Chapter 3

Uncertainties modelling CH$_4$ emissions from northern wetlands in glacial climates: the role of vegetation parameters

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3.1 Abstract

Marine Isotope Stage 3 (MIS 3) interstadials are marked by a sharp increase in the atmospheric methane (CH$_4$) concentration, as recorded in ice cores. Wetlands are assumed to be the major source of this CH$_4$, although several other hypotheses have been advanced. Modelling of CH$_4$ emissions is crucial to quantify CH$_4$ sources for past climates. Vegetation effects are generally highly generalized in modelling past and present-day CH$_4$ fluxes, but should not be neglected. Plants strongly affect the soil-atmosphere exchange of CH$_4$ and the net primary production of the vegetation supplies organic matter as substrate for methanogens. For modelling past CH$_4$ fluxes from northern wetlands, assumptions on vegetation are highly relevant since paleobotanical data indicate large differences in Last Glacial (LG) wetland vegetation composition as compared to modern wetland vegetation. Besides more cold-adapted vegetation, sphagnum mosses appear to be much less dominant during large parts of the LG than at present, which particularly affects CH$_4$ oxidation and transport. To evaluate the effect of vegetation parameters, we used the PEATLAND-VU wetland CO$_2$/CH$_4$ model to simulate emissions from wetlands in continental Europe during LG and modern climates. We tested the effect of parameters influencing oxidation during plant transport ($f_{ox}$), vegetation net primary production (NPP, parameter symbol

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36  CHAPTER 3. UNCERTAINITIES: THE ROLE OF VEGETATION

\[ P_{\text{max}}, V_{\text{transp}}, Z_{\text{root}}, f_{\text{ex}} \]  

Our model results show that modelled \( \text{CH}_4 \) fluxes are sensitive to \( f_{\text{ox}} \) and \( Z_{\text{root}} \) in particular. The effects of \( P_{\text{max}}, V_{\text{transp}} \) and \( f_{\text{ex}} \) are of lesser relevance. Interactions with water table modelling are significant for \( V_{\text{transp}} \).

We conducted experiments with different wetland vegetation types for Marine Isotope Stage 3 (MIS 3) stadial and interstadial climates and the present-day climate, by coupling PEATLAND-VU to high resolution climate model simulations for Europe. Experiments assuming dominance of one vegetation type (\textit{Sphagnum} vs. \textit{Carex} vs. \textit{Shrubs}) show that \textit{Carex}-dominated vegetation can increase \( \text{CH}_4 \) emissions by 50% to 78% over \textit{Sphagnum}-dominated vegetation depending on the modelled climate, while for shrubs this increase ranges from 42% to 72%. Consequently, during the LG northern wetlands may have had \( \text{CH}_4 \) emissions similar to their present-day counterparts, despite a colder climate. Changes in dominant wetland vegetation, therefore, may drive changes in wetland \( \text{CH}_4 \) fluxes, in the past as well as in the future.

3.2 Introduction

Interstadials during the last glacial and previous glacials show a conspicuous increase in the atmospheric \( \text{CH}_4 \) concentration, which is recorded in ice cores [46, 17]. Several studies have addressed \( \text{CH}_4 \) fluxes from wetlands during past glacial climate warming phases to explain the origin of these elevated \( \text{CH}_4 \) concentrations [276, 265, 139, 101]. Such warming phases may also serve as an analogue for the effects of present warming on northern wetlands [31]. However, a complicating factor is the effect of vegetation on \( \text{CH}_4 \) emissions. Vegetation affects \( \text{CH}_4 \) fluxes from wetlands, modifying both the transfer of labile organic carbon into anoxic soils and the transfer of \( \text{CH}_4 \) from soil to the atmosphere. In large scale \( \text{CH}_4 \) emission models, this is often overlooked and it leads to simplistic descriptions of the wetland \( \text{CH}_4 \) flux dynamics [51, 283]. Glacial-interglacial and stadial-interstadial climate changes may have induced shifts in vegetation patterns or complete biomes. Also, vegetation and ecosystems which have no analogue today may have existed. Global vegetation model simulations involving past climates might be used, although these have yielded results significantly different from paleobotanical data [124]. An example of non-analogue vegetation is the abundance of sphagnum mosses in present-day and glacial wetlands. In MIS 3 and 2 peaty deposits in Europe, sphagnum mosses are practically lacking [26, 214, 124]. In this respect, wetland flora during most of the last glacial differed markedly from modern, often sphagnum-rich peatlands and tundra vegetation. The same holds for the last glacial environments in Siberia [100, 298, 317, 319].

