and Löfroth 2009), the Swedish wetland ('våtmark') is land with the groundwater table above or near the ground surface, or vegetation-covered water areas, with at least half of the vegetation being hydrophilic (Löfroth 1991). This is also more or less used by SKB to identify the 'mires' in biosphere assessments. However, since the epilittoral areas of lakes have already been addressed above in Chapter 4, the focus of this chapter is on other wetland types. Whilst the interest in this review, and subsequently the discussion that follows, is focused, on peatlands, most of the material in this chapter is relevant also to other types of wetlands. This includes also wetlands associable with the ecosystem types addressed in the earlier chapters (e.g. drained peatland fields may still be considered wetlands, and many littoral areas of lakes could be classified also as mires). For simplicity, 'mire' has been used here as a collective name for different kinds of wetlands, and the other terms have been complementarily used as seen appropriate.

6.1 General characteristics

Peatlands comprise many different ecosystems with and without a tree and/or moss layer (Rydin and Jeglum 2006, cited in Limpens et al. 2008, p 1476), but basically they are wetlands with an organic soil layer of at least 30 cm, which may extend to a depth of 15–20 m, a mean peat thickness of 1.3–2.3 m being characteristic for northern peatlands (Clymo et al. 1998 and Turunen et al. 2002, both cited in Limpens et al. 2008, p 1475). In general, peat formation requires a surplus of water (positive water balance), absence or very low activity of organisms that are responsible for decomposition, and low or intermediate temperatures hampering the speed of most chemical and biological processes; such typically anoxic conditions make peatlands accumulators, buffers, transformers and filters for nutrients and water and are therefore considerable sinks of matter in the landscape (Nykänen et al. 1995).

There is a large variation in peatland and mire ecosystems, but there are also some unifying characteristics that apply across the types, although *Sphagnum*-dominated ones are clearly the most studied (Limpens et al. 2008, pp 1476–1477, and references therein):

- The redox potential, largely governed by the position of the water table, is decisive for many biogeochemical processes that exhibit a strongly vertically structured environment;
- The upper peat layer (about 5–40 cm) is unsaturated with water, has oxic conditions during the growing season and supports most biological activity, whereas the layer below is waterlogged and anoxic;
- The relative importance of root respiration in respect of heterotrophic respiration decreases with depth, and for example fine roots of shrubs are restricted to the upper zone that is at least intermittently unsaturated and oxic;
- The oxic–anoxic boundary shifts as a result of water table fluctuations;

- Litter degradability decreases with depth, as the ongoing decomposition produces increasingly decomposed and recalcitrant litter residues, but non-uniformly so since litter input also occurs further down in the form of dead roots, root exudates and litter leachates;
- The transport of gases and solutes slows with depth due to the decrease in diffusion coefficients in and hydraulic conductivity of the peat with increasing water saturation and compaction;
- The concentrations of electron acceptors, in particular oxygen, decrease with depth (i.e. distance from their atmospheric source) and deplete rapidly in the saturated zone, this transition being particularly sharp after longer drought periods.

Peatlands can be hydrologically and nutrient-wise classified in two main types: bogs (ombrotrophic peat soils) and fens (minerotrophic peat soils). Bogs are fed entirely by rainwater and atmospheric deposition and are usually less nutrient-rich compared to fens that receive groundwater and surface water and nutrients from surrounding areas (e.g. Joosten et al. 2017a, b; Vitt 2006, cited in Korrensalo 2017, p 7, Päivänen and Hånell 2012). Transition mires (ombro–minerotrophic peat soils) lie in between. Within the main types different subtypes of peatland are also recognized, including kettle hole mires, sloping mires, and spring water mires (e.g. Joosten et al. 2017a, b).

Bogs have lower nutrient and cation levels, particularly Ca, and lower pH than fens (Laine et al. 2000, cited in Juottonen 2008, p 4). Vegetation of northern bogs is characterised by *Sphagnum* mosses, which further acidify their surroundings, whereas fens typically have higher coverage of grass-like plants such as sedges (*Carex* spp.) with root systems largely in the anoxic peat (Päivänen and Hånell 2012, Rydin and Jeglum 2006, and many others). As an adaptation to anoxia, sedges and other typical mire vascular plants have aerenchyma, intercellular spaces which form a gas conduit and allow transport of oxygen into roots (Armstrong et al. 1991 and Koncalova 1990, both cited in Juottonen 2008, p 4; also, cf. Sections 4.4.2 and 6.4.3).

In the Forsmark region, characteristics of the wetland ecosystems vary systematically with the age of the area since the wetland formation, which is roughly proportional to the distance from the sea. The wetland areas associated with newly isolated shallow lakes are dominated by dense reed belts (*Phragmites australis*), which successively expand from the shores into the central parts of the lakes. Eventually, the reeds are replaced by vegetation communities dominated by *Bryales* and *Carex* species, forming the rich fens that are characteristic of Northern Uppland. The pH and contents of nutrients are relatively high in fen peat, which makes them suitable for cultivation after drainage. As the peat layer thickens with time, the influence of calcite-enriched groundwater diminishes. The rich-fen vegetation is replaced by poor-fen communities dominated by *Sphagnum* species. Once a raised bog has developed thereafter, the primary production on the bog plateau will be fed by rain and the connections to the groundwater table will be limited or even non-existent. (Löfgren 2010; SKB 2014, p 49, and references therein).

The link with the groundwater-mediated releases from a geological repository to the surface ecosystem depends on, and changes with, the mire succession (see also Section 6.1.1). In littoral and overgrown areas of ponds and lakes, there is a strong link also with the aquatic system and there, as well as in minerotrophic mires with a thin peat layer (fen), the releases are readily available for the biological circulation. With the development towards an ombrotrophic bog the link, in the broader picture, weakens but accumulation of the released radionuclides in deeper peat layers and their potential re-release due to subsequent change in environmental conditions (e.g. due to drainage for agriculture or forestry, which also compacts the peat deposit) becomes more important (Aro et al. 2017, Ikonen et al. 2015). Even in areas with thick peat layers, surface pools of open water can decrease the transport distance from the bedrock to the biological circulation, and cracks and pipes in the peat layer may provide preferential transport paths (Aro et al. 2017; Limpens et al. 2008, pp 1480–1481, and references therein).

6.1.1 Mire formation and succession (host processes and temporal scales)

Mires are formed through three main mechanisms. *Primary peatland* formation refers to the land surface becoming occupied by peat-forming vegetation (e.g. sedges, *Sphagnum* mosses) immediately after the retreat of water or glacial ice. In *paludification*, peat-forming vegetation replaces the original one on mineral soils due to increased wetness resulting from, for example, influence of a nearby mire, changes in surrounding water systems or climate change. *Terrestrialisation*, in turn, refers to a water body becoming overgrown by vegetation, often helped by sedimentation. With time, the peat layer grows in thickness due to the production exceeding the decay, and usually the mire also expands laterally. (E.g. Aro et al. 2017, Päivänen and Hånell 2012).

As told by Clymo and Bryant (2008, pp 2054–2055), Clymo and Pearce (1995, pp 249–250) and many others, the story of a peatland proper starts, regardless of the formation mode, with carbon being added by photosynthesis to the living plants growing on the surface of a peatland and through senescence getting deposited on the ground as litter that partly decomposes and the residual forms peat. Due to the much slower decomposition of mosses, they soon dominate the peat deposit. With the mosses, the new growth shades the older below which then withers and begins to decay mainly through the actions of fungi and bacteria. This decay is mostly aerobic (and, thus, produces mainly CO_2) since, though surprisingly opaque, the moss canopy is very porous to gases and water (Clymo and Bryant 2008, Clymo and Hayward 1982, Clymo and Pearce 1995, Hayward and Clymo 1982, 1983). Eventually the increasing load of the new growth from above and the much heavier water retained by it causes the moss structure to collapse. This reduces the space between the litter particles, as well as decreases the hydraulic conductivity, forcing the rain carrying the DOC leached from the upper layers to flow sideways off the peatland along this interface. Also, the diffusion rate of gases greatly decreases from that in the air, and the microorganisms just below the water table use up the oxygen faster than it is replenished from the air, turning conditions anoxic. Slightly deeper in the peat, anaerobic bacteria take over the production. However, the high anaerobic decay rate prevailing at a few centimetres below the water table decreases with depth without the decay ceasing even farther below, though. The hydraulic conductivity at the surface is sufficiently high so that the water table usually oscillates by only a few centimetres, but in long dry periods temporarily sinks some tens of centimetres into the usually anoxic peat. On the other hand, the excess water, for example during heavy rains, easily flows laterally in the much more conductive surface layer. All this combined keeps the peat proper practically permanently waterlogged. (Clymo and Bryant 2008, Clymo and Pearce 1995; also, cf. Figure 6-1).

Already a while ago Ivanov (1953, cited in Ingram 1978, p 225), introduced a two-layered system (the diplotelmic system) as a concept for understanding of the hydrological functioning and the peat development of raised bogs. Ingram (1978) named the two layers of this classification system *acrotelm* (the 'top peat') and *catotelm* (the waterlogged 'bottom peat'). These two horizons are often described as oxidation and reduction horizons (e.g. Clymo and Bryant 2008). The acrotelm has a relatively high hydraulic conductivity, a fluctuating water table and a relatively high rate of carbon turnover, whereas the catotelm is constantly saturated, has a low hydraulic conductivity, no access to atmospheric oxygen and a very slow carbon turnover rate (e.g. Clymo 1984, Clymo and Williams 2012, Holden and Burt 2003, Päivänen and Hånell 2012, Rydin and Jeglum 2006). The acrotelm is typically about 5–60 cm thick, but in some applications it may be useful to sub-divide into the predominantly oxic acrotelm proper or 'oxytelm' (maybe down to 20 cm) and the usually anoxic but periodically oxic *mesotelm* below it; this 'middle layer' is the subzone in which the anoxic decay, and also methanogenesis, is relatively fast (Clymo and Bryant 2008, Clymo and Pearce 1995, Clymo and Williams 2012).

The above put together, it is useful to recognize four structural layers, and four process zones which move up and down over days and years across these layers (Figure 6-1). The *green moss layer* and the euphotic (i.e. 'sunlit') zone coincide for most of the time, but the aerobic and transitional zones follow the water table down during the summer, and somewhat reduce the much more extensive anaerobic zone beneath (Clymo and Bryant 2008, Clymo and Pearce 1995, Clymo and Williams 2012). This is underlaid by the *litter-peat layer* and the *collapse-peat layer*. These three topmost functional layers are the most active, but the *peat proper* is not inactive either (cf., e.g., Section 6.2), even though often called such (Clymo and Pearce 1995). In the figure, the interface between acrotelm and catotelm can be found in the upper part of peat proper based on defining the acrotelm as the depth to which the water table sinks in a dry year (Ingram 1978, cited in Clymo and Williams 2012, p 1), but the actual local relationship between the structural layers and the process zones varies both laterally and in time. Thus, this conceptual figure rather identifies 'acrotelm proper' and 'catotelm proper', leaving room for the mesotelm in between.

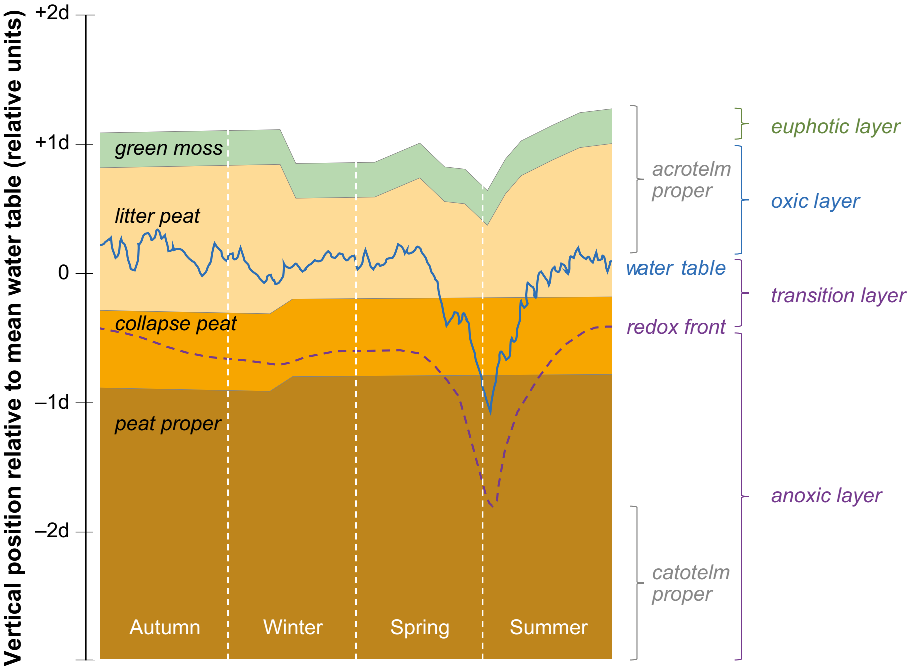

Figure 6-1. *Schematic illustration of structural layers (solid colours) and process zones (at the right) in the surface of a peatland over an annual cycle (time from left to right); the irregular blue line shows a stylised example of water table variation – the process zones (rightmost labels) move up and down following the changes in the groundwater table, as represented by the change in the position of the redox front (purple dashed line) (figure adapted from Clymo and Pearce 1995, p 251).*

In Finland and Sweden, areas with past retreating ice sheets and the still ongoing post-glacial land uplift exhibit a natural development series from minerotrophic to ombrotrophic mires. A typical sequence in the series can be characterised as a trajectory from coastal meadows and swampy fens to minerotrophic and ombrotrophic fens and spruce mires, and further through *Eriophorum*-dominated pine bogs to raised bogs as the peat thickness increases with the mire age (e.g. Aario 1932, Korhola and Tolonen 1996, Sohlenius et al. 2013, Tuittila et al. 2012). As implied above, this sequence considers rather the central areas of the mire – at the same time the mire tends to expand through paludification and develop the typical lagg and marginal slope areas around the central plateau (e.g. Päivänen and Hånell 2012, pp 30–31), and the areas further away from the central mass follow the succession sequence later, paced by the lateral expansion. The peat thickness increment is typically in the order of 0.2–4 mm y^{-1} (e.g. Korhola and Tolonen 1996, Mäkilä et al. 2013), although when considering the rate over the whole age of the peat, the peat increment in the Uppland region in Sweden is 0.5–1 mm y^{-1} (Sohlenius et al. 2013) and in Finland the highest values are in the order of 0.8 mm y^{-1} (Mäkilä et al. 2013). As the peat thickness as such, also the long-term rate of carbon accumulation in peatlands increases towards the south and is higher in younger than older mires (e.g. Korhola et al. 1995, Korhola and Tolonen 1996, Mäkilä and Goslar 2008, Päivänen and Hånell 2012, Sohlenius et al. 2013, Turunen and Tolonen 1996). Thus, carbon accumulation rates in fens (typically younger mires) tend to be higher than in bogs (older ones). Also, the accumulation rates in general are higher in fens without tree cover and in pine fens than in spruce–birch–alder fens (Turunen and Tolonen 1996); the peat accumulation rate may slow down with oligotrophy, but somewhat increase again after the bog stage has been established (Korhola et al. 1995 and Mäkilä et al. 2001, cited in Tuittila et al. 2012). On a costal transect in Finland, it was observed to take about 3 000 years for a wetland to develop from a reed stand on the seashore into a bog with about two metres of peat, or, 2 500–3 000 years for the bog vegetation to become dominant over the vegetation typical for fens (Tuittila et al. 2012).

6.1.2 Mire microforms (spatial variability)

Boreal bogs are peatland ecosystems that are often characterised by an uneven surface topography (heterogeneous on a scale of about 10 m) intimately linked with the water table and the plant communities that further link to whether there are plants facilitating aerenchymal transport or not (cf. Sections 4.4.2 and 6.4.3). They vary from hummocks rising up to 10–50 cm above the mean water table to intermediate lawn surfaces and hollows which in winter contain standing water but in summer have the water table just below their surface, and pools which permanently contain standing water (Clymo and Pearce 1995, Korrensalo 2017, Laine et al. 2009, Rydin and Jeglum 2013). The surface pattern typical to the bog state emerges as a result of self-organising processes, and these micro-topographic variations increase resilience towards environmental perturbations both through the diversity of plant species and communities they support and through variation in physical properties between microforms, although being also capable of rapid transformation to another stable state at a higher level of perturbation (Belyea and Baird 2006, Dise 2009, Heijmans et al. 2013, and Turetsky et al. 2012, all cited in Korrensalo 2017, p 27).

Even though homogeneous plant communities with comparable leaf area are known to function similarly in the ecohydrological sense, they may have different photosynthetic and respiration rates and relationships with and sensitivity on environmental variables, and thus also differ in important characteristics to the carbon cycling such as productivity, litter decomposability and association with fungi; in addition, there are many related vegetation–biogeochemistry feedbacks (Riutta et al. 2007a, b, and Williams et al. 2006, both cited in Laine et al. 2009, p 2647; Limpens et al. 2008, p 1479, and references therein):

- There is a general trade-off between *Sphagnum* species inhabiting hummocks contra those in hollows, with lower decomposability among the former, and higher productivity with the latter;
- *Sphagnum* species growing in ombrotrophic conditions are usually low in decomposability compared with most of the co-inhabiting vascular plants;
- Different plants produce peat with different structure and hydraulic conductivity, and these features in turn affect the redox status and other physico-chemical conditions;
- Plants differ in the production rate and degradability of their root exudates;
- Sedge or other grass-like plants increase methane emission through aerenchymatic tissues (see Section 6.4.3).

Both photosynthesis and respiration are dependent on the seasonally varying temperature, moisture and light conditions, as well as the amount of leaf area (Korrensalo 2017). The seasonal changes in respiration are controlled by the water table fluctuations (Fenner and Freeman 2001, cited in Korrensalo 2017, p 9) and ambient temperature (Lafleur et al. 2005, cited in Korrensalo 2017, p 9), which differ in their relative importance in dry and wet community types (Maanavilja et al. 2011, cited in Korrensalo 2017, p 9). In addition to the seasonal variability, there are also interannual changes in the conditions and in the varying responses of the plant communities (e.g. Bubier et al. 2003b, cited in Korrensalo 2017, p 9), but the seasonal timing and magnitude of changes in these environmental conditions have been found important controls also for the longer-term variation in the carbon sink (Lund et al. 2012 and Waddington and Roulet 2000, both cited in Korrensalo 2017, p 9).

As indicated above, *Sphagnum* mosses, a genus dominating boreal bog ground layer, is in a key role in shaping the surface formations by creating acidic, nutrient-poor environment of slow decomposition, which is unfavourable for many other plant species (van Breemen 1995 and Verhoeven and Liefveld 1997, cited in Korrensalo 2017, p 8). The mosses form a continuum of species along the moisture gradient according to their wetness/drought tolerance (Hayward and Clymo 1982 and Rydin 1993, cited in Korrensalo 2017, p 25; also, Korrensalo 2017, p 8, and references therein). For example, species living on hummocks have higher capillarity, they are better able to retain water and they have higher biomass per area and productivity in such nutrient-poor conditions than species dominating on hollows, allowing the hummocks to rise above the mean water table – this is contrasted by hollow-dwelling species that are more productive in terms of biomass increment and photosynthesis rate, but limited to the wet and relatively nutrient-rich surfaces due to their lower-drought resistance. The structural tissues of *Sphagnum* species on lawns are stimulated by CO_2 originating from the decomposition below, which allows them to rise above hollow species and outcompete them. These habitats created by the mosses are also favoured by different composition of vascular plant species. Dry hummocks have an aerobic layer thick enough for the roots of dwarf shrubs, which on their part have higher water potential and photosynthesis in drought conditions, and sedges have a lower drought tolerance, but also aerenchymatic tissue that allow them to transport oxygen to their roots in the wet hollow conditions.

6.1.3 Carbon in mires

As outlined above in Section 6.1.1, part of the organic matter produced by the plants accumulates and forms peat in anaerobic layers due to the incompleteness of the decay in such conditions; "the peat accumulates under the living mire plants not because of high net primary productivity but rather a slow decomposition rate" (Päivänen and Hånell 2012, p 44). Also, particularly the *Sphagnum* mosses have been found associated with microbial communities that can alleviate the nitrogen limitation through fixation of the atmospheric nitrogen; these microbes work through phototrophic, heterotrophic and methanotrophic pathways (Auman et al. 2001, Basilier et al. 1978, Bodelier and Laanbroek 2004, Davis et al. 1964, Larmola et al. 2010, and Raghoebarsing et al. 2005, all six cited in Larmola et al. 2014, pp 734–735). An important factor in the decay is how long the organic matter stays in the oxic surface layer before the raising redox front reaches and engulfs it into the anoxic catotelm. However, as a rule of thumb, 5–20 % of the primary production of mires is already initially deposited in catotelm. (Päivänen and Hånell 2012).

As the burial of organic matter implies, peatlands act as persistent sinks for atmospheric carbon, that is, their carbon uptake is greater than total carbon losses, depicted by positive net ecosystem exchange (NEE) and accumulation of the peat (Päivänen and Hånell 2012, Rydin and Jeglum 2013; also, Yu 2012 cited in Korrensalo 2017, p 7). However, the carbon uptake can be altered or even turned into net release through variations in temperature, moisture and light conditions (Alm et al. 1999, Lund et al. 2012, Nijp et al. 2015, and Waddington and Roulet 2000, all cited in Korrensalo 2017, p 9). However, peatlands are, almost as a rule, net emitters of methane originating from the final end of the degradation of the soil organic matter (e.g. the review by Hoch et al. 2014). Temporal and spatial methane efflux to the atmosphere is by several orders of magnitude more variable than that of CO_2, cumulative annual sum of which seems, in turn, to be affected more by broad-scale geographic location and physical setting than internal factors of a mire (Limpens et al. 2008).

Dissolved organic carbon (DOC) compounds that consists of leachates, exudates from roots and recent photosynthates, and are very labile, may be transported to wet depressions, increasing soil microbial respiration (Boddy et al. 2007, cited in Biasi et al. 2014, p 123). About 40–70 % of this carbon is relatively quickly released back to the atmosphere as CO_2 that is produced in plant root and shoot respiration (Gifford 2003 and Litton et al. 2007, both cited in Korrensalo 2017, p 7). Above the water table, oxygen-demanding microbes decompose dead plant material aerobically and produce CO_2. Below the water table, anoxic conditions prevail, and CH_4 is produced by anaerobic decomposers much in the same way as in lake and stream bottom sediments (Chapters 4 and 5). As a result, most of the carbon in soil organic matter is released back to the atmosphere as CO_2 and CH_4. Part of the DOC becomes laterally exported with the runoff to streams. The rest, up to 15 % of the original primary production, remains undecomposed and becomes peat (Clymo 1984; Francez and Vasander 1995 and Gorham 1991, both cited in Korrensalo 2017, p 7). Of the carbon assimilated by *Sphagnum* mosses, up to 26 % may originate from the methane production, particularly where submerged (Larmola et al. 2014; Larmola et al. 2010 and Raghoebarsing et al. 2005, both cited in Larmola et al. 2014, p 736). Water table fluctuations control the spatial variability of the carbon sink and the proportions of carbon released as CO_2 or CH_4 (Rydin and Jeglum 2013 and Updegraff et al. 2001, both cited in Korrensalo 2017, pp 7, 25). The lower the water table, the larger proportion of the readily decomposable fresh plant litter is decomposed in aerobic conditions (Korrensalo 2017) and the higher the proportion of CO_2 of the total carbon efflux. The average water table at a distinct location determines, on the other hand, habitats for different plant functional types (Rydin and Jeglum 2013, cited in Korrensalo 2017, p 25). In turn, the plant species composition has an effect on both autotrophic and heterotrophic parts of the carbon cycle through the differences in photosynthesis rate and litter quality across the plants (Bubier et al. 2003a, Riutta et al. 2007a, b, and Williams et al. 2006, all four cited in Laine et al. 2009, p 2647; Leppälä et al. 2008 and Straková et al. 2011, both cited in Korrensalo 2017, p 7). 'Plant functional groups' can be identified based on the similarities in these respects (e.g. Chapin et al. 1996 and Frolking et al. 2010, both cited in Korrensalo 2017, pp 7–8).

Since plant biomass usually decreases from the dry end of the wetness gradient towards the hollows (Korrensalo 2017; also, Moore et al. 2002 and Vasander 1982, both cited in Korrensalo 2017, p 8), also autotrophic respiration can be expected to follow the same pattern. Although the litter formed in the dry plant communities is more resistant to decomposition (Straková et al. 2011 and Turetsky et al. 2008, both cited in Korrensalo 2017, pp 8–9), heterotrophic respiration is stimulated by a thicker aerobic layer (Silvola et al. 1996, cited in Korrensalo 2017, p 9), and the decomposition of the less recalcitrant litter of hollow species is hindered by high water table (Bengtsson et al. 2016, cited in Korrensalo 2017, p 9). As a result, also the total respiration has been found to be higher in hummocks (Alm et al. 1999, Laine et al. 2006, 2007a, and Strack et al. 2006, all cited in Korrensalo 2017, p 9). However, there are also important differences in vegetation structure among studied bog sites apparently breaking the rule; almost solely dwarf-shrub-dominated, generally drier bog sites (Moore et al. 2002, cited in Korrensalo 2017, p 9) are likely to function in a different way than wetter sites having also a substantial proportion of sedge-covered areas (Laine et al. 2007a, cited in Korrensalo 2017, p 9). However, if the respiration and the photosynthesis have a rather symmetrical relationship to the water table, it can result in spatially even net ecosystem exchange (Korrensalo 2017; also, Bubier et al. 1998, cited in Korrensalo 2017, p 25).

The dominant pathways of water movement, also carrying the dissolved and particulate carbon, in most ombrotrophic peatlands are the near-surface flow through the upper peat layers and the saturation-excess overland flow. Matrix flow in deeper peat layers is severely limited. However, large preferential pathways may exist forming considerable conduits (called macro-pores or pipes, depending on the diameter) for the water and carbon flow. They may even explain some of the additional degassing from bog pools that does not seem to be accounted for by pool size alone; many pools drained for examination have been found to have a natural pipe channel. (Limpens et al. 2008, pp 1480–1481, and references therein). Natural pipes, which make an important contribution to streamflow at least in many peatlands in the UK, also transport significant amounts of CO_2 and CH_4 to the stream system (Dinsmore et al. 2011, cited in Billett and Harvey 2013, p 165).

6.2 Methane production

As outlined above, it is typical of a peatland to host two main layers in respect of the methane cycle: an anoxic subsurface zone with CH_4 production by methanogens and an aerobic superficial zone of CH_4 oxidation by methanotrophs (e.g. Whalen 2005). The base of the mesotelm (the 'transition zone') is a major site of anoxic decomposition (Belyea 1996, cited in Clymo and Williams 2012, p 8) and methane production (Clymo and Williams 2012, Eriksson et al. 2010, Kettunen et al. 1999, Segers 1998, Sundh et al. 1994). The main locus of methane production in peatlands is a relatively thin layer below the water table (Figure 6-2), but the concentrations of CO_2 and CH_4 increase with depth in the peat, suggesting that there is continued gas production (decay) in deep peat as well (Clymo and Bryant 2008). The largest CH_4 production potentials are generally measured from a few centimetres to 20 cm below the water level, and production declines in deeper, more decomposed peat (Clymo and Bryant 2008, Eriksson et al. 2010, Sundh et al. 1994; Edwards et al. 1998, Krumholz et al. 1995, Saarnio et al. 1997, Williams and Crawford 1984, all four cited in Juottonen 2008, p 6). Unlike in the catotelm, in the periodically oxic mesotelm, sulphate reduction is rapid, and this competes strongly with methanogenesis and may be as, or more, important than methanogenesis in converting carbon to gaseous forms (Watson and Nedwell 1998 and Vile et al. 2003, cited in Clymo and Bryant 2008, p 2058).

Somewhat differently from freshwater environments favouring acetate as a precursor of methane (cf. Section 4.3), either hydrogenotrophic or acetotrophic methanogenesis may dominate in mires. In addition, in permafrost conditions, stimulation of CH_4 production by methanol may imply potential for the methylotrophic pathway. (Ganzert et al. 2007, Kotsyurbenko et al. 2004, Lansdown et al. 1992, and Metje and Frenzel 2005, 2007, all cited in Juottonen 2008, p 6). However, typically, acetotrophic methanogenesis is associated to the upper peat layers with abundant labile organic carbon, whereas and H_2- and CO_2-dependent methanogenesis predominates in the more recalcitrant deeper peat layers (Hornibrook et al. 1997). Keller and Bridgham (2007), as well as Juottonen (2008, p 6, supported by several references therein), linked variation in the importance of acetotrophic methanogenesis during the growing season to the presence of root exudates, and reported that the acetotrophic pathway dominates methane productions in fens. A similar relationship was reported by Galand et al. (2010), whereas hydrogenotrophic methanogenesis has been reported to be the dominant pathway in bogs (Duddleston et al. 2002, Horn et al. 2003). That is, the pathway of methanogenesis has been observed to shift from acetotrophic in surface peat, rhizosphere, and *Carex* fens to hydrogenotrophic in more oligotrophic deeper peat and *Sphagnum*-dominated bogs. Also, seasonal fluctuations are, fittingly, more typical to the acetotrophic production (Juottonen 2008, p 6, and references therein).

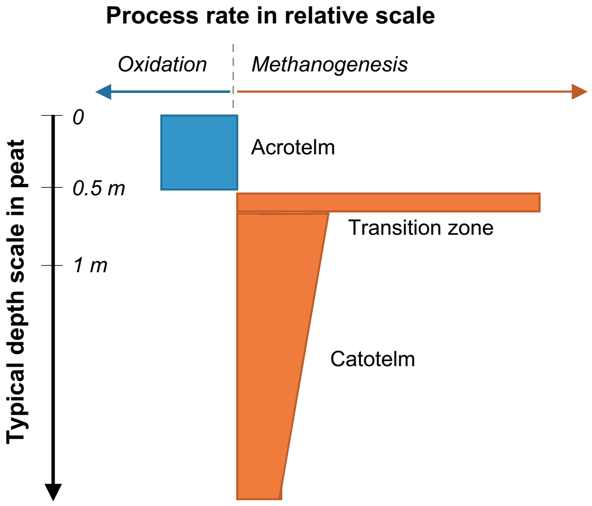

***Figure 6-2.** Schematic presentation of methane production and oxidation rates in mires (adapted from Clymo and Pearce 1995, p 257). The transition zone is sometimes associated to the mesotelm layer, conceptualised to lie between the catotelm and the acrotelm proper (Clymo and Bryant 2008).*

Methanogen communities generally change with peat depth, and shifts related to vegetation have also been reported, and intra- and inter-seasonal patterns have been demonstrated for mires (Juottonen 2008, p 11, and references therein). Bacterial communities in anoxic peat have received much less attention than those in the oxic surface layers, despite their role in carbon cycling as substrate producers to and competitors of methanogens. Based on the few molecular studies available, bacteria associated to anoxic (or most likely anoxic) peat mainly belong to *Alphaproteobacteria*, *Acidobacteria*, *Planctomycetes*, *Verrucomicrobia*, *Deltaproteobacteria*, *Actinobacteria*, *Planctomycetes*, *Firmicutes* and *Chloroflexi* (Juottonen 2008, p 16, and references therein). However, methanogens and methanogenic potential have been detected also in unsaturated peat and soils, suggesting methanogens tolerate temporary aeration (Juottonen 2008, pp 6–7, and references therein).

In the thesis of Juottonen (2008), methanogens and methane production were assessed along spatial and temporal gradients in three boreal mires in Finland. Methanogen communities and methane production changed markedly along an eco-hydrological gradient from fen to bog, with changing vegetation and pH. The most acidic *Sphagnum* bog showed mainly *Methanomicrobiales*-associated hydrogenotrophic methanogens, whereas the oligotrophic and mesotrophic fens with higher pH and sedge coverage had more diverse communities including also acetotrophic methanogens. (Juottonen 2008). Active methanogens were detected also in winter, unlike in other studies including wintertime measurements (Avery et al. 1999 and Yavitt et al. 1987, both cited in Juottonen 2008, p 29). Interestingly, the detected phyla did not markedly differ from those commonly observed in mineral soils (Juottonen 2008).

In a peat bog in southwestern Finland (Tsitko et al. 2014), bacterial communities were found to divide the deposit into five distinct strata: the *Sphagnum* layer, 0.5–3.7, 3.7–4.0 and 5.5–6.0 m deep peat layers, and the clay subsoil. The surface was dominated by *Acidobacteria* and *Alpha*- and *Betaproteobacteria*, and in the peat *Acidobacteria* consisted up to 85 % of the community with a contribution decreasing with depth in particularly in favour of *Chloroflexi* reaching their maximum contribution of nearly 35 % in the second-deepest peat layer. However, most of the taxonomic groups belonged to uncultured bacteria with unknown physiological role. Throughout the peat layer, many aerobic methanotrophs were identified, which might employ alternative metabolic routes for oxidising methane or use completely different lifestyles under anaerobic conditions; relative abundance of genes associated with methane metabolism was found fairly constant throughout the full vertical profile. (Tsitko et al. 2014).

The rate of methane production in peat is controlled by peat and substrate quality, temperature and pH (Raivonen et al. 2017, p 4667, and references therein). Also, other microbes are essential for the regulation of methanogenic activity as they often act as substrate producers to and competitors of the methanogens, and the methanogenesis is mainly limited by the substrate supply. This is ultimately regulated by the plant primary production through the input of organic matter, as carbon from fresh litter or root exudates has been shown to support the CH_4 production; this fresh organic matter has higher amount of labile carbohydrates readily available to decomposers, opposed to older material rich in recalcitrant compounds (e.g. lignin and humic substances). Also, if the groundwater level is close to the surface, organic matter reaches water-saturated peat virtually undecomposed. When the level is lower, the labile compounds are degraded more extensively in the then thicker layer of aerobic peat and become less available for methanogens. (Juottonen 2008, p 7, and references therein; Le Mer and Roger 2001; Moore and Dalva 1993, cited in Le Mer and Roger 2001, p 33; Raivonen et al. 2017, p 4666, and references therein). However, vascular plants such as *Carex* and *Eriophorum* species allocate labile carbon directly into the water-saturated layer as root exudates (Joabsson et al. 1999, cited in Juottonen 2008, p 7; also, see Section 4.4.2). The type of vegetation also influences the litter chemistry and decomposability (Juottonen 2008). Methane emissions to the air, in turn, are favoured by high peat decomposition rates (typical to warm and poorly decomposed peat), local anoxia, availability of substrates from roots, and rapid transport to the surface by ebullition and plant-mediated transport (Sections 6.4.2 and 6.4.3) (Limpens et al. 2008, p 1478, and references therein).

Methane production is also strongly dependent on temperature and usually temperature-limited in northern mires, with maximal production at 20–35 °C. Incubation of acidic peat (pH 4–5) at elevated pH has led to higher production with maximal production at pH 6–7, suggesting that also pH limits methanogenic activity in peat. Exceptions are known where higher pH had no effect or even inhibited CH_4 production. If alternative electron acceptors are present, methanogens compete for substrates, particularly H_2, with other terminal decomposers. For example, sulphate reduction due to airborne sulphate deposition may decrease CH_4 production. When the available electron acceptor is CO_2, hydrogenotrophic methanogens compete with acetogens. In some northern mires, an acetate-accumulating terminal process has been observed in connection to low CH_4 production levels. Although acetogenesis from H_2 and CO_2 occurs in cold soils and sediments, no direct evidence exists of its occurrence in peat and it has even been calculated to be thermodynamically unfavourable in peat. (Juottonen 2008, p 7, and references therein).

Also, other couplings between C, N, Fe, and S transformations play a role. Organic matter decomposition and methanogenesis are potentially influenced by the effects of extracellular enzyme activity and by the accumulation of decomposition products due to the slowness of transport processes in water saturated peat. The electron transfer processes that finally lead to, or influence, CO_2, CH_4 and DOC fluxes are almost exclusively microbially mediated and require the exo-enzymatic cleavage of complex litter and soil organic matter molecules, with phenol oxidase enzymes in a particularly important role. Recent studies also suggest that the impact of water saturation, anaerobia and associated accumulation of decomposition products can result in a near shut down of hetero- and autotrophic respiration deeper into the saturated zone of ombrotrophic peat soils where oxygen transport is impeded, likely leading to spatiotemporally variable mosaic of oxic and anoxic microenvironments with variable respiration rates and pathways. In the saturated zone, the heterotrophic respiration seems also to rely on the removal of organic matter decomposition products. Linking respiration to peatland hydrology, the water residence time, or the time that a certain volume of soil is occupied by the same body of water, may, thus, offer a promising concept. (Limpens et al. 2008, p 1478, and references therein).

In fens, the higher abundance of vascular plants, such as sedges, entails allocation of labile carbon as root exudates to the methanogenic layer and possible facilitation of the obligate and potential acetotrophic methanogens, supported by observations from a fen with pH similar to bogs (Juottonen 2008). Compared to relatively homogenous bog peat, the root system in fens creates a more heterogeneous environment. Root exudates have been shown to support CH_4 production from acetate (Ström et al. 2003, cited in Juottonen 2008, p 29). Accordingly, the oligotrophic and mesotrophic Lakkasuo fen had higher CH_4 production potential and more diverse methanogen communities including also acetotrophic *Methanosarcinales*. The mesotrophic fen has also exhibited a higher fraction of acetotrophic methanogenesis than the bog. In a chrono-sequence of mires of Finnish land-uplift coast (Merilä et al. 2006, cited in Juottonen 2008, p 29), methanogen communities of younger fens differed from a site representing a fen–bog transition stage that was reflected in both pH and vegetation. However, different communities in *Eriophorum* lawn and poorer hummock with similar pH further into an oligotrophic fen imply that not only pH but also the botanical composition of peat and substrate quality shape methanogen community composition. (Juottonen 2008, p 29, and references therein).

Low microbial activity in bogs (as contrast to fens) has been related to low pH, low nutrient levels, and recalcitrant or even inhibitory nature of *Sphagnum* residue, making bog peat poor substrate for microbes. Yet, comparisons of production rates of CH_4, CO_2, and acetate in *Sphagnum*-dominated mires have suggested that the restriction of activity may concern methanogenesis in particular, rather than total anaerobic microbial activity. Low pH as such could shape the communities and restrict acetotrophic production. Decrease of pH from 4.8 to 3.8 in incubations of Siberian bog peat reduced CH_4 production and shifted the pathway from acetotrophic to hydrogenotrophic. Another possibility is a competitive process, for example acetogenesis, which in some soils inhibits hydrogenotrophic methanogenesis especially at low temperatures. The limitation of CH_4 production has been particularly severe in bogs at temperatures < 15 °C, but similar pattern of low CH_4 production potential at ≤ 15 °C and strong increase with temperature was also observed in the Siikaneva fen, which has a low pH that is comparable to pH of bogs. (Juottonen 2008, p 28, and references therein). Methanogenic growth in bog peat could also be limited by lack of required trace elements such as Ni, Fe, and Co (Basiliko and Yavitt 2001, cited in Juottonen 2008, p 28).

In a review based on several hundred laboratory incubations (Segers 1998), it was demonstrated that the distribution of potential CH_4 production rate is skewed and the variation is large, which is consistent with CH_4 fluxes measured under field conditions. For example, CH_4 production was on average three times larger in peat from minerotrophic natural wetlands as compared to the rate in peat from oligotrophic wetlands (1.2 vs. 0.4 mmol l^{-1} day^{-1}). Moreover, CH_4 production was 20 times larger in peat collected close to, or below, the water surface as compared to samples collected 5 cm (or more) above the water table (1.4 vs. 0.07 mmol l^{-1} day^{-1}) (Segers 1998). In a study with wet peat soils, significant methane production only occurred with [dissolved] organic matter fractions associated with larger particle sizes. The >2 mm fraction contributed 90 % of the total methane production capacity, and the capacity strongly decreased with depth (indicating major role of recent plant residues) so that the 0–5 cm layer contributed to 70 % of the total methane produced (van den Pol-van Dasselaar and Oenema 1999, cited in Le Mer and Roger 2001, p 33). Estimates from depth-integrated field measurements in northern Sweden (Sundh et al. 1994) ranged from approximately 300 mg CH_4 m^{-2} day^{-1} in poor fen samples to 1400 mg CH_4 m^{-2} day^{-1} in samples from relatively wet areas (groundwater table less than 8 cm from the surface) in short and tall sedge fens.

Reports on the rate constants of acetotrophic and hydrogenotrophic methanogenesis (i.e. the production rate expressed relative to the concentration of the substrate) from natural wetland ecosystems are rare. However, at least from two studies (Keller and Bridgham 2007, Galand et al. 2010) examining the methanogenic pathways in boreal peatlands ranging from oligotrophic bogs to intermediate and rich fens, it is possible to combine production rates of CH_4, with estimates of the relative contribution of the two pathways and concentrations of the substrate (acetate or CO_2) to the approximate rate constants for acetotrophic and hydrogenotrophic methanogenesis (Table 6-1). From these results it can be seen that the turnover time (i.e. the reciprocal of the rate constant) of the acetate pool with respect to CH_4 production is in the order of days (with a median of 6 days and a range of 1–25 days), whereas the turnover of the CO_2 pool with respect to hydrogenotrophic methane production is somewhat slower (median 11 days, range 7–160 days). The mesotrophic fens in both studies stand out with a high rate of acetotrophic methanogenesis (> 150 mM day^{-1}) and a similar turnover time of the acetate pool (about 7 days). Moreover, the slowest turnover times for acetate and CO_2 are found under conditions when the respective pathway is relatively unimportant. That is, extreme values are driven by variation in rates rather than pool sizes. For example, the maximum turnover time for acetate (25 days) is found in the oligotrophic fen (Table 6-1), and thus CH_4 is produced only on a low rate through the acetotrophic pathway (3 µM day^{-1}, 11 % of CH_4 production). Also, the maximum turnover time for CO_2 (160 days) is found in the rich fen, where the contribution of the hydrogenotrophic pathway is limited (3 µM day^{-1}, 11.5 % of CH_4 production).

Table 6-1. Anaerobic carbon mineralization in boreal peatland estimated from laboratory incubations (Galand et al. 2010, Keller and Bridgham 2007). Samples were collected from horizons with a high potential for CH_4 production (0–20 cm below water level), but there were slight differences in the methods between the studies (sites), so the figures are not necessarily fully compatible.

Site	Mire type	pH	CH_4 production ($mmol\ L^{-1}\ day^{-1}$)		CH_4 rate constant (day^{-1})		CO_2 production ($mmol\ L^{-1}\ day^{-1}$)	
			Acetotr.	Hydrog.	Acetotr.	Hydrog.	Rate	Ratio*
Michigan	Bog	3.9	40	72	0.11	0.09	542	4.8
	Intermediate fen	4.8	274	117	1.23	0.09	920	2.4
	Rich fen	5.9	24	3	0.12	0.01	340	12.6
Finland	Ombrotrophic bog	3.9	19	64	0.63	0.14	93	1.1
	Oligotrophic fen	5.2	3	28	0.04	0.09	60	1.9
	Mesotrophic fen	5.3	247	186	0.31	0.11	345	0.8

* Ratio of the CO_2, production rate to the total CH_4 production rate (i.e. to the sum of acetotrophic and hydrogenotrophic production rates).

6.3 Methane oxidation

In mires, the volumetric potential for methane oxidation is typically an order of magnitude higher, and the rate is less variable, than the volumetric potential for methane production (e.g. Galand et al. 2010, Keller and Bridgham 2007, Segers 1998; the methane oxidation (or, here, CO_2 production) rates reported by the former two sources are shown also in Table 6.1). In methanogenic environments, oxygen availability is the major factor limiting the oxidation (Le Mer and Roger 2001). Thus, when the methane passes through the oxic surface layer, depending on the thickness of the layer and tortuosity of the transport path, 60–90 % or even all of the methane produced in anoxic peat may be oxidized into CO_2 by aerobic methanotrophic bacteria (Le Mer and Roger 2001; Frenzel and Karofeld 2000, Pearce and Clymo 2001, and Segers 1998, all three cited in Juottonen 2008, p 5; Raivonen et al. 2017, p 4667, and references therein). Also, even within anoxic layers of wetlands, a thin oxidising layer can exist in rhizosphere of aerenchymal plants (cf. Section 4.4.2), allowing for local methane oxidation (Le Mer and Roger 2001; Armstrong et al. 1994, cited in Shaw and Thorne 2016, p 15; Raivonen et al. 2017, p 4667, and references therein). However, this is unlikely to be very efficient due to the short residence time within the thin oxic rhizosphere layer (Shaw and Thorne 2016). In addition, methane oxidisation has been reported inside the roots and in the submerged parts of the leaf sheaths of rice plants, as well as in anoxic submerged soils (Bosse and Frenzel 1997, Gilbert and Frenzel 1995, and Murase and Kimura 1994, all cited in Le Mer and Roger 2001, p 28).