Models commonly include two groups of processes that are related to vegetation. The first group refers to production of labile organic compounds from gross primary production (GPP), used by methanogens in the anaerobic soil zone. The second group of processes is related to the transport of \( \text{CH}_4 \) to the atmosphere via plant stems and leaves [302]. The latter processes may be influential, but their parameterization is complicated as all parameters tend to be difficult to measure [291, 131]. Differences in vegetation effectively influence \( \text{CH}_4 \) fluxes as proved by [147], documenting the relation between \( \text{CH}_4 \) and net primary production (NPP) in tundra vegetation. [291] and [56] have also shown the importance of plant transport of \( \text{CH}_4 \) through their aerenchymous tissues (tissues containing channels for gas exchange) and the differences between vegetation types. During
such transport oxidation of CH$_4$ may also occur. As shown by [212], symbiosis between Sphagnum spp. and methanotrophic bacteria (methanotrophs) allows within-plant oxidation of CH$_4$ even when plants are submerged.

Considerable spatial variations in fluxes related to vegetation differences have been found in northern wetlands (e.g. [262, 295, 282, 271, 202, 203]). Such variations have been ascribed to differences in NPP, plant transport and oxidation of CH$_4$ and can be reproduced by plot-scale models, if the vegetation parameters of the model are correctly specified [283, 202]. Changes in peatland vegetation (area fraction of Carex and Sphagnum vegetation and pools) also may influence future northern wetland CH$_4$ emissions [90, 252]. For global scale model simulations of CH$_4$ fluxes, the relevance of these vegetation-related processes is difficult to determine, although wetlands generally consist of mosaics of plants which may be constant in wide geographic areas [62]. Therefore, it could be justified to lump vegetation effects all together. A precise characterization of vegetation conditions generally remains out of scope for global scale simulations, even though regional attempts have already been made using remote sensing data [156, 233].

During MIS 3, wetlands were largely dominated by Cyperaceae spp. [214] with the occurrence of bryophytes other than Sphagnum. The cause may have been the ubiquitous presence of soils with generally high pH value caused by frequent cryoturbation processes, erosion/sedimentation of fresh, relatively unweathered sediment (e.g. [214]) and deposition of generally calcareous loess ([275, 297]). Also low atmospheric CO$_2$ concentrations may have decreased the expansion of sphagnum mosses [105]. The quality of organic matter in the substrate influences microbial metabolism and can act as a major limitation factor in their growth rates [296]. Thus, vegetation characteristics affecting the transfer of photosynthesis products to labile organic carbon in the soil may also have a large effect on CH$_4$ fluxes [147], e.g. root exudation and root distribution.

We hypothesize that large differences in vegetation between modern and past northern lowlands may have influenced past northern wetland fluxes, and this article explores the effect of vegetation parameters on a large scale model of CH$_4$ fluxes for the LG and modern climate. Our modelling experiments on past glacial climates are fully described in [31], where PEATLAND-VU model output was validated with present-day fluxes from natural wetlands by using the modern climate control experiment of the paleoclimate simulations, to drive the CH$_4$ emission model. That study also explored the effects of model complexity and water table modelling. The values obtained in the experiments are annual emissions from the European region displayed in Figure 3.1 on page 38 respectively for Modern and LG MIS 3 warm/interstadial and cold/stadial climates.
Figure 3.1: Land, sea and glacial ice distribution for the MIS3 stadial (MIS3COLD), interstadial (MIS3WARM) and present-day control (MODERN) climate model experiments of the Stage 3 project (see [19] for a more extensive description of the STAGE3 climate model runs).
3.3 Effects of plants on CH\textsubscript{4} fluxes

There are three main pathways for transport of CH\textsubscript{4} from the soil to the atmosphere (e.g. \cite{126, 61}):

1. Molecular diffusion, which is dependent on soil characteristics, such as porosity and permeability of the soil. During diffusion, CH\textsubscript{4} may be consumed by methanotrophic bacteria in oxygenated soil zones.