6.4 Methane transport and emission

Methane and other gases, such as O_2, CO_2, H_2 and N_2, move through the acrotelm (the generally oxic surface layer) by three processes: 1) diffusion, 2) ebullition, and 3) through plant roots and stems (driven by the mass flow caused by diffusion and pressure gradients; also known as the plant bypass or shunt mechanism) (e.g. Clymo and Bryant 2008, Clymo and Williams 2012; Whalen 2005, cited in Juottonen 2008, p 5). For methane, oxidation into CO_2 may alter the transport path due to the differences in gas transport properties between CH_4 and CO_2. For catotelm proper (i.e. deep peat), however, only diffusion is plausible, and there CO_2 travels the same path with practically the same rate since CO_2 and CH_4 have nearly the same diffusion coefficients (Clymo and Bryant 2008, Clymo and Williams 2012) even if their solubilities differ considerably. The three main transport modes are discussed below from the perspective of studies specific to peatlands and mires, although it is to be noted that the descriptions above related to the similar processes in littoral zones of lakes (Section 4.4) are mostly applicable also to the wetland environments.

6.4.1 Diffusive fluxes

The bulk of methane transported at the catotelm–acrotelm interface seems to be mostly consumed, because the methane oxidation is significantly faster than the upward transport by diffusion (Hornibrook et al. 2009). However, if the layer with potential oxidation is thin and the transport is fast enough, more methane would potentially be emitted, as well as if the other transport pathways contribute. Therefore, the depth of the water table regulating the thickness of the oxic acrotelm is an important factor for methane emission also when considering the role of the diffusion path (e.g. Sundh et al. 1994).

Properties of the peat column also affect the diffusion of methane and oxygen in the air- and water-filled peat pores. Porosity of the soil determines the rate of diffusion; the lower it is, the slower is the diffusion. The porosity of peat is generally high (at least 80 %), so therefore peat is relatively easily passable by diffusion, compared to many other soil types. However, diffusion through the surficial peat column is thought to be a minor component in the total methane emissions from a peatland when gas-transporting vegetation (Section 6.4.3) is present at the site, because the diffusion coefficient in water is approximately four orders of magnitude lower than in gas inside the plant roots and stems, and because the probability of the methane becoming oxidised is higher when travelling through peat in contrast to the plant-facilitated bypass mechanisms. (Raivonen et al. 2017, p 4668, and references therein).

However, considering the long timescales related to groundwater-mediated discharges from the bedrock or subsoil into peat deposits, the diffusion coefficient of common gases dissolved in water is about 1×10^{-5} cm^2 s^{-1} (or more practically here, 3×10^5 cm^2 millennium^{-1}), which makes diffusion distances discussed in timescales of biochemistry small, but allows considerable diffusion distances over the millennial timescales related to the development of the (thicker) peat formations themselves (Clymo and Bryant 2008) as well as to the timescales relevant to the geological disposal of radioactive waste. That is, in an old peat deposit (with a thickness of several metres), diffusion alone can remove to the atmosphere about 95 % of the CO_2 and CH_4 generated by microbial decay at depth within the peat mass (Clymo and Williams 2012). This is further promoted by the severely limited advective groundwater flow in the deep peat layers (cf. Sections 6.1.1 and 6.1.3). However, the thinner the peat is, the more pronounced would the other transport pathways be in this respect.

6.4.2 Ebullition

Another transport pathway of produced methane in the mire is by ebullition, where methane in excess of the maximum solubility is transported as gas bubbles to the peatland surface (also, cf. Section 4.4.1). Estimates of the role of ebullition vary in the range of 0–70 % of the total methane emissions from wetlands, making it possibly a dominant pathway of methane emissions (e.g. Coulthard et al. 2006, Glaser et al. 2004; also, Peltola et al. 2018, p 938, and references therein).

In peatlands, direct ebullition to the surface is rare since ebullition events usually take place when the water table is below surface and, thus, the ebullitive gas flux is released to the air within the top-most peat layer [or moss canopy] (Peltola et al. 2018, Raivonen et al. 2017). For the origin of the gas bubbles in respect of the depth in the peat layer, there is both observational and theoretical evidence for both deep and surface locations, although for somewhat different reasons. Similarly, whether or not the vascular plants hinder the ebullition is under debate (Peltola et al. 2018, pp 946–948, and references therein). In principle, the ebullition occurs when the concentration of dissolved gases reaches saturation, but in practice, methane ebullition has been observed in wetlands already at concentrations below such limit (Raivonen et al. 2017).

In a modelling study, Peltola et al. (2018) compared alternative ebullition modelling approaches to eddy covariance measurements of methane fluxes on a boreal sedge fen in southern Finland and concluded that the simulated annual methane emissions were largely unaffected by the alternative modelling assumptions, but for temporal variability they made a considerable difference (Peltola et al. 2018).

6.4.3 Plant-mediated fluxes

Differences in methane emissions within and between mires can largely be attributed to the vascular plant community (Table 6-2). Similarly to many aquatic plants (Section 4.4.2), almost all vascular plants typical of wetlands have an internal gas transport system regarded as an adaption to low oxygen levels, where oxygen is transported downwards and carbon dioxide is transported upwards (Cronk and Fennessy 2001). The same system also ventilating out the methane from the rooting zone (Whiting and Chanton 1992, cited in Clymo and Pearce 1995, p 257). The methane transported through these plant aerenchyma largely escapes oxidation (Schimel 1995, cited in Juottonen 2008, p 5). Moreover, vascular plants do also provide additional substrate for methane production in the form of root exudates (e.g. Chanton et al. 2008). The abundance of vascular plants therefore is of importance both for the transport of methane and for stimulating the methane production – for example, methane emissions from areas with *Phragmites* spp. and *Typha* spp. in Sweden have been estimated to account for 5–10 % of the total emissions from wetlands in the country (Kasimir-Klemedtsson et al. 2001, cited in Bastviken et al. 2004, p 10). As outlined in Section 6.1.2, the plant community in mires is dependent on the type of mire and is related to its developmental stage.

Table 6-2. Percentage of CH_4 emission from wetlands attributed to plant species or communities (from Kölbener 2010).

Plant species	%	Reference
Carex spp.	25	Morrissey et al. 1993
Eriophorum angustifolium	48	Christensen et al. 2003
Phragmites australis	62	Grünfeld and Brix 1999
Carex spp.	89	Verville et al. 1998
Tundra vegetation	> 97	Bartlett et al. 1992
Eriophorum and *Carex* spp.	36	Schimel 1995
Carex spp.	60	King et al. 1998
Carex meyeriana	75–86	Ding et al. 2005
Scheuchzeria palustris	97	Frenzel and Karofeld 2000
Calamagrostis angustifolia	28–31	Ding et al. 2005
Eriophorum and *Carex* spp.	55–85	Waddington et al. 1996
Carex lasiocarpa	73–82	Ding et al. 2005
Fen vegetation	90	Whiting and Chanton 1992

For a broader picture, Leppälä et al. (2011) investigated five mires along a successional gradient, from sedge-dominated fens to a bog and found an increasing trend in methane emissions, but with a drop for the end state (i.e. the bog). The main factor controlling the emissions was the water table that fluctuated more in the younger fens and was more constant in the bog. They concluded that the effect of vegetation (mainly, the presence of vascular plants) was secondary to the control from water table fluctuations (as presented in Section 6.1.2, the development of the plant community is coupled with the development of the wetness). A fluctuating water table will also affect the available substrates for methanogenesis and possibly also inhibit the methanogenic population through aerobiosis, which will further affect the potential methane production and oxidation (Segers 1998).

Roots of sedges typical to fens (particularly those of the *Carex* species) extend to deep soil and therefore they have a large contact surface with the anoxic peat, especially the fine roots and the tips of coarser roots acting as gas-permeable passages. Isotopic studies have shown that passive diffusion along the concentration gradient dominates the methane transport in sedges, but there are, however, contrasting findings about where the key resistance for the flux lays. (Raivonen et al. 2017, p 4667, and references therein).

Variations in the methane transport through aerenchyma between night- and daytimes can be related either to stomata opening (*Scirpus* spp.) or to a convection phenomenon related to temperature (*Phragmites* spp.) (Van Der Nat et al. 1998, cited in Le Mer and Roger 2001, p 29). Plants possessing aerenchyma are mostly herbaceous, but also include trees such as *Alnus* species (Rusch and Rennenberg 1998, cited in Le Mer and Roger 2001, p 29). In laboratory experiments with submerged soils planted with *Spartina patens* and rice, it was observed that redox potential (Eh) that varied between −200… +100 mV affected not only methanogenesis but also gas transfer through the plant. At a lower Eh the aerenchyma formation increased and the size of the roots decreased, and a further decrease of Eh from −200 to −300 mV induced a ten-fold increase in methane production and a 17-fold increase in its emission (Kludze and Delaune 1995, and Kludze et al. 1993, both cited in Le Mer and Roger 2001, p 33).

Marked diurnal fluctuations in the plant-mediated efflux of methane have been reported not only for lakes (see Section 4.4.2) but also for mires. Higher night-time values have been observed for dry, but not for wet, communities in a boreal mire, a *Carex rostrata* dominated mire, wet tundra, and an *Eriophorum angustifolium* lawn (Mikkelä et al. 1995, Thomas et al. 1996, Waddington et al. 1996 and Whalen and Reeburgh 1988, all cited in Juutinen et al. 2004, p 10). A small maximum in the efflux in the afternoon, explainable by the effect of temperature on the production and diffusion of the methane, has been found in a sedge fen and on non-vegetated sediment surface (Van Der Nat et al. 1998 and Whiting and Chanton 1992, cited in Juutinen et al. 2004, p 10). However, no diurnal trends have been observed for example in *Carex* and *Calamagrostis* dominated wetland sites or in an *Equisetum fluviatile* stand (Hyvönen et al. 1998 and Moosavi and Crill 1997, both cited in Juutinen et al. 2004, p 10). As for the diel variability of aerenchymal transport in lake plants, it needs to be noted also here that these results relate to relatively short-term measurements only, and in a recent study (Milberg et al. 2017), published after the initial literature search for the current review, the diel patterns were found to vary much between measuring occasions. That is, the role and variability of the plant-mediated transport is likely rather strongly coupled with the other transport mechanisms and their variability over the different timescales.

6.5 Whole-mire methane budgets

Factors that favour methane emission from wetlands are mostly submersion and availability of low-molecular-weight organic matter. Usually, the methane emissions and the net productivity of submerged soils are positively correlated; about 3 % of the daily productivity is emitted as methane (Dacey et al. 1994 and Whiting and Chanton 1993, cited by Le Mer and Roger 2001, p 35).

Regional methane emissions by mire types in Sweden are available, for example, from the data of Nilsson et al. (2001) and Sundh et al. (1994) (Table 6-3). Nilsson et al. (2001) also provide corresponding upscaled annual fluxes of 2.5 ± 0.9, 1.5 ± 1.1, 5.5 ± 3.3 and 8.7 ± 3.8 g CH_4 m_{-2} y−1 for the Central-Swedish *Sphagnum*–dwarf shrub, transitional, short-sedge and tall-sedge fens, respectively (with ± 95 % confidence intervals). Generally, the sedge-dominated mire types have the highest fluxes and, overall, fluxes for the central parts of the country are somewhat lower than those for the northern part (except for flark surfaces). Somewhat more recently, Nilsson et al. (2008) estimated the methane emissions from an oligotrophic mire in northern Sweden to be 9 and 14 g CH_4-C m^{-2} y^{-1} in two consecutive years, respectively, and Rinne et al. (2007) estimated the methane emission in a minerotrophic fen in southern Finland to yield 9 g CH_4-C m^{-2} y^{-1}. These data are reasonably similar to those presented in Table 6-3, although derived with different methods.

Table 6-3. Rates of CH_4 production (estimated from laboratory incubations) and emission rates (estimated from field chambers) from boreal wetlands in Sweden, as well as the ratios of the rates. For the emissions from mires in central Sweden, also the standard error of the measurements is presented. The water table is indicated in terms of metres below the mire surface.

Region and mire type	Water table (m)	Production (mg m^{-2} day^{-1})	Emission (mg m^{-2} day^{-1})	Emission: production
Northern Sweden (Sundh et al. 1994)				
Poor fen, flark	0.02	340	72	21 %
Poor fen, hummock	0.19	300	1	0.3 %
Short-sedge fen, dry	0.14	400	−3	–
Short-sedge fen, wet	0.07	1 300	5	0.4 %
Mesotrophic tall-sedge fen, flark	0.08	1 450	70	5 %
Mesotrophic tall-sedge fen, slope	0.15	385	8	2 %
Central Sweden (Nilsson et al. 2001)				
Sphagnum – dwarf shrub (n=41)	0.32		13 ± 2	
Transitional fens (n=4)	0.37		8 ± 2	
Short-sedge fens (n=80)	0.31		29 ± 9	
Tall-sedge fens (n=43)	0.23		46 ± 10	

Emissions from different areas of the same wetland can also vary, due to micro-topography and differences between how fast the peat decomposes in different areas (Susiluoto et al. 2018, p 1200), as well as due to the variation in plant communities (Section 6.4.3). Temporal and spatial variability of the methane efflux to the atmosphere is by several orders of magnitude larger than that of the net ecosystem exchange (i.e. efflux of CO_2). The cumulative annual sum of the CO_2 efflux seems more affected by broad-scale geographic location and physical setting than that of the methane efflux, more reflecting the influence of internal factors. (Limpens et al. 2008). Drier bogs with persistently low water table, with or without permafrost, have very small methane efflux (< 1 g C m^{-2} y^{-1}; Christensen et al. 2004 and Roulet et al. 2007, both cited in Limpens et al. 2008, p 1482), while wetter bogs can have intermediate fluxes (5–8 g C m^{-2} y^{-1}; Laine et al. 2007b, cited in Limpens et al. 2008, p 1482). In fens, particularly when sedges are predominant, the efflux is the highest and can exceed 15 g C m^{-2} y^{-1} (Shurpali et al. 1993 and Suyker et al. 1996, both cited in Limpens et al. 2008, p 1482).

What comes to the role of the different methane transport (and emission) pathways, for example Wania et al. (2010) presented the modelled relative contribution between the three pathways for seven reference sites that was compared to the model estimates. These represented a span of 68–85 %, 16–31 % and 0–1.4 % of plant-mediated, diffusion and ebullition fluxes, respectively. In typical open-water wetlands plant-mediated transport accounts for 12–98 %, diffusion about 5 % (in contrast to the > 90 % for the well-drained oxic upland systems) and ebullition 10–60 % of the soil-produced methane emitted to the atmosphere (Xu et al. 2016, p 3738, and references therein; note that the ranges consist of estimates derived from separate studies and as a whole do not fully agree together). For annual balances for a sedge fen in southern Finland, Peltola et al. (2018) derived modelling estimates of 61–94 % of the methane emissions (measured total emissions 11.9–14.7 g CH_4 m^{-2} y^{-1}) being due to the aerenchymal transport, the remainder being released through diffusion and ebullition fluxes (the shares of the diffusive and ebullitive fluxes varied with the modelling assumptions used). For the same fen, also the modelling results of Susiluoto et al. (2018) indicated a contribution of 75–95 % for the plant-mediated methane releases.

6.6 Peatland drainage and restoration

Drained soils of organic origin may have the potential for both methanogenesis and methanotrophy (cf. Chapter 3). Methane production occurs mainly below the groundwater table, and the draining of a peatland will limit the potential methane production and also increase the potential methane oxidation by increasing the distance from the bottom of the unsaturated zone to the atmosphere. Moreover, the plant community will shift towards a community less adapted to water inundation and oxygen deficiency (i.e. a community lacking the potential of plant-mediated methane transport to the atmosphere, cf. Sections 4.4.2 and 6.4.3).

When draining lowers the water table, the methanogenic domain needs to move into more decomposed peat, and a higher mass of organic matter becomes aerobically degraded. However, the lower substrate availability than at the earlier water table and the increased (but still low) oxygen level may benefit certain methanogen groups that already reside at or below the new water table, particularly those more tolerant to oxygen (Juottonen 2008, p 29, and references therein). In addition to loss of peat-forming vegetation, drainage of peat soils significantly enhances particulate organic carbon loss through concentrated flow in the drainage channels and also increases sub-surface peat erosion and soil piping (Holden et al. 2006, cited in Limpens et al. 2008, p 1483). This most likely affects the substrate availability to the methanogens, since the most easily degradable material also tends to leach out first.

The reduction in methane emissions after the onset of drought, or drainage, can be due to a reduction in methanogenesis within the peat rather than an increase in the oxidation capacity (Freeman et al. 2002, cited in Shaw and Thorne 2016, p 16). However, on the opposite, in mire restoration (rewetting), the methane emissions may grow higher than either in the undrained or drained state of the mire (Koskinen 2017). Even though there are also indications of only low methane emissions from restored forestry-drained peatlands (Juottonen et al. 2012, cited in Koskinen 2017, pp 11, 28), high emissions have been reported also in studies on restored cutover peatlands (Wilson et al. 2009, 2013, cited in Koskinen 2017, p 28) especially when the water table fluctuates near the surface causing inundation and intermittent periods of plant growth (Koh et al. 2009, Hahn-Schlöfl et al. 2011, and Vanselow-Algan et al. 2015, all cited in Koskinen 2017, p 29).

Methane emission measurements on organic soils drained for forestry in Finland show that the emissions are located to ditches with vegetation; fluxes from areas in between were insignificant (Minkkinen et al. 1997). In three cultivated peat soils in southern Finland with the water table 0.8 m below the soil surface, a net uptake of methane (0.06–4 mg CH_4-C m^{-2} y^{-1}) was measured during two consecutive years, but similar cultivated peat soils having the water table 0.4 m below surface in northern Finland emitted methane with a considerably higher range (3.6–300 mg CH_4-C m^{-2} y^{-1}), suggesting that only poorly drained cultivated peat soils may act as a net source for methane (Regina et al. 2007). In a Danish study on drained organic soils that have been used for agricultural purposes for decades, there were none or very small emissions of methane, with the exception of three sampling points hosting tussocks of *Juncus effusus* (able to ventilate methane along aerenchyma and indicating poor drainage) showing consistent emission throughout the year (Petersen et al. 2012). Measurements from Swedish organic soils used for agricultural purposes since the 1930s showed consistently insignificant methane emissions unless the water table was located closer than 0.5 m from the soil surface, and even then the highest emissions were only about 80 mg CH_4-C m^{-2} y^{-1} (Kasimir-Klemedtsson et al. 2009). A small net uptake (i.e. influx) was also recorded in a barley field suggesting the presence of a methanotrophic community (Kasimir-Klemedtsson et al. 2009). Berglund and Berglund (2011) showed insignificant methane emissions from two Swedish cultivated peat soils drained in 1920 and 1938. Both these areas were previously minerotrophic fens with brown mosses (rich fen) in one case and *Phragmites* peat in the other. Such vegetation communities are characteristic also to fens in the Forsmark area today (Löfgren 2010). Utilisation of the sulphate forms of nitrogen fertilisers reduce methane emission from cultivated wetlands (Le Mer and Roger 2001).

The insignificant emissions from most cultivated organic soils seems to be related to a low or insignificant methanogenesis, whereas the potential methane oxidation seems to be more resistant to drying, in combination yielding in net uptake of methane from the atmosphere (i.e. influx in the order of, e.g., up to 37 mg CH_4-C m^{-2} y^{-1}; Maljanen et al. 2003).

7 Summary and conclusions

In this chapter, first a tentative conceptual model of methane cycling in general, based on the findings of the literature review above is outlined. For references for the underlying details, see the respective sections in the earlier chapters. This drawing of the conceptual view is followed by site-specific considerations of the methane cycling at Forsmark. In the final section in this chapter, conclusions on the implications of the current work for biosphere assessments of geological repositories (at Forsmark) are drawn.

7.1 Tentative conceptual model of methane cycling

Radioactive carbon from a geological repository may enter surface ecosystems such as natural wetlands, lakes or streams through the discharge of deep groundwater. A significant fraction of the radiocarbon released can be expected to be in the form of low-weight organic molecules, such as acetate, or in the form of inorganic carbon (CO_2, H_2CO_3). Biochemical transformations of this radiocarbon entering an ecosystem will depend on the environmental conditions and the presence of microbial populations. This report, and, thus, also the tentative conceptual model outlined here, focuses on the potential transformation of acetate and CO_2 to CH_4 and the further transport, transformation and emission of the methane in various ecosystems. Whereas forests, grassland and arable or agricultural systems typically are net consumers of methane (i.e. atmospheric methane is drawn into the soil to supply the oxidation), net methane effluxes occur in freshwater bodies and wetlands. Since the focus of the current work is to investigate whether part of the repository-originated C-14 releases could avoid uptake by plants (and thus further entering the food webs through herbivory) by evading the methane oxidation, the discussion below primarily considers these wetter environments. However, it needs to be noted that, regardless of the carbon forms used and produced, the microbial transformation results in the incorporation of part of the possibly C-14 bearing carbon in the microbial biomass and further in the food web.

Acetotrophic methanogenesis

Acetate (CH_3COOH) is the anion of acetic acid, and it is common in natural environments both as such and as a degradation product of other organic molecules. Under aerobic conditions it is readily metabolised by microorganisms and converted to CO_2 and microbial biomass on the timescale of days (Wu et al. 1997), but in anaerobic conditions methanogens can produce CH_4 from acetate under strongly reducing condition (typically < -200 mV) or acetate may also be transformed to CO_2 by anaerobic respiration (e.g. by denitrification or reduction of sulphate, iron or manganese). Acetate may also be transported by groundwater advection to oxic environments before it is biochemically transformed. However, in anaerobic environments (such as subsurface layers in lake and stream sediments or in peatlands), where acetate is an important metabolic end product from fermentation, acetate acts as an important substrate to methanogenesis. In sulphate-rich environments, acetate can be consumed also by sulphate-reducing bacteria (SRB) thus competing with the acetotrophic methanogens. Some studies have indicated that presence of sulphate, nitrate or ferrihydrite can inhibit the acetotrophic methanogenesis in particular. In freshwater environments, the acetotrophic pathway has been estimated to provide two thirds of the produced methane. In mires, the acetotrophic pathway is more typical to the upper peat layers whereas the hydrogenotrophic one seems more typical at depth and in oligotrophic bogs than at surface or in minerotrophic fens (Juottonen 2008).

Hydrogenotrophic methanogenesis

Whereas the acetotrophic methanogenesis is typical to environments with abundant labile organic carbon, the hydrogenotrophic (autotrophic) methanogenesis tends to have a larger role in more recalcitrant anoxic layers. These microbes grow by reducing carbon dioxide with hydrogen. Some hydrogenotrophic microbes also use formate and produce both carbon dioxide and hydrogen that are then further utilised by them. In addition to the hydrogenotrophic pathway having an increasing role deeper in the peat deposit, it also seems to increase towards oligotrophy (i.e. with the succession from fens to bogs).

Methylotrophic methanogenesis

The third main pathway of methane production uses methylated compounds such as methanol, methylamines or dimethyl sulphide, but is usually considered a minor contributor except in marine environments and in wetlands where the other substrates are more efficiently utilised by non-methanogenic bacteria (e.g. SRB). Particularly in some marine systems and in permafrost peatlands, the methylotrophic production may play a larger role (Juottonen 2008, Xu et al. 2016).

Aerobic methanogenesis

There is also some evidence of methane production occurring also in oxic water layers, proposed to explain a considerable part of methane concentrations in the epilimnion in some cases. The role of this mechanism remains yet unclear, though (e.g. Wu et al. 2016).

General regulation of methanogenesis

Regulation of methanogenesis is a complex aggregate of biogeochemical processes, and it is affected by several environmental factors including redox conditions, substrate supply, pH, temperature, competition (e.g. reduction of nitrate, ferric iron or sulphate) and microbiological inhibition (e.g. heavy metals). However, even if ferric iron supplies competitors of methanogens, high iron content in soils also enhances the low redox potential after submersion, which favours methanogenesis in periodically flooded soils. In sulphate-rich soil layers the methanogenesis is characteristically suppressed. The methanogen activity is usually at the optimum around neutral or slightly alkaline conditions, but at least some methanogens have adapted to considerably acidic environments typically met in peatlands. The methanogenesis is also considered highly sensitive to temperature (optimum at +30…40 °C), even though significant methane production has been observed in aquatic sediments (near +4 °C for a considerable time of year at northern latitudes) as well as in wetland and forest soils also in wintertime (even below +1 °C). The temperature effects are also subdued in sediments of deeper parts of water bodies, in contrast to littoral areas.

The highest potential for transformation of carbon to CH_4 is confined to a relatively narrow zone close to, or just below, the redox front (i.e. the average water table in terrestrial systems, or the thermocline/oxycline/metalimnion or the sediment–water interface in water bodies). In open-water areas of lakes, this narrow zone proximal to the redox front is overlaid by a thicker (oxic) water column somewhat reducing the possibilities of methane escaping to the atmosphere (see below). In littoral areas of lakes, the situation is somewhat between of those prevailing in the open-water areas and in peatlands. If there is also sulphate reduction occurring in the sediment (more usual in marine environments, though) or in peat, the main horizon of methanogenesis lies beneath that front due to the biochemical competition.

In peatlands, the most active zone of methanogenesis (mesotelm) has a hydrological conductivity that may be an order of magnitude higher than that of deeper catotelm peat, resulting in considerable periodical losses via lateral runoff, and it also has a relatively high rate of gas exchange with the atmosphere despite of saturated conditions. However, under hummocks, there is a thicker relatively well aerated layer of moss canopy and vascular plant roots and stems potentially trapping or retaining gas fluxes. On the other hand, methane production occurs also in deeper peat layers, with rates decreasing with depth.

In addition, root exudates of vascular plants tend to associate particularly with acetotrophic methanogenesis through supplying low-molecular-weight organic carbon (LMWOC) more or less proportionately to the plant density. Other sources of easily metabolisable substrate to methanogens include the decomposition of plant litter and detritus (in both water bodies and peatlands) and the anoxic decomposition of peat.

Transport and effluxes of methane (and CO_2)

The methane transport mechanisms are essentially the same in all ecosystems, particularly among mires (and other wetlands) and freshwater bodies. As briefly explained below, these include the release from the sediment, catotelm peat or anoxic soil layers, water mixing and/or stratification and related storage flux in water bodies, efflux from surface water/soil/peat, ebullition, and plant-mediated transport.

Typically, the transport of the methane produced in soil profile or under water takes from minutes to days, or in frozen conditions up to a season. During this time, the methane may get oxidised (see below). In methane-producing horizons, the advective transport often plays a minor role, enhancing the relevance of the relatively slow diffusion, and the transport time is thus regulated for example by temperature, water-saturation, water and air pressure, and soil/sediment texture, including the pore structure and connectivity. Cracks and pipes in deeper peat layers may be an exception to this, by providing preferential (advective) flow routes for water and gas. However, there are also considerably faster gas transport routes, as summarised in the following.

Considerable production and release of methane into the water column also aids in oxygen depletion and development of stratification, unless the export to the air is fast enough. This further weakens the concentration gradient between the sediment and the water column, and decreases the transport rate. However, in stratified conditions in deeper parts of a water body, a considerable anoxic and methane-rich water volume may develop, and this methane inventory then typically becomes diffused relatively rapidly at the spring or autumn overturn in the rest of the water body; this is called the storage flux. On the other hand, high oxygen concentration in bottom water considerably enhances the diffusion of methane from the sediment to the water. Similar effect has been observed also with turbulence and bottom shear stress (in lakes mainly from wind exposure). Regardless of the arrival mode, dissolved methane reaching the surface water by diffusion or advection (water mixing) further diffuses to the atmosphere unless transported away by water flows (for transport as gas bubbles, see below). This efflux from the water surface is driven by the 'piston velocity' (also 'gas transport velocity'), which is a result of turbulence at the water–air interface and thus depends mostly on the wind speed, but exhibits considerable spatial variability, although usually in a relatively well constrained manner in lakes and other wider water bodies. With ice cover, this water-to-air flux is considerably suppressed, which may result in relatively large and rapid emission of stored methane at the ice break. In streams, this efflux mode is usually predominant, but spatially highly variable due to the 'step-stair continuum' of small waterfalls, riffles and pools. In mires, the moss layer or other emergent vegetation effectively reduces the piston velocity. Also, due to the proximity of the water table and thermally well insulating peat layer, no notable stratification and storage flux occurs, with the potential exceptions of some open-water pools or seasonal accumulation under ice or ground frost. However, periodically, the advective runoff along the mesotelm–acrotelm surface layer can be considerable. In such environments, the ventilation to the surface peat and further to the atmosphere resembles more the situation with upland soils, described right below. Littoral areas of lakes, in turn, represent a transition between the open-water environment and mires, with increasing proportion of ebullitive and aerenchymal transport (see further below in this subsection) towards areas with denser vegetation.

In the well-aerated oxic upland soils, the gas exchange (including both CH_4 and CO_2) seems to be largely governed by diffusion and 'wind-induced pressure pumping', both affected by the soil moisture content; this is reflected also by the general trend of increasing methane and carbon dioxide fluxes – as well as increasing degree of methane oxidation in the upland soils – with the increasing wetness and decreasing efficiency of gas exchange. In very dry periods, this may be enhanced by the suppression of microbial activity due to desiccation stress. Presence and type of vegetation affect also both the pore structure of and the moisture conditions in the soil.

Ebullition (transport with gas bubbles) is often considered the largest contributor to the methane emissions from a lake and likely at least as important in mires and wetlands, but field studies are sensitive to the time period of the measurements, as well as to spatial variability. This is since an ebullition events are episodic and easily triggered by changes in air or water pressure. However, there must be a sufficiently high gas pressure built up in the anoxic sediment or peat layer to allow the bubbles to escape in the first place; the ebullition flux is basically a function of the net methane accumulation (production minus losses). In practice, also changes in temperature, other gases or 'impurities' affect the bubble formation and release, as well as the water (or peat) depth affecting the pressure threshold to be overcome. Thus, shallower areas are more prone to ebullition than deeper ones. The short ebullition events also indicate that the transfer through the water column is indeed rapid, and little oxidation can occur on the way. In mires, though, the emerging gas bubbles may be trapped in the oxic moss canopy or dense root system of vascular plants, particularly under hummocks. High ebullition fluxes have been associated to elevated substrate and nutrient concentrations, but this may rather indicate enhanced methane production than increased proneness to ebullition per se.

Plant-mediated transport refers to the gas exchange through the aerenchyma in some aquatic and wetland plants (e.g. common reed, cattails, water lilies and some sedges), which primarily supplies the otherwise anoxic root layer with oxygen, allowing at the same time opposite flux of methane and other gases from the rooting zone to the air. Depending on the plant type, the gases move through the aerenchyma either by diffusion alone (concentration gradient) or by both diffusion and convective flow. This is related to the plant respiration, and is thus affected by the ambient temperature and humidity, as well as (partly) associated to solar irradiation. Consequently, many studies report considerable diel variability in these methane fluxes, although some others have found the diel patterns highly variable over longer measurement periods. The plant-mediated fluxes are also seasonal and peak typically in late summer, when they may temporarily dominate the overall methane emissions. Particularly with lakes, though, the role of the pathway decreases with the increasing lake size, since the aerenchymal vegetation is typically restricted to water depths less than about 1.5 metres.

It needs to be borne in mind, though, that only a few studies have measured diffusive, ebullitive and aerenchymal fluxes simultaneously, and even fewer over a longer time period. Since there are several methane transport pathways acting simultaneously, but regulated differently, coherent estimation of the fractionation of the methane emissions over a larger area (such as a lake or a mire) and multi-annual averaging is challenging.

Some transport and ‘loss’ of methane, relevant for establishing a mass balance, occurs also due to its incorporation in microbial biomass (methane oxidation, see below), grazing these methanotrophs by (aquatic) organisms and further trophic transfer in the food web. This is discussed readily relatively briefly already in Section 4.5. For mass balances, it also needs to be noted that the oxidation of the methane may considerably contribute to the dissolved inorganic carbon (DIC) pool as well.

Methane oxidation

Methane oxidation occurs prevalently in aerobic environments by methanotrophic bacteria that utilise the methane as their sole energy source. However, also more limited anaerobic oxidation by other types of microbes have been observed mainly in marine, freshwater and wetland environments, but also to an extent in soils, with seemingly decreasing contribution towards the drier conditions. Although found everywhere in soils, methanotrophs are concentrated at the redox fronts (i.e. near the anaerobic regions producing the methane). This includes also the rhizosphere of aerenchymal plants supporting microscale aerobic conditions. They seem particularly active in zones with periodical anaerobiosis (e.g. mesotelm in peatlands). In water bodies, most but not necessarily all of methane oxidation tends to occur at the interface of anoxic and oxic sediment layers or in the metalimnion separating the anoxic and oxic water layers.

As already touched upon above, the likelihood of a molecule of methane to be oxidised is dictated by the transport pathway of the molecule, from the point of production to the open air (Megonigal et al. 2003, cited in Shaw and Thorne 2016, p 15). The thicker the aerobic layer of soil [or water] overlying the anoxic locus of methanogenesis, the greater the degree of oxidation (Hoch et al. 2014, Shaw and Thorne 2016). In cultivated mineral soils, a characteristic length scale of tens of centimetres is needed to convert the methane into CO_2 (Hoch et al. 2014). This seems similar to the characteristic micro-topographical scale of many mires (hummocks–hollows) that also has been associated to the local variability in the methane and CO_2 effluxes. Such length scale also fits well to typical drainage depths for agriculture and forestry and to the common observations of consumption of atmospheric methane by the methanotrophs in such drained soils. Conversely, the shallower the oxic epilimnion layer in water bodies, the higher the fraction of the methane in the water column that potentially can leave the system unoxidised; this is particularly contrasted between the shallower littoral zones and the deeper open-water parts. Similarly, a large fraction of the methane escapes from streams due to relatively shallow water, high methane concentrations (often even supersaturated) and high turbulence.

The methane oxidation is a series of biochemical steps via methanol, formaldehyde and formate in combination with incorporation into microbial biomass. It is also enzyme-catalysed. Thus, methanotrophy is not a simple first-order process (except approximately so in low methane concentrations), but rather follows Michaelis–Menten kinetics, or in case of being also oxygen-limited, a double

Monod expression (see Section 2.2). Furthermore, preincubation of soils in a high-methane environment has been demonstrated to change the kinetics towards enhanced oxidation rates. On the other hand, the oxidation capacity of the bacteria is limited and particularly rapid methane pulses may remain partly unoxidised. In the literature, often methanotrophs of low and high affinity for methane are distinguished, operating in high and low methane concentrations, respectively. The high-concentration and low-affinity methanotrophy typically relates to the proximity of methanogenic environments or otherwise methane-enriched conditions, whereas the low-concentration and high-affinity system is more typical to well-drained oxic upland soils. For the reaction-kinetic formulas, these affinities relate to differences in the Michaelis constant of the system.

Effectively, the methane oxidation rate depends on the methane and oxygen supply, the presence and adaptation of particular methanotroph populations, and possible stimulation dynamics with a higher methane input rate at a somewhat earlier time. As with other biochemical processes, also methanotrophy is affected by the temperature. However, methane oxidation has been observed also in freezing temperatures. High levels of nitrate and other nitrogen compounds (and thus also fertilisers) may inhibit methanotrophy to a varying degree. However, the effect of this seems to be dependent also on the microbial communities involved (e.g. Bodelier 2011). Tilling of cultivated soil also tends to destroy aerated micro-niches suitable for methanotrophs. pH per se seems to affect little methane oxidation rates.

Open issues

There are also some methane-cycling mechanisms under debate, including aerobic methane production within plant tissue, methane production by fungi, and anaerobic methane production from the cleavage of methyl phosphonate (e.g. Wu et al. 2016, pp 3746–3747, and references therein). Methane production in oxic water layers has been reported as well. Anaerobic methane oxidation has been demonstrated in marine systems, but significance for other ecosystem types remains inconclusive (Xu et al. 2016). It is recognised, however, that considerable amount of literature on this topic has been published during and after this review conducted in early 2017. Whether or not vascular plants hinder the ebullitive escape of the methane in mires is also under debate (Peltola et al. 2018, pp 946–948, and references therein).

Conceptual presentation

Based on the methane-related processes in general (addressed in Chapter 2) and the further information on the methane cycling in wetlands (Chapter 6), a tentative conceptual model of the key carbon species involved and their transformations in the soil layer of a generic mire is outlined in Figure 7-1. New organic carbon is added from the top by the primary production (mainly plant litter, root exudates, etc.). The subsequent carbon transformation pathways in the peat vary according to the changes in the redox state, following the variations in the water table (indicated also with the curve on the right-hand side of the graph illustrating relative profile of the oxygen partial pressure). The potential input of radiocarbon species released from the repository into the mineral subsoil beneath the peat layers is indicated with the blue arrows. For methane transport pathways from these layers to the atmosphere, see Figure 2-1 in Chapter 2.

When compared to the general harmonised structure in the biosphere assessment models (Figure 7-2) and to the schematic presentation of methane pathways in a stratified lake presented already earlier in Figure 4-2, it can be seen that this tentative conceptual model could be elaborated with small adjustments from the mire context into a more general setting of littoral areas of lakes, or maybe even also for the open-water areas of lakes and streams; this would require the addition of oxic and anoxic open-water layers in the conceptual model, and generalising the changing (ground)water table into a seasonally moving oxycline (the redox front; whether in water column or within peat/sediment, depending on the ecosystem). Such generalisation would also host addressing drainage of lakes or wetlands, or rewetting of peatlands, in a coherent framework.

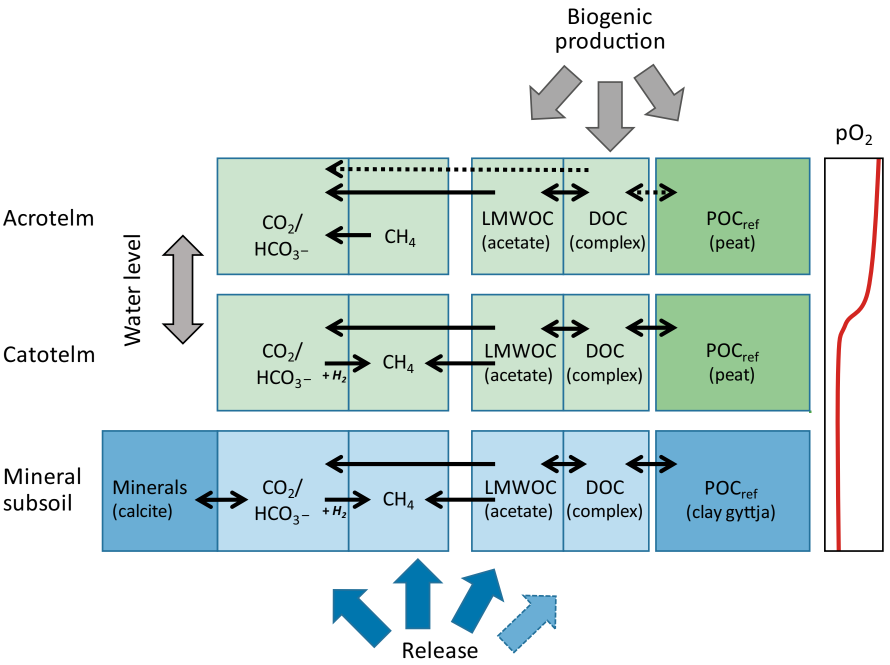

Figure 7-1. *Tentative conceptual model of storages of carbon species and their transformations in a mire. LMWOC denotes low-molecular-weight organic carbon, DOC dissolved organic carbon, POC_{ref} refractory (recalcitrant) particulate organic carbon, and pO_2 the partial pressure of oxygen at the different vertical zones (the pO_2 curve has been adapted from Limpens et al. 2008, p 1477). Note that the transformation from CO_2/HCO_3^- to CH_4 requires also H_2 resulting from the fermentation supplied by the LMWOC and DOC pools.*

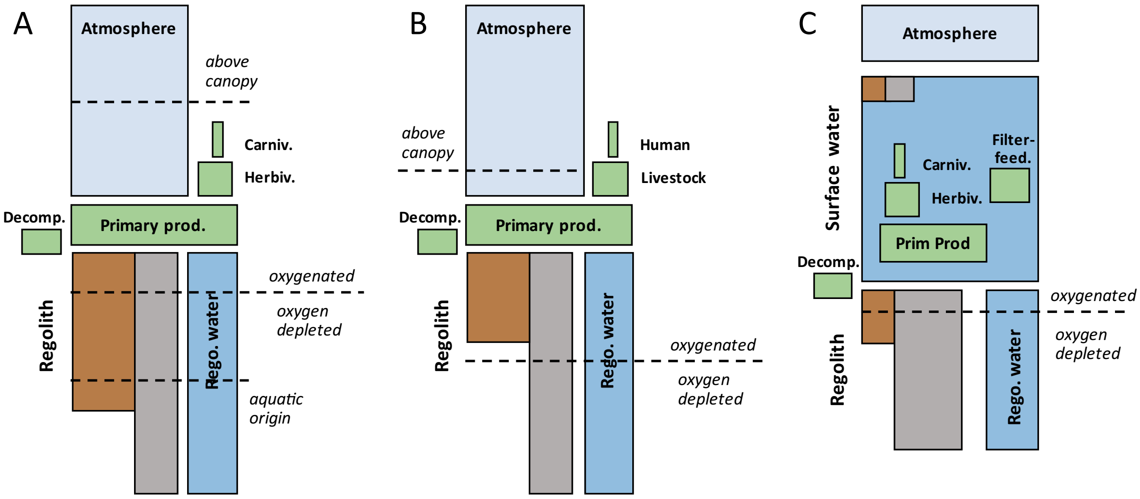

Figure 7-2. *Biosphere components identified as important for the transport and fate of radionuclides in A) mire, B) agricultural and C) aquatic ecosystems (Saetre et al. 2013, pp 25, 27). Green indicate radionuclide inventories in organisms, blue indicates inventories of dissolved radionuclides. Grey and brown indicate radionuclide inventories associated with regolith solid states, i.e. adsorbed radionuclides (grey) and radionuclides stored in organic matter (brown). The horizontal line indicates the boundary between oxygenated and oxygen depleted aquatic sediments (regolith).*

7.2 Methane in Forsmark landscape

To establish coarse estimates of the relative contribution of the methane emission pathways in Forsmark lakes, their size range (0.01–0.75 km²; Andersson 2010) is used here to translate the results of Bastviken et al. (2004) into full-lake emission rates. These are based on a reasonably coherent dataset on the relative role of the different emission fluxes, albeit only for a limited range of conditions that are not necessarily fully representative to the Forsmark area. Regardless, this is judged to illustrate the relative magnitudes to a relevant extent. In this study of Bastviken et al. (2008), epilimnetic sediments down to water depths of about two metres produced most of the methane emissions, and the maximal water depth in the Forsmark lakes is 2.2 m (Andersson 2010). This might indicate that most of the sediments in Forsmark lakes may emit a large proportion of their methane inventory, especially during summer periods. On this same basis, methane emissions through the various pathways in the Forsmark lakes (Table 7-1) can be roughly estimated, with the regression equations presented by Bastviken et al. (2004, p 6) using the lake area alone.

These results indicate that approximately half of the methane emission to the atmosphere would occur through ebullition, the other half consisting of the diffusive efflux. The possible contribution of the storage flux would remain anyway at 5–13 %. However, the lakes in the region are shallow and the littoral habitat with emergent macrophytes is the dominant habitat in the lakes (on average comprising 69 % of the lake area, with a range of 34–96 %) (Andersson 2010), and thus there may not be any anoxic hypolimnion of a considerable volume to store the methane. Also, due to the high coverage of emergent macrophytes, the plant-mediated efflux of methane could potentially be an important pathway for many of the Forsmark lakes, although difficult to set a number for. In a broader perspective, this pathway may become more relevant at the landscape level as land uplift and succession occur converting sea bays into lakes, and lakes into mires (also, cf. below in this section).

Table 7-1. Methane emission rates for Forsmark lakes estimated based on the lake areas (0.01–0.75 km²; Andersson 2010) alone by employing the regression equations established by Bastviken et al. (2008, p 6). Note that such regressions are not readily available for the plant-mediated (i.e. aerenchymal) emissions and, thus, they are omitted in this scoping calculation.

Emission pathway	Flux (mg CH_4 m^{-2} day^{-1})
Ebullitive flux	1.4–2.8
Diffusive flux	1.4–1.9
Storage flux	0.15–0.68
Total	2.9–5.4

As the streams in the Forsmark area are small and to a large extent covered by vegetation, and as many of the stream stretches are dry during summer, the methane production, oxidation and emission conditions vary considerably and it seems difficult to make quantitative estimates without a more in-depth study. However, the study made in southwest Sweden (Natchimuthu et al. 2017; also, see Chapter 5 here) would provide reasonable first estimates for the non-dry periods. For the dry periods, then, it seems plausible that the situation would develop similar to lake margins, wetlands or even poorly-drained upland soils if the drying is severe enough.