2. Ebulition, effective when a threshold CH\textsubscript{4} concentration is reached in water-saturated soil, so that CH\textsubscript{4} bubbles can form and rise to the soil surface.

3. Plant transport from the root zone through aerenchymous tissue of plants. This may provide a fast shortcut to bypass methanotrophic bacteria in oxygenated topsoil. On the other hand, CH\textsubscript{4} may be exposed to oxidation in the root zone and during transport in the plant as well.

\cite{69} ranks the importance of each pathway in percentage terms, allocating 2% of the total fluxes to molecular diffusion, while ebullition is held responsible for 48% and plants account for the remaining 50%. As the vegetation density increases, so does the proportion of the fluxes released to the atmosphere through plants; conversely the value for ebullition-related emissions decreases \cite{23}. Otherwise ebullition can be very efficient in completely water-saturated soils \cite{158}, due to the low solubility of CH\textsubscript{4} in water and the rapid transfer of bubbles \cite{44}, and can be enhanced by a decrease in atmospheric or hydrostatic pressure \cite{261, 251}. Oxidation of CH\textsubscript{4} is mainly associated with the root system of wetland plants, although it also occurs inside plants and at their surface. Methanotrophs occupy oxic zones at the root-soil interface \cite{272, 210, 247, 120} where oxygen is supplied by plant transport. Plants can actively drive gas exchange and therefore, this gas exchange rate is partly dependent on metabolism \cite{302}. Ström et al. \cite{254} demonstrated considerable differences in rhizosphere CH\textsubscript{4} oxidation between wetland plants; \textit{Juncus effusus} and \textit{Eriophorum vaginatum} showed high oxidation (>90%) compared to \textit{Carex rostrata} (20-40%). The high oxidation in the root system of \textit{Juncus effusus} is attributed to an efficient oxygen supply to the roots \cite{247}. Popp et al. \cite{210} found lower oxidation for \textit{Carex} (0 to 3-4%). However, the oxidation in the root system is difficult to determine, and Popp et al. \cite{210} note considerable differences between methods. According to an experiment by Berestovskaya et al. \cite{29}, CH\textsubscript{4} oxidation was found to occur in bog water, in green parts of peat moss and in all the soil horizons investigated, while its production was recorded in peat horizons, in clay with plant roots, and in peaty moss areas. Gas consumption by CH\textsubscript{4}-oxidizing bacteria in the vegetation is also supported by data from the incubation of marsh plants with up to 88% CH\textsubscript{4} depletion \cite{57}. Heilman et al. \cite{106} demonstrate oxidation at the surfaces of submerged plants. Raghoebarsing et al. \cite{212} have described a symbiosis of methanotrophs with \textit{Sphagnum} species. The methanotrophs live inside the plant between leaf cells and convert CH\textsubscript{4} to CO\textsubscript{2}, providing the plant with CO\textsubscript{2} for photosynthesis. \cite{148} have demonstrated the widespread occurrence of this symbiosis; high oxidation rates were measured in particular from samples derived from northeast Siberian tundra \cite{202}, collected by the first author of this paper. \textit{Sphagnum} species are able to decrease CH\textsubscript{4} fluxes from the soil by 40% to 90% of what would otherwise have been emitted into the atmosphere \cite{148, 202}. For global scale modeling of CH\textsubscript{4} emissions, it would be useful to extend the widely used concept of Plant Functional Type (PFT) with
these fundamental aspects of the carbon cycle. \cite{307} introduced two PFTs specifically for wetland methane modeling (flood-tolerant C3 graminoids and sphagnum mosses). Similarly, we grouped wetland plants according to their CH$_4$ transport and oxidation capacity, suited to model CH$_4$ emissions. The following two factors were taken into account in this classification:

1. The oxidation of CH$_4$ during plant transport. A major role is played by the metabolism of the plant, whether or not there is a bacterial community able to decompose CH$_4$ and whether it is supplied with oxygen.