Regarding the mires in the Forsmark area, the estimates of methane emission by Nilsson et al. (2001) for central Sweden (see Section 6.5 and Table 6-3) can be applied as an approximation. The low-sedge and tall-sedge vegetation types can be regarded more representative for the early successional minerotrophic mires of Forsmark, whereas the transitional fen represents the border communities surrounding these early mire types. However, in the Forsmark region, the very first successional stage of an in-filled lake is dominated by *Phragmites australis*. This stage has been identified as a major contributor to methane emissions (e.g. Van Der Nat et al. 1998, Sugimoto and Fujita 1997, Johansson et al. 2004), possibly due to the ability of the species for convective aerenchymal ventilation in contrast to the *Carex* species (that are more typical to fens) that only facilitate passive diffusion through the aerenchyma (Vasander and Kettunen 2006, Laanbroek 2010). Regardless, it is also notable that in such *Phragmites*-dominated areas of *lakes* in general the methane emission rates (1.3–316 mg CH_4 m^{-2} day^{-1}, with short-term estimates up to 6160 mg CH_4 m^{-2} day^{-1}; Section 4.4.2) are mostly about one order of magnitude larger than those for Swedish *mires* (8–72 mg CH_4 m^{-2} day^{-1}; Table 6-3), but less different from estimates for Swedish littoral reedbeds (140–310 mg CH_4 m^{-2} day^{-1}; Kasimir-Klemedtsson et al. 2001). As mentioned in Section 6.5, it seems that older mires (bogs) emit less methane than the younger ones (fens). However, also the connection of the plant community to the groundwater ceases with the mire turning ombrotrophic (a fen into a bog) after a certain age (due to the thickness of peat accumulated), which limits direct root access of the plants to radionuclide releases from the bedrock.

For cultivated peatlands and upland soils (see Sections 3.1 and 6.6), it seems that methane emissions are practically always minor due to the high oxidation potential of the surface layer.

7.3 Implications for biosphere assessments

Radioactive carbon (C-14) from a geological repository may enter surface ecosystems, and a significant fraction of this radiocarbon released is expected to be in the form of low-weight organic molecules or inorganic carbon that may undergo biochemical transformations depending on the environmental conditions and microbial activity. The potential transformation of acetate and CO_2 to CH_4 and the further transport, transformation and emission of the methane in various ecosystems have been reviewed based on literature at hand – not aiming at a comprehensive account, but to provide an overall view improving the present knowledge basis in the biosphere assessments – and described in this report, as summarised in Sections 7.1 and 7.2 just above.

Mires and especially fens are by long assessment experience more typical locations to convey releases from the repository into the food web than older bogs in the present and future landscape of Forsmark. These systems emit considerable amounts of methane, so at least part of the repository-originated methane releases could be ventilated to the atmosphere and escape incorporation to the primary production and food webs. However, the main dose pathways relate to former mires that have been turned into cultivated peatlands. For example, in the SR-PSU assessment the main exposure pathway was rather the exposure directly from the groundwater than the exposure resulting from a radiocarbon storage accumulated in the peat matrix (object 157_2; Saetre and Ekström 2017). Thus, even if some radiocarbon released from the repository would be ventilated away as methane rather than being retained in the biological circulation in fens, implications to the doses would likely remain relatively minor. Furthermore, in drained and cultivated cropland, the fraction of the methane getting oxidised to carbon dioxide near the ground surface, and therefore available for uptake by crops, would anyway be considerable (Section 6.6). Also, in well-drained upland soils the oxidised fraction seems to be very high, as practically all the methane would be oxidised if the sufficiently aerated top soil is thicker than a few decimetres (i.e. in the order of less than 0.5 metres) (e.g. Hoch et al. 2014, Shaw and Thorne 2016). Consequently, accounting for radiocarbon from repositories that bypass the carbon uptake by primary producers in the form of methane likely would not decrease doses to humans substantially.

In lakes, that are relevant to the dose assessment particularly in earlier stages in the development of landscape, methane released or produced from radioactive or stable carbon can get oxidised into CO_2 along the diffusive path to the water surface, unless sufficiently strong stratification and consequently seasonally large storage in an anoxic water volume can be assumed. If such an anoxic volume can be assumed, it would allow major methane efflux events at lake turnover. However, there also is evidence that the radiocarbon could be transported into the aquatic food web, including fish, through the microbial biomass of methanotrophs (Section 4.5). In littoral areas and in epilittoral sediments of lakes, much of the methane could still escape from the oxidisation and plant uptake through ebullition or plant-mediated transport (or via sufficiently short diffusive path that seems considerably more unlikely to occur). This is largely similar to what would occur in undrained mires, and very fittingly the SKB biosphere assessments (e.g. SKB 2014, 2019b) readily handle such littoral parts of lakes as mire-type objects. Even though a clear minimum value for the methane escaping the oxidation cannot be readily defined for general application to littoral or mire systems, there would seem to be potential for further study if the location of the releases entering the combined system of open-water parts of the lake versus the bordering littoral/mire areas could be characterised better also for the biosphere objects in future landscapes.

As evident from the review, and its summary in Section 7.1, it is difficult to make a balanced estimate of the relative roles of the methane transport pathways, since so many regulating factors are in the play at the same time and since there is also potentially considerable spatial and temporal variability involved. In addition, the methane production and oxidation processes, too, are affected by the intimate coupling of vegetation, other sources of substrate, water table, biogeochemical conditions and microbial communities. Literature allows to characterise the individual processes and their couplings, though, and there has also been a considerable amount of new relevant literature published since the collection of material for this review in the first half of 2017. In any case, however, there would be merit in gaining better overall view on a more structured basis. The summary discussion in Section 7.1 paves a way to the identification of a common set of components and state variables across the relevant ecosystems and indicates that, largely, also the processes and their controls are common albeit functioning at different rates in different conditions. In other words, in the view of the author here, the material calls for organisation and complementation into an interaction matrix (for examples, see e.g. Avila et al. 2006 or SKB 2010). A matrix version general to all the ecosystems could also be modified to more specific circumstances by at least suppressing components, state variables and processes that are practically absent in the particular context. Description of the matrix constituents would also facilitate an organised way to collate also quantitative information where available and identify gaps warranting further search of literature or totally new research. However, it is recognised that this may not be a straightforward task due to the heterogeneity of the literature to be synthesised.

As partially touched upon above regarding lakes and lake/mire systems, for a more quantitative view of the potential fraction of methane escaping oxidation and incorporation into higher organisms, it would seem essential to first try to constrain how focused or dispersed the repository-originated C-14 releases can be expected to be in environments appropriately representing the relevant plausible future landscapes, and in which parts of the ecosystem they could enter (e.g. whether the releases would be with a high confidence into the littoral zones of a lake rather than to the relatively deep areas). Taking the large uncertainties inherent to the future landscape development into account this may not be conceivable, though, but also in that case there could be merit of studying the impact of postulated releases to certain types of areas on the radiological implications, and then at least qualitatively pondering the plausibility of such situations occurring under the different assessment scenarios and cases.

If quantitative modelling of the methane sources, transport and losses were to be strived for, to complement the process-based synthesis, for example Peltola et al. (2018), Raivonen et al. (2017), Susiluoto et al. (2018) and Xu et al. (2016) review and provide useful modelling tools for mires and terrestrial environments in general, as well as do Shaw and Thorne (2016) with their example of scoping calculations for upland agricultural soils. Whereas at least some of the former ones can readily handle submerged soil/peat, and would, thus, fit reasonably well to represent also the lake littoral zones, none of these seem to encompass the whole range of processes of concern, so some further model formulation work would seem necessary. However, it seems tedious to compile coherent and sufficiently representative datasets for the models, in contrast to the many pieces of data collated also in this report but remaining short of allowing clear quantitative conclusions. For more solid data basis for modelling efforts, readily completed or ongoing field observation campaigns on mires and freshwater bodies would likely be most fruitful, if the data were available in sufficient detail. In any case, the models should also be validated against sufficiently solid empirical data on the natural methane processes and their controls, even if then used to support assessment models with much longer timescales. As outlined already above, further review of literature and a systematic synthesis could help to better fit also the partial data together, though. Anyway, it would be very useful to iterate between improvements in modelling, data and synthesising of general knowledge on the key processes.

Regarding stream environments, the situation is on one hand similar to the lake littoral zones and mires, but on the other hand it is more complicated due to the inherent small-scale variability of streams. Due to their smaller role in SKB's biosphere assessments, the stream environments have not been addressed in this review to the same elaborateness as lakes and mires. However, if the fate of radiocarbon in streams raises as an issue worth the investment, the studies of natural methane production, transport and losses summarised in Chapter 5 would seem to provide a reasonably good basis for further development. Also in this case, the proposed systematic overall view of the processes and their couplings likely would be of good use.

For potential special scenarios of rapid or extensive release of methane (or analogously low-weight organic carbon species) from the repository, it needs to be noted that evidence from both the experiments with upland agricultural soils in the UK (Shaw and Thorne 2016, particularly their p 12) and from landfill examples (Section 3.2) indicate that in some situations the release could overwhelm the metabolic capacity of the soil microbial community, even if the methanotrophic organisms were readily stimulated by the presence of abundant quantities of methane. This could thus result in a considerable fraction of the releases passing the plant uptake and instead venting to the air. Such situation could be modelled though the Michaelis–Menten kinetics summarised in Section 2.2, together with literature or, preferably, specific experimental data to derive values for the kinetic parameters representative to the particular conditions.

As an overall conclusion, the present assumption that all C-14 released from the repository will be transformed into CO_2 and entering food chain through plant uptake is pessimistic but not unjustifiably so, since such situations cannot be completely ruled out in any of the recipient environments. However, as recommended above, there could be merit for a more systematic grasp of the interactive web of processes regulating the whole-system methane behaviour, primarily to strengthen the knowledge basis and secondarily possibly striving for enhanced process-level modelling supported by comprehensive empirical datasets. In addition, there may be further aspects to be considered for the radiological protection of the biota, even though current assessments indicate only very minor levels of exposure.

References

SKB's (Svensk Kärnbränslehantering AB) publications can be found at www.skb.com/publications. SKBdoc documents will be submitted upon request to document@skb.se.

Aario L, 1932. Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. Fennia 55, 1–179. (In German.)

Alm J, Schulman L, Walden J, Nykänen H, Martikainen P J, Silvola J, 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80, 161–174.

Alperin M J, Reeburg W S, 1984. Geochemical observations supporting anaerobic methane oxidation. In Crawford R L, Hanson R S (eds). Microbial growth on C_1 compounds. Washington DC: American Society for Microbiology, 282–298.

Amaral J A, Knowles R, 1995. Growth of methanotrophs in methane and oxygen counter gradients. FEMS Microbiology Letters 126, 215–220.

Amiro B D, Ewing L L, 1992. Physiological conditions and uptake of inorganic carbon-14 by plant roots. Environmental and Experimental Botany 32, 203–211.

Andersson E (ed), 2010. The limnic ecosystems at Forsmark and Laxemar-Simpevarp. SKB TR-10-02, Svensk Kärnbränslehantering AB.

Anthony C, 1982. The biochemistry of methylotrophs. London: Academic Press.

Arkebauer T J, Chanton J P, Verma S B, Kim J, 2001. Field measurements of internal pressurization in *Phragmites australis* (Poaceae) and implications for regulation of methane emissions in a midlatitude prairie wetland. American Journal of Botany 88, 653–658.

Armstrong W, Justin S, Beckett P M, Lythe S, 1991. Root adaptation to soil waterlogging. Aquatic Botany 39, 57–73.

Armstrong W, Strange M E, Cringle S, Beckett P M, 1994. Microelectrode and modelling study of oxygen distribution in roots. Annals of Botany 74, 287–299.

Aro L, Ikonen A, Kangasniemi V, 2017. Groundwater-sourced radionuclide transport in different development stages of mires: conceptual models. In 4th International Conference on Radioecology & Environmental Radioactivity, 3–8 September 2017, Berlin: Abstracts book. Fontenay-aux-Roses: Institut de Radioprotection et de Sûreté Nucléaire (IRSN), 606–607.

Auman A J, Speake C C, Lidstrom M E, 2001. *nifH* sequences and nitrogen fixation in Type I and Type II methanotrophs. Applied and Environmental Microbiology 67, 4009–4016.

Avery G B, Shannon R D, White J R, Martens C S, Alperin M J, 1999. Effect of seasonal changes in the pathways of methanogenesis on the $\delta^{13}C$ values of pore water methane in a Michigan peatland. Global Biogeochemical Cycles 13, 475–484.

Avery G B, Shannon R D, White J R, Martens C S, Alperin M J, 2003. Controls on methane production in a tidal freshwater estuary and a peatland: methane production via acetate fermentation and CO_2 reduction. Biogeochemistry 62, 19–37.

Avila R, Pröhl G, 2008. Models used in the SFR 1 SAR-08 and KBS-3H safety assessments for calculation of C-14 doses. SKB R-08-16, Svensk Kärnbränslehantering AB.

Avila R, Kovalets I, 2016. Models of C-14 in the atmosphere over vegetated land and above a surface-water body. SKB R-15-09, Svensk Kärnbränslehantering AB.

Avila R, Thiry Y, Gilbin R, Agüero A, Thorne M, Sheppard M, Tamponnet C, Ikonen A, Xu S, 2006. Recommendations for improving predictions of the long-term environmental behaviour of ^{14}C, ^{36}Cl, ^{99}Tc, ^{237}Np and ^{238}U: Findings of the IUR Waste and Radioecology Task Force. International Union of Radioecology. (IUR Report 6:2006)

Baker J F, Fritz P, 1981. Carbon isotopic fractionation during microbial methane oxidation. Nature 293, 289–291.

Bartlett K B, Crill P M, Sass R L, Harriss R C, Dise N B, 1992. Methane emissions from tundra environments in the Yukon-Kuskokwim delta, Alaska. Journal of Geophysical Research: Atmospheres 97, 16645–16660.

Basilier K, Granhall U, Stenström T-A, 1978. Nitrogen fixation in wet minerotrophic moss communities of a subarctic mire. Oikos 31, 236–246.

Basiliko N, Yavitt J B, 2001. Influence of Ni, Co, Fe, and Na additions on methane production in *Sphagnum*-dominated Northern American peatlands. Biogeochemistry 52, 133–153.

Bastviken D, 2009. Methane. In Likens G E (ed). Encyclopedia of inland waters. Vol 2. Oxford: Elsevier, 783–805.

Bastviken D, Ejlertsson J, Tranvik L, 2002. Measurement of methane oxidation in lakes: a comparison of methods. Environmental Science & Technology 36, 3354–3361.

Bastviken D, Ejlertsson J, Sundh I, Tranvik L, 2003. Methane as a source of carbon and energy for lake pelagic food webs. Ecology 84, 969–981.

Bastviken D, Cole J, Pace M, Tranvik L, 2004. Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. Global Biogeochemical Cycles 18, GB4009. doi:10.1029/2004GB002238

Bastviken D, Cole, J J, Pace M L, Van de Bogert M C, 2008. Fates of methane from different lake habitats: Connecting whole-lake budgets and CH_4 emissions. Journal of Geophysical Research: Biogeosciences 113, G02024. doi:10.1029/2007JG000608

Bastviken D, Santoro A L, Marotta H, Pinho L Q, Calheiros D F, Crill P, Enrich-Prast, A, 2010. Methane emissions from Pantanal, South America, during the low water season: toward more comprehensive sampling. Environmental Science & Technology 44, 5450–5455.

Bastviken D, Tranvik L J, Downing J A, Crill P M, Enrich-Prast A, 2011. Freshwater methane emissions offset the continental carbon sink. Science 331, 50. doi:10.1126/science.1196808

Belyea L R, 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos 77, 529–539.

Belyea L R, Baird A J, 2006. Beyond "the limits to peat bog growth": cross-scale feedback on peatland development. Ecological Monographs 76, 299–322.

Bender M, Conrad R, 1993. Kinetics of methane oxidation in oxic soils. Chemosphere 26, 687–696.

Bender M, Conrad R, 1994. Methane oxidation activity in various soils and fresh-water sediments: Occurrence, characteristics, vertical profiles, and distribution on grain-size fractions. Journal of Geophysical Research: Atmospheres 99, 16531–16540.

Bender M, Conrad R, 1995. Biological formation and consumption of methane. Soil Biology and Biochemistry 27, 1517–1527.

Bendix M, Tornbjerg T, Brix H, 1994. Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L.: 1. Humidity-induced pressurization and convective throughflow. Aquatic Botany 49, 91–105.

Bengtsson F, Granath G, Rydin H, 2016. Photosynthesis, growth, and decay traits in *Sphagnum*: a multispecies comparison. Ecology and Evolution 6, 3325–3341.

Berglund Ö, Berglund K, 2011. Influence of water table level and soil properties on emissions of greenhouse gases from cultivated peat soil. Soil Biology and Biochemistry 43, 923–931.

Bergström I, Mäkelä S, Kankaala P, Kortelainen P, 2007. Methane efflux from littoral vegetation stands of southern boreal lakes: an upscaled regional estimate. Atmospheric Environment 41, 339–351.

Biasi C, Jokinen S, Marushchak M E, Hämäläinen K, Trubnikova T, Oinonen M, Martikainen P J, 2014. Microbial respiration in Arctic upland and peat soils as a source of atmospheric carbon dioxide. Ecosystems 17, 112–126.

Billett M F, Harvey F H, 2013. Measurements of CO_2 and CH_4 evasion from UK peatland headwater streams. Biogeochemistry 114, 165–181.

Billet M F, Charman D J, Clark J M, Evans C D, Evans M G, Ostle N J, Worrall F, Burden A, Dinsmore K J, Jones T, McNamara N P, Parry L, Rowson J G, Rose R, 2010. Carbon balance of UK peatlands: current state of knowledge and future research challenges. Climate Research 45, 13–29.

Boddy E, Hill P W, Paul W, Farrar J, Jones D L, 2007. Fast turnover of low molecular weight components of the dissolved organic carbon pool of temperate grassland field soils. Soil Biology and Biochemistry 39, 827–835.

Bodelier P L E, 2011. Interactions between nitrogenous fertilizers and methane cycling in wetland and upland soils. Current Opinion in Environmental Sustainability 3, 379–388.

Bodelier P L E, Laanbroek H J, 2004. Nitrogen as a regulatory factor of methane oxidation in soils and sediments. FEMS Microbiology Ecology 47, 265–277.

Bogard M J, del Giorgio P A, Boutet L, Garcia Chaves M C, Prairie Y V, Merante A, Derry A M, 2014. Oxic water column methanogenesis as a major component of aquatic CH_4 fluxes. Nature Communications 5, 5350. doi:10.1038/ncomms6350

Bosse U, Frenzel P, 1997. Activity and distribution of methane-oxidizing bacteria in flooded rice soil microcosms and in rice plants (*Oryza sativa*). Applied and Environmental Microbiology 63, 1199–1207.

Brönmark C, Hansson L-A, 2005. The biology of lakes and ponds. 2nd ed. Oxford, UK: Oxford University Press.

Bubier J L, Moore T R, 1994. An ecological perspective on methane emissions from northern wetlands. Trends in Ecology and Evolution 9, 460–464.

Bubier J, Crill P, Moore T, Savage K, Varner R, 1998. Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. Global Biogeochemical Cycles 12, 703–714.

Bubier J L, Bhatia G, Moore T R, Roulet N T, Lafleur P M, 2003a. Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. Ecosystems 6, 353–367.

Bubier J, Crill P, Mosedale A, Frolking S, Linder E. 2003b. Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers: Peatland responses to interannual moisture. Global Biogeochemical Cycles 17, 1066. doi:10.1029/2002GB001946

Bull I D, Parekh N R, Hall G H, Ineson P, Evershed R P, 2000. Detection and classification of atmospheric methane oxidizing bacteria in soil. Nature 405, 175–178.

Bussmann I, 2005. Methane release through resuspension of littoral sediment. Biogeochemistry 74, 283–302.

Capone D G, Kiene R P, 1988. Comparison of microbial dynamics in marine and freshwater sediments: contrasts in anaerobic carbon catabolism. Limnology and Oceanography 33, 725–749.

Carpenter S R, 1983. Lake geometry: Implications for production and sediment accretion rates. Theoretical Biology 105, 273–286.

Casper P, Maberly S C, Hall G H, Finlay B J, 2000. Fluxes of methane and carbon dioxide from a small productive lake to the atmosphere. Biogeochemistry 49, 1–19.

Chanton J P, Martens C S, Kelley C A, Crill P M, Showers W J, 1992. Methane transport mechanisms and isotope fractionation in emergent macrophytes of an Alaskan tundra lake. Journal of Geophysical Research: Atmospheres 97, 16681–16688.

Chanton J, Chaser L, Glasser P, Siegel D, 2005. Carbon and hydrogen isotopic effects in microbial methane from terrestrial environments. In Flanagan L B, Ehleringer J R, Pataki D E (eds). Stable isotopes and biosphere-atmosphere interactions: processes and biological control. San Diego: Academic Press, 85–105.

Chanton J P, Glaser P H, Chasar L S, Burdige D J, Hines M E, Siegel D I, Tremblay L B, Cooper W T, 2008. Radiocarbon evidence for the importance of surface vegetation on fermentation and methanogenesis in contrasting types of boreal peatlands. Global Biochemical Cycles 22, GB4022. doi:10.1029/2008GB003274

Chanton J P, Powelson D K, Green R B, 2009. Methane oxidation in landfill cover soils, is a 10 % default value reasonable? Journal of Environmental Quality 38, 654–663.

Chapin F S, Bret-Harte M S, Hobbie S E, Zhong H, 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science 7, 347–358.

Charman D, 2002. Peatlands and environmental change. Chichester: Wiley.

Chowdhury T R, Dick R, 2011. Type II aerobic methane oxidizing bacteria (AMOB) drive methane oxidation in pulsed wetlands as indicated by ^{13}C-phospholipid fatty acid composition. Nature Proceedings. doi:10.1038/npre.2011.6291.1

Christensen T R, Panikov N, Mastepanov M, Joabsson A, Stewart A, Öquist M, Sommerkorn M, Reynaud S, Svensson B, 2003. Biotic controls on CO_2 and CH_4 exchange in wetlands – a closed environment study. Biogeochemistry 64, 337–354.

Christensen T R, Johansson T, Åkerman H J, Mastepanov M, 2004. Thawing sub-artic permafrost: effects on vegetation and methane emissions. Geophysical Research Letters 31, L04501. doi:10.1029/2003GL018680

Clymo R S, 1984. Limits to peat bog growth. Philosophical Transactions of the Royal Society, London, B 303, 605–654.

Clymo R S, Bryant C L, 2008. Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised peat bog. Geochimica et Cosmochimica Acta 72, 2048–2066.

Clymo R S, Hayward P M, 1982. The ecology of *Sphagnum*. In Smith A J E (ed). The ecology of bryophytes. London: Chapman & Hall, 229–289.

Clymo R S, Pearce D M E, 1995. Methane and carbon dioxide production in, transport through, and efflux from a peatland. Philosophical Transactions of the Royal Society, London, A 350, 249–259.

Clymo R S, Williams M M R, 2012. Diffusion of gases dissolves in peat pore water. Mires and Peat 10, 6.

Clymo R S, Turunen J, Tolonen K, 1998. Carbon accumulation in peatland. Oikos 81, 368–388.

Cole J J, Caraco N F, 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF_6. Limnology and Oceanography 43, 647–656.

Cole J J, Pace M L, 1998. Hydrologic variability of small, Northern Michigan lakes measured by the addition of tracers. Ecosystems 1, 310–320.

Cole J J, Carpenter S R, Kitchell J, Pace M L, Solomon C T, Weidel B, 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. Proceedings of the National Academy of Sciences 108, 1975–1980.

Conrad R, 1989. In Andreae M O, Schimel D S (eds). Exchange of trace gases between terrestrial ecosystems and the atmosphere. Chichester: Wiley, 39–58.

Conrad R, 1996. Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO). Microbiological Reviews 60, 609–640.

Conrad R, 1999. Contribution of hydrogen to methane production and control of hydrogen concentrations in methanogenic soils and sediments. FEMS Microbiology Ecology 28, 193–202.

Conrad R, 2009. The global methane cycle: recent advances in understanding the microbial processes involved. Environmental Microbiology Reports 1, 285–292.

Coulthard T J, Baird A J, Ramirez J, Waddington J M, 2006. Methane dynamics in peat: importance of shallow peats and a novel reduced-complexity approach for modelling ebullition. In Baird A J, Belyea L R, Comas X, Reeve A S, Slater L D (eds). Carbon cycling in northern peatlands. Washington D.C., American Geophysical Union, 173–186. (Geophysical Monograph Series, 184). doi:10.1029/2008GM000811

Cronk J K, Fennessy M S, 2001. Wetland plants: biology and ecology. Boca Raton, FL: Lewis Publishers.

Czepiel P M, Crill P M, Harriss R C, 1995. Environmental factors influencing the variability of methane oxidation in temperate zone soils. Journal of Geophysical Research: Atmospheres 100. 9359–9364.

Dacey J W H, Klug M J, 1979. Methane efflux from lake sediments through water lilies. Science 203, 1253–1254.

Dacey J W H, Drake B G, Klug M J, 1994. Stimulation of methane emission by carbon dioxide enrichment of marsh vegetation. Nature 370, 47–49.

Davis J B, Coty V F, Stanley J P, 1964. Atmospheric nitrogen fixation by methane-oxidizing bacteria. Journal of Bacteriology 88, 468–472.

De Visscher A, Tomas D, Boeckx P, Van Cleemput O, 1999. Methane oxidation in simulated landfill cover soil environments. Environmental Science & Technology 33, 1854–1859.

Deines P, Bodelier P L E, Eller G, 2007. Methane-derived carbon flows through methane-oxidizing bacteria to higher trophic levels in aquatic systems. Environmental Microbiology 9, 1126–1134.

Del Grosso S J, Parton W J, Mosier A R, Ojima D S, Potter C S, Borken W, Brumme R, Butterbach-Bahl K, Crill P M, Dobbie K, Smith K A, 2000. General CH_4 oxidation model and comparison of CH_4 oxidation in natural and managed systems. Global Biogeochemical Cycles 14, 999–1019.

DelSontro T, Boutet L, St-Pierre A, del Giorgio P A, Prairie Y T, 2016. Methane ebullition and diffusion from northern ponds and lakes regulated by the interaction between temperature and system productivity. Limnology and Oceanography 61, S62–S77.

Deppenmeier U, 2002. The unique biochemistry of methanogenesis. Progress in Nucleic Acid Research and Molecular Biology 71, 223–283.

Ding W X, Cai Z C, Tsuruta H, 2005. Plant species effects on methane emissions from freshwater marshes. Atmospheric Environment 39, 3199–3207.

Dinsmore K J, Smart R P, Billett M F, Holden J, Baird A J, Chapman P J, 2011. Greenhouse gas losses from peatland pipes: a major pathway for loss to the atmosphere? Journal of Geophysical Research: Biogeosciences 116, G03041. doi:10.1029/2011JG001646

Dise N, 2009. Peatland response to global change. Science 325, 810–811.

Dlugokencky E J, Steele L P, Lang P M, Masarie K A, 1994. The growth-rate and distribution of atmospheric methane. Journal of Geophysical Research: Atmospheres 9, 17021–17043.

Donis D, Flury S, Stöckli A, Spangenberg J E, Vachon D, McGinnis D F, 2017. Full-scale evaluation of methane production under oxic conditions in a mesotrophic lake. Nature Communications 8, 1661. doi:10.1038/s41467-017-01648-4

Dove A, Roulet N, Crill P, Chanton J, Bourbonniere R, 1999. Methane dynamics of a northern boreal beaver pond. Écoscience 6, 577–586.

Duddleston K N, Kinneyet M A, Kiene R P, Hines M E, 2002. Anaerobic microbial biogeochemistry in a northern bog: Acetate as a dominant metabolic end product. Global Biogeochemical Cycles 16, 1063. doi:10.1029/2001GB001402

Dunfield P, Knowles R, 1995. Kinetics of inhibition of methane oxidation by nitrate, nitrite, and ammonium in a humisol. Applied and Environmental Microbiology 61, 3129–3135.

Dunfield P, Knowles R, Dumont R, Moore T R, 1993. Methane production and consumption in temperate and subarctic peat soils − response to temperature and pH. Soil Biology and Biochemistry 25, 321–326.

Edwards C, Hales B A, Hall G H, McDonald I R, Murrell J C, Pickup R, Ritchie D A, Saunders J R, Simon B M, Upton M, 1998. Microbiological processes in the terrestrial carbon cycle: methane cycling in peat. Atmospheric Environment 32, 3247–3255.

Eriksson T, Öquist M G, Nilsson M B, 2010. Effects of decadal deposition of nitrogen and sulfur, and increased temperature, on methane emissions from a boreal peatland. Journal of Geophysical Research 115, G04036. doi:10.1029/2010JG001285

Fallon R D, Harrits S, Hanson R S, Brock T D, 1980. The role of methane in internal carbon cycling in Lake Mendota during summer stratification. Limnology and Oceanography 25, 357–360.

Fechner-Levy E J, Hemond H F, 1996. Trapped methane volume and potential effects on methane ebullition in a northern peatland. Limnology and Oceanography 41, 1375–1383.

Fendinger N J, Adams D D, Glotfelty D E, 1992. The role of gas ebullition in the transport of organic contaminants from sediments. Science of the Total Environment 112, 189–201.

Fenner N, Freeman C, 2001. Drought-induced carbon loss in peatlands. Nature Geoscience 4, 895–900.

Ferry J G, 1992. Methane from acetate. Journal of Bacteriology 174, 5489–5495.

Flechard C R, Neftel A, Jocher V, Ammann C, Leifeld J, Fuhrer J, 2007. Temporal changes in soil pore space CO_2 concentration and storage under permanent grassland. Agricultural and Forest Meteorology 142, 66–84.

Francez A J, Vasander H, 1995. Peat accumulation and peat decomposition after human disturbance in French and Finnish mires. Acta Oecologica 16, 599–608.

Freeman C, Nevison G B, Kang H, Hughes S, Reynolds B, Hudson J A, 2002. Contrasted effects of simulated drought on the production and oxidation of methane in a mid-Wales wetland. Soil Biology and Biochemistry 34, 61–67.

Frenzel P, Karofeld E, 2000. CH_4 emission from a hollow-ridge complex in a raised bog: The role of CH_4 production and oxidation. Biogeochemistry 51, 91–112.

Frenzel P, Thebrath B, Conrad R, 1990. Oxidation of methane in the oxic surface layer of a deep lake sediment (Lake Constance). FEMS Microbiology Letters 73, 149–158.

Frolking S, Roulet N T, Tuittila E-S, Bubier J L, Quillet A, Talbot J, Richard P J H, 2010. A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. Earth System Dynamics 1, 1–21.

Galand P E, Yrjälä K, Conrad R, 2010. Stable carbon isotope fractionation during methanogenesis in three boreal peatland systems. Biogeosciences 7, 3893–3900.

Ganzert L, Jurgens G, Münster U, Wagner D, 2007. Methanogenic communities in permafrost-affected soils of the Laptev Sea coast, Siberian Arctic, characterized by 16S rRNA gene fingerprints. FEMS Microbiology Ecology 59, 476–488.

Garcia J L, Patel B K C, Ollivier B, 2000. Taxonomic, phylogenetic, and ecological diversity of methanogenic Archae. Anaerobe 6, 205–226.

Gifford R M, 2003. Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. Functional Plant Biology 30, 171–186.

Gilbert B, Frenzel P, 1995. Flux to the atmosphere of CH_4 and CO_2 from wetland ponds on the Hudson Bay lowlands (Hbls). Soil Biology and Biochemistry 25, 621–630.

Giller P S, Malmqvist B, 1998. The biology of streams and rivers. Oxford, UK: Oxford University Press.

Glaser P H, Chanton J P, Morin P, Rosenberry D O, Siegel D I, Ruud O, Chasar L I, Reeve A S, 2004. Surface deformations as indicators of deep ebullition fluxes in a large northern peatland. Global Biochemical Cycles 18, GB1003. doi:10.1029/2003GB002069

Gonzalez-Gil G, Schroth G M H, Gomez K, Papritz A, Zeyer J, 2008. Diffusional and microbial isotope fractionation of methane during gas push–pull tests. Geochimica et Cosmochimica Acta 72, 2115–2124.

Gorham E, 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1, 182–195.

Grey J, 2016. The incredible lightness of being methane-fuelled: Stable isotopes reveal alternative energy pathways in aquatic ecosystems and beyond. Frontiers in Ecology and Evolution 4, 8. doi:10.3389/fevo.2016.00008

Grossart H-P, Frindte K, Dziallas C, Eckert W, Tang K V, 2011. Microbial methane production in oxygenated water column of an oligotrophic lake. Proceedings of the National Academy of Sciences 108, 19657–19661.

Grünfeld S, Brix H, 1999. Methanogenesis and methane emissions, effects of water table, substrate type and presence of *Phragmites australis*. Aquatic Botany 64, 63–75.

Gunnarsson U, Löfroth M, 2009. Våtmarksinventeringen – resultat från 25 års inventeringar. Nationell slutrapport för våtmarksinventeringen (VMI) i Sverige. Stockholm: Naturvårdsverket. (Rapport 5925) (In Swedish.)

Hahn-Schöfl M, Zak D, Minke M, Gelbrecht J, Augustin J, Freibauer A. 2011. Organic sediment formed during inundation of a degraded fen grassland emits large fluxes of CH_4 and CO_2. Biogeosciences 8, 1539–1550.

Hanson R S, Hanson T E, 1996. Methanotrophic bacteria. Microbiological Review 60, 439–471.

Hayward P M, Clymo R S, 1982. Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. Proceedings of the Royal Society, London, B 215, 299–325.

Hayward P M, Clymo R S, 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. Journal of Ecology 71, 845–863.

Heijmans M M P D, van der Knaap Y A M, Holmgren M, Limpens J, 2013. Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events. Global Change Biology 19, 2240–2250.

Hoch A R, Lever D A, Shaw G, 2014. Uptake of carbon-14 in the biosphere: Summary report. NPO004437, AMEC/004041/008 Issue 2, Radioactive Waste Management Limited.

Hoch A R, Rochelle C A, Humphreys P N, Lloyd J R, Heath T G, Thatcher K E, 2016. Carbon-14 Project Phase 2: Formation of a gas phase and its migration. AMEC/200047/007 Issue 1, AMEC, UK.

Holden J, Burt T P, 2003. Hydrological studies on blanket peat: the significance of the acrotelm-catotelm model. Journal of Ecology 91, 86–102.

Holden J, Evans M G, Burt T P, Horton M, 2006. Impact of land drainage on peatland hydrology. Journal of Environmental Quality 35, 1764–1778.

Horn M A, Matthies C, Küsel K, Schramm A, Drake H L, 2003. Hydrogenotrophic methanogenesis by moderately acid-tolerant methanogens of a methane-emitting acidic peat. Applied and Environmental Microbiology 69, 74–83.

Hornibrook E R C, Longstaffe F J, Fyfe W S, 1997. Spatial distribution of microbial methane production pathways in temperate zone wetland soils: Stable carbon and hydrogen isotope evidence. Geochimica et Cosmochimica Acta 61, 745–753.

Hornibrook E R C, Bowes H L, Culbert A, Gallego-Sala A V, 2009. Methanotrophy potential versus methane supply by pore water diffusion in peatlands. Biogeosciences 6, 1491–1504.

Houser J, Bade D, Cole J, Pace M, 2003. The dual influences of dissolved organic carbon on hypolimnetic metabolism: organic substrate and photosynthetic reduction. Biogeochemistry 64, 247–269.

Huber-Humer M, Gebert J, Hilger H, 2008. Biotic systems to mitigate landfill methane emissions. Waste Management & Research 26, 33–46.

Humer M, Lechner P, 1999. Alternative approach to the elimination of greenhouse gases from old landfills. Waste Management & Research 17, 443–452.

Humer M, Lechner P, 2001. Design of a landfill cover layer to enhance methane oxidation: results from a two year field investigation. In Christensen T H, Cossu R, Stegmann R (eds). Proceedings of SARDINIA 2001 – Eight International Waste Management and Landfill Symposium, Margherita di Pula, Italy, Vol. II: Leachate and landfill gas, 14–18 October 2001. Cagliari, Italy: CISA Environmental Sanitary Engineering Centre, 541.

Hütsch B W, Webster C P, Powlson D S, 1994. Methane oxidation in soil as affected by land use, soil pH and N fertilization. Soil Biology and Biochemistry 26, 1613–1622.

Huttunen J T, Väisänen T, Heikkinen M, Hellsten S, Nykänen H, Nenonen O, Martikainen P J, 2002. Exchange of CO_2, CH_4 and N_2O between the atmosphere and two northern boreal ponds with catchments dominated by peatlands or forests. Plant and Soil 242, 137–146.

Huttunen J T, Alm J, Liikanen A, Juutinen S, Larmola T, Hammar T, Silvola J, Martikainen P J, 2003. Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. Chemosphere 52, 609–621.

Hyvönen T, Ojala A, Kankaala P, Martikainen P, 1998. Methane release from stands of water horsetail (*Equisetum fluviatile*) in a boreal lake. Freshwater Biology 40, 275–284.

IAEA 1997. The Joint Convention on the Safety of Spent Fuel Management and on the Safety of Radioactive Waste Management. Vienna: International Atomic Energy Agency. (Information Circular INFCIRC/546)

ICRP 2013. Radiological protection in geological disposal of long-lived radioactive waste. Annals of the ICRP 42, 1–57. (ICRP Publication 122)

Ikonen A, Aro L, Mustonen J, 2015. Conceptual models of groundwater-related radionuclide transport in different development stages of mires. In Kuznetsov O L, Znamenskiy S R, Kantserova L V (eds). Болота Северной Европы: разнообразие, динамика и рациональное использование; Международный симпозиум (Петрозаводск, 2–5 сентября 2015 г.), тезисы докладов – Mires of Northern Europe: biodiversity, dynamics, management; international symposium (Russia, Petrozavodsk, September 2–5, 2015), abstracts. Petrozavodsk: Karelian Research Centre of the Russian Academy of Science, 88.

Ingram H A P, 1978. Soil layers in mires: function and terminology. Journal of Soil Science 29, 224–227.

IPCC, 2006. Guidelines for national greenhouse gas inventories. Available at: http://www.ipcc-nggip.iges.or.jp/public/2006gl/index.html [1 December 2008].

Ivanov K E, 1953. Гидрология болот. Leningrad: Gidrometeoizdat. (In Russian.)

Jang I, Lee S, Hong J-H, Kang H, 2006. Methane oxidation rates in forest soils and their controlling variables: a review and a case study in Korea. Ecological Research 21, 849–854.

Jensen S, Olsen R A, 1998. Atmospheric methane consumption in adjacent arable and forest soil systems. Soil Biology and Biochemistry 30, 1187–1193.

Joabsson A, Christensen T R, Wallen B, 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Trends in Ecology & Evolution 14, 385–388.

Johansson A E, Gustavsson A M, Öquist M G, 2004. Methane emissions from a constructed wetland treating wastewater–seasonal and spatial distribution and dependence on edaphic factors. Water Research 38, 3960–3970.

Jones R I, Grey J, 2011. Biogenic methane in freshwater food webs. Freshwater Biology 56, 213–229.

Jones R I, Carter C E, Kelly A, Ward S, Kelly D J, Grey J, 2008. Widespread contribution of methane-cycle bacteria to the diets of lake profundal chironomid larvae. Ecology 89, 857–864.

Joosten H, Clarke D, 2002. Wise use of mires and peatlands – background and principles including a framework for decision-making. Saarijärvi: International Mire Conservation Group and International Peatland Society.

Joosten H, Couwenberg J, Moen A, Tanneberger F, 2017a. Mire and peatland terms and definitions in Europe. In Joosten H, Tanneberger F, Moen A (eds). Mires and peatlands of Europe: Status, distribution and conservation. Stuttgart: E. Schweitzerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), 65–96.

Joosten H, Moen A, Couwenberg J, Tanneberger F, 2017b. Mire diversity in Europe: mire and peatland types. In Joosten H, Tanneberger F, Moen A (eds). Mires and peatlands of Europe: Status, distribution and conservation. Stuttgart: E. Schweitzerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), 5–64.

Juottonen H, 2008. *Archaea*, *Bacteria*, and methane production along environmental gradients in fens and bogs. PhD thesis. Viikki Graduate School in Molecular Biosciences, University of Helsinki.

Juottonen H, Hynninen A, Nieminen M, Tuomivirta T T, Tuittila E-S, Nousiainen H, Kell D K, Yrjälä K, Tervahauta A, Fritze H, 2012. Methane-cycling microbial communities and methane emissions in natural and restored peatlands. Applied and Environmental Microbiology 78, 6386–6389.

Juutinen S, Alm J, Larmola T, Huttunen J T, Morero M, Martikainen P J, Silvola J, 2003. Major implication of the littoral zone for methane release from boreal lakes. Global Biogeochemical Cycles 17, 1117. doi:10.1029/2003GB002105

Juutinen S, Alm J, Larmola T, Saarnio S, Martikainen P J, Silvola J, 2004. Stand-specific dynamics of CH_4 fluxes in boreal lakes: Patterns and controls. Journal of Geophysical Research 109, D19313. doi:10.1029/2004JD004782

Juutinen S, Rantakari M, Kortelainen P, Huttunen J T, Larmola T, Alm J, Silvola J, Martikainen P J, 2009. Methane dynamics in different boreal lake types. Biogeosciences 6, 209–223.

Kalff J, 2002. Limnology. Upper Saddle River, NJ: Prentice Hall.

Kankaala P, Ojala P A, Käki T, 2004. Temporal and spatial variation in methane emissions from a flooded transgression shore of a boreal lake. Biogeochemistry 68, 297–311.

Kankaala P, Taipale S, Grey J, Sonninen E, Arvola L, Jones R I, 2006. Experimental δC-13 evidence for a contribution of methane to pelagic food webs in lakes. Limnology and Oceanography 51, 2821–2827.

Kankaala P, Taipale S, Nykänen H, Jones R I, 2007. Oxidation, efflux, and isotopic fractionation of methane during autumnal turnover in a polyhumic, boreal lake. Journal of Geophysical Research: Biogeosciences 112, G02003. doi:10.1029/2006JG000336

Kasimir-Klemedtsson Å, Nilsson M, Sundh I, Svensson B H, 2001. Växthusgasflöden från myrar och organogena jordar. Stockholm: Naturvårdsverket. (Rapport 5132). (In Swedish.)

Kasimir-Klemedtsson Å, Weslien P, Klemedtsson, L, 2009. Methane and nitrous oxide fluxes from a farmed Swedish Histosol. European Journal of Soil Science 60, 321–331.

Kautsky U, Lindborg T, Valentin J, 2013. Humans and ecosystems over the coming millennia: Overview of a biosphere assessment of radioactive waste disposal in Sweden. Ambio 42, 383–392.

Kautsky U, Saetre P, Berglund S, Jaeschke B, Nordén S, Brandefelt J, Keesmann S, Näslund J-O, Andersson E, 2016. The impact of low and intermediate-level radioactive waste on humans and the environment over the next one hundred thousand years. Journal of Environmental Radioactivity 151, 395–403.

Kayler Z E, Sulzman E W, Rugh W D, Mix A C, Bond B J, 2010. Characterizing the impact of diffusive and advective soil gas transport on the measurement and interpretation of the isotopic signal of soil respiration. Soil Biology and Biochemistry 42, 435–444.

Keller J K, Bridgham S D, 2007. Pathways of anaerobic carbon cycling across an ombrotrophic-minerotrophic peatland gradient. Limnology and Oceanography 52, 96–107.

Keller M, Goreau T J, Wofsy S C, Kaplan W A, McElroy M B, 1983. Production of nitrous oxide and consumption of methane by forest soils. Geophysical Research Letters 10, 1156–1159.

Kettunen A, Kaitala V, Lehtinen A, Lohila A, Alm J, Silvola J, Martikainen P J, 1999. Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires. Soil Biology and Biochemistry 31, 1741–1749.

Kightley D, Nedwell D B, Cooper M, 1995. Capacity for methane oxidation in landfill cover soils measured in laboratory-scale soil microcosms. Applied and Environmental Microbiology 61, 592–601.

Kim J, Verma S B, Billesbach D P, 1998. Seasonal variation in methane emission from a temperate *Phragmites*-dominated marsh, effect of growth stage and plant-mediated transport. Global Change Biology 5, 433-440.

King G M, 1990. Regulation by light of methane emission from a Danish wetland. Nature 345, 513–515.

King G M, Roslev P, Skovgaard H, 1990. Distribution and rate of methane oxidation in sediments of the Florida Everglades. Applied and Environmental Microbiology 56, 2902–2911.

King J Y, Reeburgh W S, Regli S K, 1998. Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment. Journal of Geophysical Research: Atmospheres 103, 29083–29092.

King J Y, Reeburgh W S, Thieler K K, Kling G W, Loya W M, Johnson L C, Nadelhoffer K J, 2002. Pulse-labeling studies of carbon cycling in Arctic tundra ecosystems: The contribution of photosynthates to methane emission. Global Bioegeochemical Cycles 16, 1062. doi:10.1029/2001GB001456

Kjeldsen P, Dalager A, Broholm K, 1997. Attenuation of methane and nonmethane organic compounds in landfill gas affected soils. Journal of the Air & Waste Management Association 47, 1268–1275.