2. The transport rate. For most vascular wetland plants, aerenchymous tissue in roots and stems allows passive or active transport of gases from the atmosphere to the root system, to exchange reduced soil gases for oxygen \cite{291,131,200}.

Species displaying any combination of low oxidation and fast transport will give CH$_4$ fluxes higher than those species with high oxidation and low transport. Therefore, transport rate itself cannot be sufficient to define the effectiveness of a plant relative to CH$_4$ emissions. For usage in our model experiments outlined below, we distinguish three main classes of wetland vegetation with respect to their functionality in CH$_4$ soil-atmosphere transport (Table 3.1, on page 50):

1. Graminoid vegetation dominated by Cyperaceae and Gramineae. As indicated above, oxidation can vary between different species from low to high (e.g. Carex sp. vs. Juncus). However, this vegetation is usually dominated by Carex species in northern wetlands, and in paleobotanical sections, abundant remains of Carex are usually found. Therefore, we denote it here as Carex-type vegetation and assume domination by Carex species. Its main characteristics are the dominance of aerenchymous gas transport through hollow roots and stems and low oxidation rate. This results in high CH$_4$ emissions rates in wetlands (e.g. \cite{282,283,202,203}). Based on the inter-species variability in the rhizosphere oxidation rate, more classes could be distinguished with intermediate or high oxidation (e.g. Juncus), but the paleobotanical significance of these distinctions would be speculative.

2. Vegetation dominated by sphagnum mosses, non-vascular plants without a root system, and a well-documented symbiosis with methanotrophic bacteria \cite{212}. Therefore, CH$_4$ emissions from areas dominated by these mosses are usually smaller than others.

3. Shrubs, such as Salix ssp., have been also taken into account, because they may be abundant in some wetland types. The few data that exist on CH$_4$ oxidation and transport properties suggest intermediate behavior, showing neither rapid rates of transport nor high oxidation potential. For instance, the oxidation in Salix nigra was moderated by decreased root density in wet conditions \cite{247}. Generally these plants occupy drier sites in northern wetlands and are adapted to occasional flooding only.

These classes are not meant to represent a full classification of wetland PFTs but to represent classification end members of wetland vegetation with respect to vegetation-mediated CH$_4$ emission, designed on behalf of our model experiments. Other species
groups from drier habitats have not been included here as they cannot affect CH$_4$ emissions \cite{116,157}. Other vegetation characteristics, for instance the leaf area index (LAI), have no direct effect on CH$_4$ fluxes, although high primary production enhances substrate availability for methanogens.

3.4 Modelling experiments

3.4.1 The PEATLAND-VU model

PEATLAND-VU is a process-based model, for CO$_2$ and CH$_4$ emission from wetland soils under various climate scenarios. It consists of four sub-models: a soil physics sub-model to calculate temperature (including soil freezing) and water saturation of the soil layers, a CO$_2$ sub-model, a CH$_4$ sub-model, and an organic production sub-model \cite{302,284}. The model includes several labile and refractory organic matter reservoirs (peat substrate, manure, roots and litter, root exudates and refractory humic matter). In the CH$_4$ sub-model, gas production below the water table linearly depends on labile organic carbon concentration, multiplied by a production rate factor R$_0$. We assumed a small contribution from peat to CH$_4$ formation using a rate constant R$_0_{\text{peat}}$ of 0.01 × the R$_0$ for labile organic matter in the model. The labile carbon pool is produced by the transfer of net primary production (NPP) into root exudates and plant litter. This depends on linear conversion factors for root-shoot and root-exudate allocation of NPP ($f_{\text{shoots}}, f_{\text{ex}}$), and the vertical root density distribution (exponential, determined by maximum rooting depth $Z_{\text{roots}}$). NPP depends on a maximum daily NPP $P_{\text{max}}$. Above the water table, CH$_4$ is oxidized by methanotrophs, which depends on CH$_4$ concentration and is modelled using a Michaelis-Menten relation \cite{302}. Soil-atmosphere transport includes diffusion, ebullition and transport by plants. Ebullition depends on a soil CH$_4$ concentration threshold. Plant transport depends on soil CH$_4$ concentration, root density, plant growth rate, and a vegetation-dependent factor, $V_{\text{transp}}$. During transport, part of the CH$_4$ may be oxidized, which is modelled using a plant oxidation factor $f_{\text{ox}}$. This includes all plant-related oxidation (within the rhizosphere, in plant tissue and at the plant surface). To summarize, vegetation processes influencing CH$_4$ fluxes in this model are: maximum NPP, a factor for all CO$_2$ that is oxidized during plant transport, partitioning of NPP among shoot and root production and the fraction of NPP transferred into below-ground labile organic carbon (the main substrate for methanogens), and a factor quantifying plant transport rate \cite{284,302}. Several of these parameters are poorly quantified, yet strongly determine model results \cite{283}. These parameters are displayed in Table 3.2, on page 51.