Kludze H K, Delaune R D, 1995. Gaseous exchange and wetland plant-response to soil redox intensity and capacity. Soil Science Society of America Journal 59, 939–945

Kludze H K, Delaune R D, Patrick W H, 1993. Aerenchyma formation and methane and oxygen exchange in rice. Soil Science Society of America Journal 57, 386–391.

Koh H-S, Ochs C A, Kewei Y, 2009. Hydrologic gradient and vegetation controls on CH_4 and CO_2 fluxes in a spring-fed forested wetlands. Hydrobiologia 630, 271–286.

Kohl J-G, Henze R, Kühl H, 1996. Evaluation of the ventilation resistance to convective gas-flow in the rhizomes of natural reed beds of *Phragmites australis* (Cav.) Trin. ex Steud. Aquatic Botany 54, 199–210.

Koncalova H, 1990. Anatomical adaptations to waterlogging in roots of wetland graminoids: Limitations and drawbacks. Aquatic Botany 38, 127–134.

Korhola A, Tolonen K, 1996. The natural history of mires in Finland and the rate of peat accumulation. In Vasander H (ed). Peatlands in Finland. Helsinki: Finnish Peatland Society, 20–26.

Korhola A, Tolonen K, Turunen J, Jungner H, 1995. Estimating long-term carbon accumulation rates in boreal peatlands by radiocarbon dating. Radiocarbon 37, 575–854.

Korrensalo A, 2017. Behind the stability of boreal bog carbon sink: Compositional and functional variation of vegetation across temporal and spatial scales. PhD thesis. University of Eastern Finland. (Dissertationes Forestales 240) doi:10.14214/df.240

Koskinen M, 2017. Impacts of restoration of forestry-drained peatlands on nutrient and organic carbon exports and methane dynamics. PhD thesis. University of Helsinki. (Dissertationes Forestales 232) doi:10.14214/df.232

Kotsyurbenko O R, Chin K J, Glagolev M V, Stubner S, Simankova M V, Nozhevnikova A N, Conrad R 2004. Acetoclastic and hydrogenotrophic methane production and methanogenic populations in an acidic West-Siberian peat bog. Environmental Microbiology 6, 1159–1173.

Krumholz L R, Hollenback J L, Roskes S J, Ringelberg D B, 1995. Methanogenesis and methanotrophy within a *Sphagnum* peatland. FEMS Microbiology Ecology 18, 215–224.

Kuivila K M, Murray J W, Devol A H, Novelli P C, 1989. Methane production, sulfate reduction and competition for substrates in the sediments of Lake Washington. Geochimica et Cosmochimica Acta 53, 409–416.

Käki T, Ojala A, Kankaala P, 2001. Diel variation in methane emissions from stands of *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha latifolia* L. in a boreal lake. Aquatic Botany 71, 259–271.

Kölbener A, 2010. Influence of plants upon methane emissions from wetlands. Ph.D. thesis. Swizz Federal Institute of Technology, Zürich. (DISS. ETH Nr. 19246)

Laanbroek H J, 2010. Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes: a mini-review. Annals of Botany 105, 141–153.

Lafleur P M, Moore T R, Roulet N T, Frolking S, 2005. Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. Ecosystems 8, 619–629.

Laine J, Minkkinen K, Laiho R, Tuittila E-S, Vasander H, 2000. Suokasvit: turpeen tekijät. Helsinki: University of Helsinki. (Publications from the Department of Forest Ecology 24) (In Finnish.)

Laine A, Sottocornola M, Kiely G, Byrne K A, Wilson D, Tuittila E-S, 2006. Estimating net ecosystem exchange in a patterned ecosystem: example from blanket bog, Agricultural and Forest Meteorology 138, 231–243.

Laine A, Byrne K A, Kiely G, Tuittila E-S, 2007a. Patterns in vegetation and CO_2 dynamics along a water level gradient in a lowland blanket bog. Ecosystems 10, 890–905.

Laine A, Wilson D, Kiely G, Byrne K A 2007b. Methane flux dynamics in an Irish lowland blanket bog. Plant and Soil 299, 181–193.

Laine A, Riutta T, Juutinen S, Väliranta M, Tuittila E-S, 2009. Acknowledging the spatial heterogeneity in modelling/reconstructing carbon dioxide exchange in a northern aapa mire. Ecological Modelling 220, 2646–2655.

Lansdown J M, Quay P D, King S L, 1992. CH_4 production via CO_2 reduction in a temperate bog: a source of ^{13}C-depleted CH_4. Geochimica et Cosmochimica Acta 56, 3493–3503.

Larmola T, Alm J, Juutinen S, Huttunen J T, Martikainen P J, Silvola J, 2004. Contribution of vegetated littoral zone to winter fluxes of carbon dioxide and methane from boreal lakes. Journal of Geophysical Research: Atmospheres 109, D19102. doi:10.1029/2004JD004875

Larmola T, Tuittila E-S, Tiirola M, Nykänen H, Martikainen P J, Yrjälä K, Tuomivirta T, Fritze H, 2010. The role of *Sphagnum* mosses in the methane cycling of a boreal mire. Ecology 91, 2356–2365.

Larmola T, Leppänen S M, Tuittila E-S, Aarva M, Merilä P, Fritze H, Tiirola M, 2014. Methanotrophy induces nitrogen fixation during peatland development. Proceedings of the National Academy of Sciences 111, 734–739.

Le Mer J, Roger P, 2001. Production, oxidation, emission and consumption of methane by soils: A review. European Journal of Soil Biology 37, 25–50.

Le Mer J, Escoffier S, Chessel C, Roger P A, 1996. Microbiological aspects of methane emission by a ricefield soil from Camargue (France): 2. Methanotrophy and related microflora. European Journal of Soil Biology 32, 71–80.

Leppälä M, Kukko-Oja K, Laine J, Tuittila E-S, 2008. Seasonal dynamics of CO_2 exchange during primary succession of boreal mires as controlled by phenology of plants. Écoscience 15, 460–471.

Leppälä M, Oksanen J, Tuittila E-S, 2011. Methane flux dynamics during mire succession. Oecologia 165, 489–499.

Lieberman R L, Rosenzweig A C, 2004. Biological methane oxidation: regulation, biochemistry, and active site structure of particulate methane monooxygenase. Critical Reviews in Biochemistry and Molecular Biology 39, 147–164.

Limer L (ed), 2019. C-14 in the biosphere: Report of an international workshop. BIOPROTA Forum.

Limer L, Ota M, Tanaka T, Thorne M, Walke R, 2017. C-14 terrestrial model-data comparisons: final report. BIOPROTA Forum.

Limer L M C, Smith K, Albrect A, Marang L, Norris S, Smith G M, Thorne M C, Xu S, 2012. C-14 long-term dose assessment: data review, scenario development, and model comparison. Stockholm: Swedish Radiation Safety Authority. (SSM Report 2012:47)

Limer L, Thorne M C, Towler G H, 2011. Assessment calculations for C-14 labelled gas for the LLWR 2011 ESC. LLW Repository Ltd. (QRS-1443Z-1 Version 4.0)

Limpens J, Berendse F, Blodau C, Canadell J G, Freeman C, Holden J, Roulet N, Rydin H, Schaepman-Strup G, 2008. Peatlands and the carbon cycle: from local processes to global implications – a synthesis. Biogeosciences 5, 1475–1491.

Litton C M, Raich J W, Ryan M G, 2007. Carbon allocation in forest ecosystems. Global Change Biology 13, 2089–2109.

Lovley D R, Klug M J 1982. Intermediary metabolism of organic matter in the sediments of a eutrophic lake. Applied and Environmental Microbiology 43, 552–560.

Lund M, Christensen T R, Lindroth A, Schubert P, 2012. Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland. Environmental Research Letters 7, 045704. doi:10.1088/1748-9326/7/4/045704

Löfgren A (ed), 2010. The terrestrial ecosystems at Forsmark and Laxemar-Simpevarp. SKB TR-10-01, Svensk Kärnbränslehantering AB.

Löfroth M, 1991. Våtmarkerna och deras betydelse. Solna: Naturvårdverkets Förlag. (In Swedish.)

Maanavilja L, Riutta T, Aurela M, Pulkkinen M, Laurila T, Tuittila E-S, 2011. Spatial variation in CO_2 exchange at a northern aapa mire. Biogeochemistry 104, 325–345.

Maljanen M, Liikanen A, Silvola J, Martikainen P J, 2003. Methane fluxes on agricultural and forested boreal organic soils. Soil Use and Management 19, 73–79.

Mattson M D, Likens G E, 1990. Air pressure and methane fluxes. Nature 347, 718–719.

Maxfield P J, Hornibrook E R C, Evershed R P, 2006. Estimating high-affinity methanotrophic bacterial biomass, growth, and turnover in soil by phospholipid fatty acid ^{13}C labeling. Applied and Environmental Microbiology 72, 3901–3907.

McDonald I R, Hall G H, Pickup R W, Murrell J C, 1996. Methane oxidation potential and preliminary analysis of methanotrophs in blanket bog peat using molecular ecology techniques. FEMS Microbiology Ecology 21, 197–211.

Megonigal J P, Hines M E, Visscher P T, 2003. Anaerobic metabolism: linkages to trace gases and aerobic processes. In Schlesinger W H (ed). Treatise on geochemistry, vol. 8: Biogeochemistry. Oxford: Pergamon, 317–424.

Megraw S R, Knowles R, 1987. Methane production and consumption in a cultivated humisol. Biology and Fertility of Soils 5, 56–60.

Merilä P, Galand P E, Fritze H, Tuittila E-S, Kukko-oja K, Laine J, Yrjälä K, 2006. Methanogen communities along a primary succession transect of mire ecosystems. FEMS Microbiology Ecology 55, 221–229.

Metje M, Frenzel P, 2005. Effect of temperature on anaerobic ethanol oxidation and methanogenesis in acidic peat from a northern wetland. Applied and Environmental Microbiology 71, 8191–8200.

Metje M, Frenzel P, 2007. Methanogenesis and methanogenic pathways in a peat from subarctic permafrost. Environmental Microbiology 9, 954–964.

Michmerhuizen C M, Striegl R G, McDonald M E, 1996. Potential methane emission from north-temperate lakes following ice melt. Limnology and Oceanography 41, 985–991.

Mikkelä K, Sundh I, Svensson B H, Nilsson M, 1995. Diurnal variation in methane emission in relation to the water table, soil temperature, climate and vegetation cover in a Swedish acid mire. Biogeochemistry 28, 93–114.

Milberg P, Törnqvist L, Westerberg L M, Bastviken D, 2017. Temporal variations in methane emissions from emergent aquatic macrophytes in two boreonemoral lakes. AoB Plants 9, plx029.

Minkkinen K, Laine J, Nykänen H, Martikainen P J, 1997. Importance of drainage ditches in emissions of methane from mires drained for forestry. Canadian Journal of Forest Research 27, 949–952.

Mobbs S, Smith K, Thorne M, Smith G, 2014. Modelling approaches to C-14 in soil-plant systems and in aquatic environments. Stockholm: Swedish Radiation Safety Authority. (SSM Report 2014:30)

Moore T R, Dalva M, 1993. The influence of temperature and water-table position on carbon-dioxide and methane emissions from laboratory columns of peatland soils. European Journal of Soil Science 44, 651–664.

Moore T R, Bubier J L, Frolking S E, Lafleur P M, Roulet N T, 2002. Plant biomass and production and CO_2 exchange in an ombrotrophic bog, Journal of Ecology 90, 25–36.

Moosavi S C, Crill P, 1997. Controls on CH_4 and CO_2 emissions along two moisture gradients in the Canadian boreal zone. Journal of Geophysical Research 102, 29261–29277.

Morrissey L A, Zobel D B, Livingston G P, 1993. Significance of stomatal control on methane release from *Carex*-dominated wetlands. Chemosphere 26, 339–355.

Mosier A R, Delgado J A, Keller M, 1998. Methane and nitrous oxide fluxes in an acid Oxisol in western Puerto Rico: effects of tillage, liming and fertilization. Soil Biology and Biochemistry 30, 2087–2098.

Murase J, Kimura M, 1994. Methane production and its fate in paddy fields. 7. Electron acceptors responsible for anaerobic methane oxidation. Soil Science and Plant Nutrition 40, 647–654.

Murase J, Sakai Y, Kametani A, Sugimoto A. 2005. Dynamics of methane in mesotrophic Lake Biwa, Japan. Ecological Research 20, 377–385.

Mäkilä M, Goslar T, 2008. The carbon dynamics of surface peat layers in southern and central boreal mires of Finland and Russian Karelia. Suo 59, 49–69.

Mäkilä M, Saarnisto M, Kankainen T, 2001. Aapa mires as a carbon sink and source during the Holocene. Journal of Ecology 89, 589–599.

Mäkilä M, Säävuori H, Kuznetsov O, Grundström A, 2013. Age and dynamics of peatlands in Finland. Espoo: Geological Survey of Finland. (Report of Peat Investigation 443)

Natchimuthu S, Sundgren I, Gålfalk M, Klemedtsson L, Crill P, Danielsson Å, Bastviken D, 2016. Spatio-temporal variability of lake CH_4 fluxes and its influence on annual whole lake emission estimates. Limnology and Oceanography 61, S13–S26.

Natchimuthu S, Wallin M B, Klemedtsson L, Bastviken D, 2017. Spatio-temporal patterns of stream methane and carbon dioxide emissions in a hemiboreal catchment in Southwest Sweden. Scientific Reports 7, 39729. doi:10.1038/srep39729

Neue H U, Roger P A, 1994. Potential of methane emission in major rice ecologies. In Zepp R G (ed). Climate biosphere interaction: Biogenic emissions and environmental effects of climate change. Chichester: Wiley, 39–54.

Neue H U, Becker-Heidmann P, Scharpenseel H W, 1990. Organic matter dynamics, soil properties, and cultural practices in ricelands and their relationship to methane production. In Bouwman A F (ed). Soils and the greenhouse effect. Chichester: Wiley, 457–466.

Nijp J J, Limpens J, Metselaar K, van der Zee S E A T M, Berendse F, Robroek B J M, 2015. Can frequent precipitation moderate the impact of drought on peatmoss carbon uptake in northern peatlands? New Phytologist 203, 70–80.

Nilsson M, Mikkelä C, Sundh I, Granberg G, Svensson B H, Ranneby B, 2001. Methane emissions from Swedish mires: national and regional budgets and dependence on mire vegetation. Journal of Geophysical Research: Atmospheres 106, 20847–20860.

Nilsson M, Sagerfors J, Buffam I, Laudon H, Eriksson T, Grelle A, Klemedtsson L, Weslien P, Lindroth A, 2008. Contemporary carbon accumulation in a boreal oligotrophic minerogenic mire – a significant sink after accounting for all C-fluxes. Global Change Biology 14, 2317–2332.

Nykänen H, Alm J, Lång K, Silvola J, Martikainen P J, 1995. Emissions of CH_4, N_2O and CO_2 from a virgin fen and a fen drained for grassland in Finland. Journal of Biogeography 22, 351–357.

Oades J M, 1988. The retention of organic matter in soils. Biogeochemistry 5, 35–70.

Pace M L, Cole J J, Carpenter S R, Kitchell J F, Hodgson J R., Van de Bogert M C, Bade D L, Kritzberg E S, Bastviken D, 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427, 240–243.

Pearce D M E, Clymo R S, 2001. Methane oxidation in a peatland core. Global Biogeochemical Cycles 15, 709–720.

Peltola O, Raivonen M, Li X, Vesala T, 2018. Technical Note: Comparison of methane ebullition modelling approaches used in terrestrial wetland models. Biogeosciences 15, 937–951.

Petersen S O, Hoffmann C C, Schäfer C-M, Blicher-Mathiesen G, Elsgaard L, Kristensen K, Larsen S E, Torp S B, Greve M H, 2012. Annual emissions of CH_4 and N_2O, and ecosystem respiration, from eight organic soils in western Denmark managed by agriculture. Biogeosciences 9, 403–422.

Powelson D, Chanton J, Abichou T, Morales J, 2006. Methane oxidation in compost and water spreading biofilters. Waste Management & Research 29, 528–536.

Powelson D K, Chanton J P, Abichou T, 2007. Methane oxidation in biofilters measured by mass-balance and stable isotope methods. Environmental Science & Technology 41, 620–625.

Päivänen J, Hånell B, 2012. Peatland ecology and forestry – a sound approach. Helsinki: University of Helsinki, Department of Forest Sciences, and Swedish University of Agricultural Sciences, Department of Forest Ecology and Management. (University of Helsinki Department of Forest Sciences Publications 3)

Raghoebarsing A A, Smolders A J P, Schmid M C, Rijpstra W I C, Wolters-Arts M, Derksen J, Jetten M S M, Schouten S, Sinninghe Damsté J S, Lamers L P M, Roelofs J G M, Op den Camp H J M, Strous M, 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 436, 1153–1156.

Raivonen M, Smolander S, Backman L, Susiluoto J, Aalto T, Markkanen T, Mäkelä J, Rinne J, Peltola O, Aurela M, Lohila A, Tomasic M, Li X, Larmola T, Juutinen S, Tuittila E-S, Heimann M, Sevanto S, Kleinen T, Brovkin V, Vesala T, 2017. HIMMELI v1.0: HelsinkI Model of MEthane buiLd-up and emIssion for peatlands. Geoscientific Model Development 10, 4665–4691.

Regina K, Pihlatie M, Esala M, Alakukku L, 2007. Methane fluxes on boreal arable soils. Agriculture, Ecosystems & Environment 119, 346–352.

Repo M E, Huttunen J T, Naumov A V, Chichulin A V, Lapshina E D, Bleuten W, Martikainen P J, 2007. Release of CO_2 and CH_4 from small wetland lakes in western Siberia. Tellus B 59, 788–796.

Riera J L, Schindler J E, Kratz T K, 1999. Seasonal dynamics of carbon dioxide and methane in two clear-water lakes and two bog lakes in northern Wisconsin, USA. Canadian Journal of Fisheries and Aquatic Sciences 56, 265–274.

Rinne J, Riutta T, Pihlatie M, Aurela M, Haapanala S, Tuovinen J P, Tuittila E-S, Vesala T, 2007. Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique. Tellus B 59, 449–457.

Riutta T, Laine J, Aurela M, Rinne J, Vesala T, Laurila T, Haapanala S, Pihlatie M, Tuittila E-S, 2007a. Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. Tellus B 59, 838–852.

Riutta T, Laine J, Tuittila E-S, 2007b. Sensitivity of CO_2 exchange of fen ecosystem components to water level variation. Ecosystems 10, 718–733.

Rosenberry D O, Glaser P H, Siegel D I, 2006. The hydrology of northern peatlands as affected by biogenic gas: current developments and research needs. Hydrological Processes 20, 3601–3610.

Roulet N T, Lafleur P M, Richard P J H, Moore T R, Humphreys E R, Bubier J, 2007. Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. Global Change Biology 13, 397–411.

Rudd J M W, Hamilton R D, 1978. Methane cycling in a eutrophic shield lake and its effects on whole lake metabolism. Limnology and Oceanography 23, 337–349.

Rudd J W M, Taylor C D, 1980. Methane cycling in aquatic environments. In Droop M R, Jannasch H W (eds). Advances in aquatic microbiology. London: Academic Press, 77–150.

Rusch H, Rennenberg H, 1998. Black alder (*Alnus glutinosa* (L.) Gaertn.) trees mediate methane and nitrous oxide emission from the soil to the atmosphere. Plant and Soil 201, 1–7.

Rydin H, 1993. Interspecific competition between Sphagnum mosses on a raised bog. Oikos 66, 431–423.

Rydin H, Jeglum J K, 2006. The biology of peatlands. 1st ed. New York: Oxford University Press.

Rydin H, Jeglum J K, 2013. The biology of peatlands. 2nd ed. Oxford, UK: Oxford University Press.

Saari A, Rinnan R, Martikainen P J, 2004. Methane oxidation in boreal forest soils: kinetics and sensitivity to pH and ammonium. Soil Biology and Biochemistry 36, 1037–1046.

Saarnio S, Alm J, Silvola J, Lohila A, Nykänen H, Martikainen P J, 1997. Seasonal variation in CH_4 emissions and production and oxidation potentials at microsites on an oligotrophic pine fen. Oecologia 110, 414–422.

Saetre P, Ekström P-A, 2017. Kompletterande beräkningar om biosfärsobjekt. SKBdoc 1571087 ver 1.0, Svensk Kärnbränslehantering AB. (In Swedish.)

Saetre P, Nordén S, Keesmann S, Ekström P-A, 2013. The biosphere model for radionuclide transport and dose assessment in SR-PSU. SKB R-13-46, Svensk Kärnbränslehantering AB.

Sakai Y, Murase J, Sugimoto A, Okubo K, Nakayama E, 2002. Resuspension of bottom sediments by an internal wave in lake. Lakes & Reservoirs 7, 339–344.

Sanseverino A M, Bastviken D, Sundh I, Pickova J, Enrich-Prast A, 2012. Methane carbon supports aquatic food webs to the fish level. PLoS ONE 7, e42723. doi:10.1371/jounal.pone.0042723

Sass R L, Fisher F M, Lewis S T, Jund M F, Turner F T, 1994. Methane emissions from ricefields: Effect of soil properties. Global Biogeochemical Cycles 8, 135–140.

Saunois M, Bousquet P, Poulter B, Peregon A, Ciais P, Canadell J G, Dlugokencky E J, Etiope G, Bastviken D, Houweling S, Janssens-Maenhout G, Tubiello F N, Castaldi S, Jackson R B, Alexe M, Arora V K, Beerling D J, Bergamaschi P, Blake D R, Brailsford G, Brovkin V, Bruhwiler L, Crevoisier C, Crill P, Covey K, Curry C, Frankenberg C, Gedney N, Höglund-Isaksson L, Ishizawa M, Ito A, Joos F, Kim H-S, Kleinen T, Krummel P, Lamarque J-F, Langenfelds R, Locatelli R, Machida T, Maksyutov S, McDonald K C, Marshall J, Melton J R, Morino I, Naik V, O'Doherty S, Parmentier F-J W, Patra P K, Peng C, Peng S, Peters G P, Pison I, Prigent C, Prinn R, Ramonet M, Riley W J, Saito M, Santini M, Schroeder R, Simpson I J, Spahni R, Steele P, Takizawa A, Thornton B F, Tian H, Tohjima Y, Viovy N, Voulgarakis A, van Weele M, van der Werf G R, Weiss R, Wiedinmyer C, Wilton D J, Wiltshire A, Worthy D, Wunch D, Xu X, Yoshida Y, Zhang B, Zhang Z, Zhu Q, 2016. The global methane budget 2000–2012. Earth System Science Data 8, 697–751.

Schilder J, Bastviken D, van Hardenbroek M, Kankaala P, Rinta P, Stotter T, Heiri O, 2013. Spatial heterogeneity and lake morphology affect diffusive greenhouse gas emission estimates of lakes. Geophysical Research Letters 40, 5752–5756.

Schimel J P, 1995. Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. Biogeochemistry 28, 183–200.

Schmidt U, Conrad R, 1993. Hydrogen, carbon monoxide, and methane dynamics in Lake Constance. Limnology and Oceanography 38, 1214–1226.

Schnell S, King G M, 1996. Response of methanotrophic activity in soils and cultures to water stress, Applied Environmental Microbiology 62, 3303–3209.

Schubert C J, Diem T, Eugster W, 2012. Methane emissions from a small wind shielded lake determined by eddy covariance, flux chambers, anchored funnels, and boundary model calculations: a comparison. Environmental Science & Technology 46, 4515–4522.

Schütz H, Holzapfel-Pschorn A, Conrad R, Rennenberg H, Seiler W, 1989. A three years continuous record on the influence of daytime, season and fertilizer treatment on methane emission rates from an Italian rice paddy field. Journal of Geophysical Research: Atmospheres 94, 16405–16416.

Schütz H, Schröder P, Rennenberg H, 1991. Role of plants in regulating the methane flux to the atmosphere. In Sharkey T D, Holland E A, Mooney H A (eds). Trace gas emission by plants. San Diego: Academic Press, 29–63.

Sebacher D I, Harriss R C, Bartlett K B, 1985. Methane emissions to the atmosphere through aquatic plants. Journal of Environmental Quality 14, 40–46.

Segers R, 1998. Methane production and methane consumption: a review of processes underlying wetland methane fluxes. Biogeochemistry 41, 23–51.

Seiler W, Conrad R, 1987. Contribution of tropical ecosystems to the global budgets of trace gases especially CH_4, H_2, CO, and N_2O. In Dickinson R E (ed). The geophysiology of Amazonia: vegetation and climate interactions. New York: Wiley, 33–162.

Shannon R D, White J R, 1996. The effects of spatial and temporal variations in acetate and sulfate on methane cycling in two Michigan peatlands. Limnology and Oceanography 41, 435–443.

Shaw G, Atkinson B, 2014. A review of literature in support of experimental and modelling studies of carbon-14 behaviour in the biosphere. AMEC/Nott/004041/001, Radioactive Waste Management Directorate, Nuclear Decommissioning Authority.

Shaw G G, Thorne M C, 2016. The oxidation of methane in soil as a factor in determining the radiological impact of a geological disposal facility. RWM005675, AMEC/200047/001 Issue 1, Radioactive Waste Management Limited.

Shen L, Wu H, Gao Z, 2015. Distribution and environmental significance of nitrite-dependent anaerobic methane-oxidising bacteria in natural ecosystems. Applied Microbiology and Biotechnology 99, 133–142.

Shurpali N J, Verma S B, Clement R J, Billesbach D P, 1993. Seasonal distribution of methane flux in a Minnesota peatland measured by eddy-correlation. Journal of Geophysical Research: Atmospheres 98, 20649–20655.

Silvola J, Alm J, Ahlholm U, Nykänen H, Martikainen P J, 1996. The contribution of plant roots to CO_2 fluxes from organic soils. Biology and Fertility of Soils 23, 126–131.

SKB, 2010. Components, processes and interactions in the biosphere. SKB R-10-37, Svensk Kärnbränslehantering AB.

SKB, 2011. Long-term safety for the final repository for spent nuclear fuel at Forsmark. Main report of the SR-Site project. SKB TR-11-01, Svensk Kärnbränslehantering AB.

SKB, 2014. Biosphere synthesis report for the safety assessment SR-PSU. SKB TR-14-06, Svensk Kärnbränslehantering AB.

SKB, 2015. Safety analysis for SFR. Long-term safety. Main report for the safety assessment SR-PSU. Revised edition. SKB TR-14-01, Svensk Kärnbränslehantering AB.

SKB, 2019a. Post-closure safety for a proposed repository concept for SFL. Main report for the safety evaluation SE-SFL. SKB TR-19-01, Svensk Kärnbränslehantering AB.

SKB, 2019b. Biosphere synthesis for the safety evaluation SE-SFL. SKB TR-19-05, Svensk Kärnbränslehantering AB.

Smith K (ed), 2015. Long-term dose assessment for carbon-14: Report of an international workshop. BIOPROTA Forum.

Smith L K, Lewis W M, 1992. Seasonality of methane emissions from five lakes and associated wetlands of the Colorado Rockies. Global Biogeochemical Cycles 6, 323–338.

Smith K, Smith G (eds), 2014. C-14: data, ecosystems and dose assessment; report of an international workshop, Aix-en-Provence, 1–3 April 2014. BIOPROTA Forum.

Sohlenius G, Schoning K, Baumgartner A, 2013. Development, carbon balance and agricultural use of peatlands – overview and examples from Uppland Sweden. SKB TR-13-20, Svensk Kärnbränslehantering AB.

SSM, 2009. The Swedish Radiation Safety Authority's regulations and general advice concerning the protection of human health and the environment in connection with the final management of spent nuclear fuel and nuclear waste. Stockholm: Swedish Radiation Safety Authority. (SSMFS 2008:37)

Stern J C, Chanton J, Abichou T, Powelson D, Yuan L, Escoriza S, Bogner J, 2007. Use of a biologically active cover to reduce landfill methane emissions and enhance methane oxidation. Waste Management 27, 1248–1258.

Steudler P A, Bowden R D, Melillo J M, Aber J D, 1989. Influence of nitrogen fertilization on methane uptake in temperate forest soil. Nature 341, 314–316.

Steven M, Smith K L, Beardsley M D, Colls J J, 2006. Oxygen and methane depletion in soil affected by leakage of natural gas. European Journal of Soil Science 57, 800–807.

St. Louis V L, Kelly C A, Duchemin É, Rudd J W M, Rosenberg D M, 2000. Reservoir surfaces as sources of greenhouse gases to the atmosphere: a global estimate. BioScience 50, 766–775.

Strack M, Waddington J M, Rochefort L, Tuittila E-S, 2006. Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown: water table and peatland CO_2 exchange. Journal of Geophysical Research: Biogeosciences 111, G02006. doi:10.1029/2005JG000145

Straková P, Niemi R M, Freeman C, Peltoniemi K, Toberman H, Heiskanen I, Fritze H, Laiho R, 2011. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. Biogeosciences 8, 2741–2755.

Ström L, Ekberg A, Mastepanov M, Christensen T R, 2003. The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Global Change Biology 9, 1185–1192.

Stumm W, Morgan J J, 1996. Aquatic chemistry: chemical equilibria and rates in natural waters. New York: Wiley.

Sugimoto A, Fujita N, 1997. Characteristics of methane emission from different vegetations on a wetland. Tellus B 49, 382–392.

Sundh I, Nilsson M, Granberg G, Svensson B H, 1994. Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. Microbial Ecology 27, 253–265.

Sundh I, Bastviken D, Tranvik L J, 2005. Abundance, activity, and community structure of pelagic methane-oxidizing bacteria in temperate lakes. Applied and Environmental Microbiology 71, 6746–6752.

Susiluoto J, Raivonen M, Backman L, Laine M, Mäkelä J, Peltola, O, Vesala T, Aalto T, 2018. Calibrating the sqHIMMELI v1.0 wetland methane emission model with hierarchical modeling and adaptive MCMC. Geoscientific Model Development 11, 1199–1228.

Suyker A E, Verma S B, Clement R J, Billesbach D P, 1996. Methane flux in a boreal fen: Season-long measurement by eddy correlation. Journal of Geophysical Research: Atmospheres 101, 28637–28647.

Taipale S, Kankaala P, Jones R I, 2007. Contributions of different organic carbon sources to *Daphnia* in the pelagic food web of a small polyhumic lake: results from mesocosm $DI^{13}C$-additions. Ecosystems 10, 757–772.

Taipale S, Kankaala P, Hämäläinen H, Jones R I, 2009. Seasonal shifts in the diet of lake zooplankton revealed by phospholipid fatty acid analysis. Freshwater Biology 54, 90–104.

Thanh Duc N, Crill P, Bastviken D, 2010. Implications of temperature and sediment characteristics on methane formation and oxidation in lake sediments. Biogeochemistry 100, 185–196.

Thomas K L, Benstead J, Davies K L, Lloyd D, 1996. Role of wetland plants in the diurnal control of CH_4 and CO_2 fluxes in peat. Soil Biology & Biochemistry 28, 17–23.

Thorne M C, MacKenzie J, 2005. The treatment of waste-derived gas in the biosphere in Nirex safety and performance assessments. Quintessa Limited/UK Nirex Limited. (QRS-1248A-1, version 2.0)

Thorne M, Smith K, Kovalets I, Avila R, Walke R, 2018. C-14 in the biosphere: terrestrial model-data comparisons and review of carbon uptake by fish. BIOPROTA Forum.

Torn M S, Chapin F S III, 1993. Environmental and biotic controls over methane flux from arctic tundra. Chemosphere 26, 357–368.

Tsitko I, Lusa M, Lehto J, Parviainen L, Ikonen A T K, Lahdenperä A-M, Bomberg M, 2014. The variation of microbial communities in a depth profile of an acidic, nutrient-poor boreal bog in southwestern Finland. Open Journal of Ecology 4, 832–859.

Tuittila E-S, Juutinen S, Frolking S, Väliranta M, Laine A M, Miettinen A, Seväkivi M-L, Quillet A, Merilä P, 2012. Wetland chronosequence as a model of peatland development: Vegetation succession, peat and carbon accumulation. The Holocene 23, 25–35.

Turetsky M R, Crow S E, Evans R J, Vitt D H, Wieder R K, 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. Journal of Ecology 96, 1297–1305.

Turetsky M R, Bond-Lamberty B, Euskirchen E, Talbot J, Frolking S, McGuire A D, Tuittila E-S, 2012. The resilience and functional role of moss in boreal and arctic ecosystems. New Phytologist 196, 49–67.

Turunen J, Tolonen K, 1996. Rate of carbon accumulation in boreal peatlands and climate change. In Lappalainen E (ed). Global peat resources. International Peat Society, 21–28.

Turunen J, Tomppo E, Tolonen K, Reinikainen A, 2002. Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. Holocene 12, 69–80.

Updegraff K, Bridgham S, Pastor J, Weishampel P, Harth C, 2001. Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. Ecological Applications 11, 311–326.

USEPA, 2004. Direct emissions from landfilling municipal solid waste. Washington, D.C.: United States Environmental Protection Agency.

Utsumi M, Nojiri Y, Nakamura T, Nozawa T, Otsuki A, Takamura N, Watanabe M, Seki H 1998. Dynamics of dissolved methane and methane oxidation in dimictic Lake Nojiri during winter. Limnology and Oceanography 43, 10–17.

van Breemen N, 1995. How *Sphagnum* bogs down other plants. Trends in Ecology & Evolution 10, 270–275.

van den Pol-van Dasselaar A, Oenema O, 1999. Methane production and carbon mineralisation of size and density fractions of peat soils. Soil Biology & Biochemistry 31, 877–886.

Van Der Nat F, Middelburg J J, 1998. Effects of two common macrophytes on methane dynamics in freshwater sediments. Biogeochemistry 43, 79–104.

Van Der Nat F J W A, Middelburg J J, van Meteren D, Wielemakers A, 1998. Diel methane emission patterns from *Scirpus lacustris* and *Phragmites australis*. Biogeochemistry 41, 1–22.

Vanselow-Algan M, Schmidt S R, Greven M, Fiencke C, Kutzbach L, Pfeiffer E M, 2015. High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. Biogeosciences 12, 4361–4371.

Vasander H, 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Annales Botanici Fennici 19, 103–125.

Vasander H, Kettunen A, 2006. Carbon in boreal peatlands. In Wieder R K, Vitt D H (eds). Boreal peatland ecosystems. Berlin: Springer Verlag. (Ecological studies 188), 165–194.

Verhoeven J, Liefveld W, 1997. The ecological significance of organochemical compounds in *Sphagnum*. Plant Biology 46, 117–130.

Verville J H, Hobbie S E, Chapin F S III, Hooper D U, 1998. Response of tundra CH_4 and CO_2 flux to manipulation of temperature and vegetation. Biogeochemistry 41, 215–235.

Vile M A, Bridgham S D, Wieder R K, Novák M, 2003. Atmospheric sulfur deposition alters pathways of gaseous carbon production in peatlands. Global Biogeochemical Cycles 17, 1058. doi:10.1029/2002GB001966

Vitt D H, 2006. Functional characteristics and indicators of boreal peatlands. In Wieder R K, Vitt D H (eds). Boreal peatland ecosystems. Berlin: Springer Verlag. (Ecological Studies 188), 9–24.

von Fischer J C, Butters G, Duchateau P C, Thelwell R J, Siller R, 2009. In situ measures of methanotroph activity in upland soil: a reaction–diffusion model and field observation of water stress. Jounal of Geophysical Research 114, G01015. doi:10.1029/2008JG000731

Waddington J M, Roulet N T, 2000. Carbon balance of a boreal patterned peatland. Global Change Biology 6, 87–97.

Waddington J M, Roulet N T, Swanson R V, 1996. Water table control of CH_4 emission enhancement by vascular plants in boreal peatlands. Journal of Geophysical Research: Atmospheres 101, 22775–22785.

Wallin M B, Öquist M G, Buffam I, Billett M F, Nisell J, Bishop K H, 2011. Spatiotemporal variability of the gas transfer coefficient (K_{CO2}) in boreal streams; implications for large scale estimates of CO_2 evasion. Global Biogeochemical Cycles 25, GB3025.

Walter K M, Zimov S A, Chanton J P, Verbyla D, Chapin F S, 2006. Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. Nature 443, 71–75.

Walter K M, Smith L C, Chapin F S III, 2007. Methane bubbling from northern lakes: Present and future contributions to the global methane budget. Philosophical Transactions of The Royal Society A 365, 1657–1676.

Wang Z P, Delaune R D, Masscheleyn P H, Patrick W H, 1993. Soil redox and pH effects on methane production in a flooded rice soil. Soil Science Society of America Journal 57, 382–385.

Wang H J, Lu J W, Wang W D, Yang L Y, Yin C Q, 2006. Methane fluxes from the littoral zone of hypereutrophic Taihu Lake, China. Journal of Geophysical Research: Atmospheres 111, D17109.

Wania R, Ross I, Prentice I C, 2010. Implementation and evaluation of a new methane model with a dynamic global vegetation model: LPJ-WHyME v1.3.1. Geoscientific Model Development 3, 565–584.

Watson A, Nedwell D B, 1998. Methane production and emission from peat: the influence of anions (sulphate, nitrate) from acid rain. Atmospheric Environment 32, 3239–3245.

Weisner S E B, 1987. The relation between wave exposure and distribution of emergent vegetation in a eutrophic lake. Freshwater Biology 18, 537–544.

Wetzel R G, 2001. Limnology: lake and river ecosystems. San Diego, CA: Academic Press.

Weyhenmeyer C E, 1999. Methane emissions from beaver ponds: Rates, patterns, and transport mechanisms. Global Biogeochemical Cycles 13, 1079–1090.

Whalen S C, 2005. Biogeochemistry of methane exchange between natural wetlands and the atmosphere. Environmental Engineering Science 22, 73–94.

Whalen S C, Reeburgh W S, 1988. A methane flux time series for tundra environments. Global Biogeochemical Cycles 2, 399–409.

Whalen S C, Reeburgh W S, Sandbeck K A, 1990. Rapid methane oxidation in a landfill cover soil. Applied and Environmental Microbiology 65, 3405–3411.

Whiticar M J, 1999. Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane. Chemical Geology 161, 291–314.

Whiticar M J, Faber E, Schoell M, 1986. Biogenic methane formation in marine and freshwater environments: CO_2 reduction vs. acetate fermentation–isotope evidence. Geochimica et Cosmochimica Acta 50, 693–709.

Whiting G J, Chanton J P, 1992. Plant-dependent CH_4 emission in subarctic Canadian fen. Global Biogeochemical Cycles 6, 225–231.

Whiting G J, Chanton J P, 1993. Primary production control of methane emission from wetlands. Nature 364, 794–795.

Wik M, Crill P M, Varner R K, Bastviken D, 2013. Multiyear measurements of ebullitive methane flux from three subarctic lakes. Journal of Geophysical Research: Biogeosciences 118, 1–15.

Williams R T, Crawford R L, 1984. Methane production in Minnesota peatlands. Applied and Environmental Microbiology 47, 1266–1271.

Williams M, Street L E, van Wijk M T, Shaver G R, 2006. Identifying differences in carbon exchange among arctic ecosystem types. Ecosystems 9, 288–304.

Wilson D, Alm J, Laine J, Byrne K A, Farrell E P, Tuittila E-S, 2009. Rewetting of cutaway peatlands: Are we re-creating hot spots of methane emissions? Restoration Ecology 17, 796–806.

Wilson D, Farrell C, Mueller C, Hepp S, Renou-Wilson F, 2013. Rewetted industrial cutaway peatlands in western Ireland: a prime location for climate change mitigation. Mires and Peat 11, 1–22.

Wu H, Green M, Scranton M I, 1997. Acetate cycling in the water column and surface sediment of Long Island Sound following a bloom. Limnology and Oceanography 42, 705–713,

Yavitt J B, Lang G E, Wieder R K, 1987. Control of carbon mineralization to CH_4 and CO_2 in anaerobic, *Sphagnum*-derived peat from Big Run Bog, West Virginia. Biogeochemistry 4, 141–157.

Yavitt J B, Downey D M, Lang G E, Sexstone A J, 1990. Methane consumption in two temperate forest soils. Biogeochemistry 9, 39–52.

Yu Z C, 2012. Northern peatland carbon stocks and dynamics: a review. Biogeosciences 9, 4071–4085.

Yvon-Durocher G, Allen A P, Bastviken D, Conrad R, Gudasz C, St-Pierre A, Thanh-Duc N, del Giorgio P A, 2014. Methane fluxes show consistent temperature dependence across microbial to ecosystem scales. Nature 507, 488–491.

Xu X, Yuan F, Hanson P J, Wullschleger S D, Thornton P E, Riley W J, Song X, Graham D E, Song C, Tian H, 2016. Reviews and syntheses: Four decades of modeling methane cycling in terrestrial ecosystems. Biogeosciences 13, 3735–3755.

Zaiss U, Winter P, Kaltwasser H, 1982. Microbial methane oxidation in the River Saar. Zeitschrift für allgemeine Mikrobiologie 22, 139–148.

Appendix 1

Biota nomenclature

The names used for the biota species and groups throughout the report have been compiled in Table A1-1 together with their corresponding common English and Swedish, as well as scientific, names. The following Internet resources have been used in the compilation of the table (September 2017): https://www.itis.gov/; https://artfakta.artdatabanken.se/; https://mesh.kib.ki.se/

Table A1-1. Names of biota species mentioned in this report.

Common English name	Scientific name	Common Swedish name
Acidobacteria	Acidobacteria	Acidobakterier
Actinobacteria	Actinobacteria	Aktinobakterier
Alder	Alnus spp.	Alar
Alphaproteobacteria	Alphaproteobacteria	Alphaproteobakterier
Archaea	Archaea	Arkéer
Arthropods	Arthropoda	Leddjur
Bacteria	Bacteria	Bakterier
Beaked sedge	Carex rostrata	Flaskstarr
Beaver	*Castor* spp.	Bäver
Bog arum	Calla palustris	Missne
Broadleaf cattail	Typha latifolia	Bredkaveldun
Brown mosses	–	Brunmossor
–	*Bryales* spp.	(Bladmossor)
–	*Calamagrostis* spp.	Rörsläktet
Carex sedges	*Carex* spp.	Starrar
–	Carex meyeriana	–
Cattails	*Typha* spp.	Kaveldun
Chara	*Chara* spp.	Sträfsen
–	Chloroflexi	–
Common cottongrass	Eriophorum angustifolium	Ängsull
Common reed	Phragmites australis	Bladvass
Common rush	Juncus effusus	Veketåk
Cottongrass	Eriophorum spp.	Ängsulls
Deltaproteobacteria	Deltaproteobacteria	Deltaproteobakterier
Fewseed sedge	Carex oligosperma	Starr växt
Firmicutes	Firmicutes	Firmikuter
Glassworm	*Chaoborus* spp. (larvae)	(Ett släkte av) tofsmygglarver
Graminoids	–	–
Grasses	Poaceae	Gräs
Leatherleaf	Chamaedaphne calyculata	Finnmyrten
Lotus	*Nelumbo* spp.	Lotusväxter
–	Methanomicrobiales	–
–	Methanosarcinales	–
Narrowleaf cattail	Typha angustifolia	Smalkaveldun
Norway spruce	Picea abies	Gran
Peat moss	*Sphagnum* spp. (pl. *Sphagna*)	Vitmossa
–	*Phragmites* spp.	Vassläktet
–	Planctomycetes	–
Pond-lilies (waterlilies)	*Nuphar* spp.	Gula näckrosor
Pondweeds	*Potamogeton* spp.	Natar
Prairie sphagnum	Sphagnum palustre	Sumpvitmossa
Proteobacteria	Proteobacteria	Proteobakterier
Purple marshlocks	Potentilla palustris	Kråkklöver
Purple small-reed	Calamagrostis canescens	Grenrör
Rannoch-rush	Scheuchzeria palustris	Kallgräs

Common English name	Scientific name	Common Swedish name
Reed grass	Calamagrostis angustifolia	(En art i släktet rör)
Rice	*Oryza* spp.	Ris
Rusty bogmoss	Sphagnum fuscum	Rostvitmossa
Saltmeadow cordgrass	Spartina patens	(En art av) marskgräs
Scots pine	Pinus sylvestris	Tall
Sedges	Cyperaceae	Halvgräs
Sitka spruce	Picea sitchensis	Sitkagran
Slender sedge	Carex lasiocarpa	Trådstarr
Spikerush	Eleocharis	Småsävs
Water horsetail	Equisetum fluviatile	Sjöfräken
Waterlilies (family)	Nymphaeaceae	Näckrosväxter
Waterlilies (genus)	Nymphaea	Vita näckrosor
Water sedge	Carex aquatilis	Norrlandsstarr
–	Verrucomicrobia	–
Yellow water-lily	Nuphar lutea	Gul näckros

Arkitektkopia AB, Bromma, 2022

SKB is responsible for managing spent nuclear fuel and radioactive waste produced by the Swedish nuclear power plants such that man and the environment are protected in the near and distant future.

skb.se