3.4.2 Climate model input to PEATLAND-VU

These experiments link the PEATLAND-VU model to the climate model experiments for the Stage 3 project on climate and landscape of Middle Weichselian Europe \cite{266,19}. They simulate the LG stadial and interstadial climates, together with a modern climate control experiment, at a high spatial resolution over Europe. The simulations focus on the climate of the MIS 3 stadials and interstadials. The climate model experiments were coupled interactively to the BIOME 3.5 global vegetation model. PEATLAND-VU is linked to the climate model by the output of monthly-averaged near-surface air temperature, precipitation and evaporation. These drive PEATLAND-VU and a water table model based
CHAPTER 3. UNCERTAINTIES: THE ROLE OF VEGETATION

The PEATLAND-VU output is integrated over a topography derived湿lands map which includes the areas that are exposed at the lower sea level stands of theLG [31], denoted as “seafloor” below. We show the results separately for present-day land and exposed seafloor. This distinction of exposed seafloor fluxes is crucial, to separate the effects of changes in global topography from other climate- and vegetation-induced fluxes. For a complete description of the model input see [31]. We use here the climate simulations for stadial and interstadial conditions, representing a typical MIS 3 stadial and interstadial (MIS3COLD and MIS3WARM simulations respectively), and the presentday climate control experiment (MODERN hereafter). The MIS3WARM (interstadial) simulation matches paleoclimate data more closely than the other simulations of the STAGE 3 experiments; the MIS3COLD climate model experiment shows higher temperatures than several paleoclimate proxies indicate, e.g. the extent of permafrost [286, 31]. The mean annual air temperatures over the land area in the model domain for MIS3WARM, MIS3COLD and MODERN are respectively 2.6°C, 2.2°C, and 6.6°C, mean January temperatures 8.1°C, 8.5°C, and 19.5°C. MIS3WARM is distinctly wetter than MIS3COLD, with mean annual precipitation over the land area of 732 vs. 674mm (MODERN: 972 mm). The domain with land, sea and land ice distribution is shown in Figure 3.1 on page 38. The land areas for the model domains of MIS3COLD, MIS3WARM and MODERN are 9.31×10^6 km^2, 9.76×10^6 km^2, and 9.29×10^6 km^2; the area for MIS3WARM is the largest because of a relatively wider area of exposed seafloor and a smaller ice cap.

3.4.3 Model runs

A number of model runs have been performed to test the sensitivity of vegetation-related parameters separately (see Table 3.2 on page 51):

- CH₄ oxidation during plant transport \( f_{ox} \);
- maximum NPP \( P_{max} \);
- plant transport rate factor \( V_{transp} \);
- root exudation factor \( f_{ex} \); and
- maximum rooting depth \( Z_{root} \).

These runs have been restricted to the MIS3WARM climate only, since only relative differences between the experiments are relevant here, rather than the climate itself. The water table (WT) greatly influences the CH₄ emissions, which are usually decreasing nearly exponentially when WT drops below the soil surface [190, 189, 227, 282]. We used two approaches to model the WT: a simple, fixed WT in which the WT is assumed to be at the soil surface throughout the year [276] (FIXEDWT hereafter) or a simulated WT based on the precipitation and temperature output of the climate model [31], cf. [60] (MODELWT hereafter). The latter model results generally in a high spring and early summer water table and a decrease of the water table in late summer, depending on the precipitation amount. Some model parameters are expected to interact with WT, since they are influenced by the (exponential) vertical root distribution: \( V_{transp}, f_{ex} \). Therefore, we also tested these parameters with both approaches of water table modelling. In the introduction, we mentioned how MIS3 wetland vegetation differed considerably from actual northern wetlands. To test the effects of observed differences between MIS 3 wetlands and present-day moss-rich tundra vegetation, we undertook experiments with
the three dominant wetland vegetation types outlined in Table 3.1 on page 50: Carex, Sphagnum, and shrubs (VEGETATION experiment). For each vegetation type, we used the parameter values as listed in Table 3.3 on page 52. These parameters are based on the morphology of the plants, on the literature discussed above, and on previous model optimization [283, 202]. We assume a higher CH$_4$ production rate for the Carex type than for Sphagnum as indicated by sensitivity experiments by Van Huissteden et al. [283] and Parmentier et al. [202], probably reflecting better substrate quality.

These sensitivity experiments also indicate value ranges for $f_{ox}$ and $V_{transp}$, for Carex and Sphagnum. The oxidation rate $f_{ox}$ is set to a low value for shrubs and Carex, and maximum for Sphagnum. The transport rate $V_{transp}$ and rooting depth $Z_{root}$ are set to a low value for Sphagnum vegetation and near maximum for Carex vegetation. In each case, we assume 100% cover of each vegetation type. These experiments include the MIS3COLD, MIS3WARM and MODERN climate model runs. For these experiments, the NPP ($P_{max}$) values were derived from the BIOME 3.5 model. All fluxes in the experiments are calculated in Gigatons CH$_4$ per year (GT yr$^{-1}$) for the entire model domain shown in Figure 3.1 on page 38. For all model runs, the soil profile is assumed uniform throughout the model domain and consists of an organic layer of 35 cm with 80% organic matter overlying mineral soil based on typical MIS 3 wetland paleosoils [275, 276, 31]. Van Huissteden et al. [283] have shown that the model is relatively insensitive to soil parameters.

### 3.5 Results

Figure 3.2 on page 44 shows the effect of oxidation of CH$_4$ during plant transport (the $f_{ox}$ parameter). Increasing $f_{ox}$, while keeping the other parameters constant, results in a linear decrease of the CH$_4$ flux. Both in the model and in real vegetated wetland ecosystems, the plant flux is the dominant flux [302, 69]. Since oxidation during plant transport is linearly related to the plant flux, this is an expected result. Likewise, increasing NPP ($P_{max}$ parameter) also results in a linear increment of the CH$_4$ flux (Table 3.4 on page 53). CH$_4$ production relates linearly to the amount of available labile organic carbon substrate, of which the production is also related linearly to NPP in the model.

Because of the possible interactions between water table and plant transport outlined above, the experiments for $V_{transp}$ have been carried out using two different approaches for water table, FIXEDWT and MODELWT. Figure 3.3 on page 44 displays the results for different values of $V_{transp}$ for both approaches. An increase of $V_{transp}$ does not result in large changes of the CH$_4$ flux. Again this is not unexpected, given the model structure. Although $V_{transp}$ is a multiplication factor in modelling the plant-mediated CH$_4$ flux, the flux is limited by the balance between CH$_4$ production and oxidation, and cannot be higher than the net production plus soil storage change. However, the interaction with the water table model causes opposing results. For FIXEDWT, the flux increases with rising $V_{transp}$, for MODELWT it decreases. In the model, the amount of plant-mediated transport is limited by the amount of roots below WT, which is exponentially distributed. With MODELWT, this produces a decrease of the flux at low WT, which is stronger at high values of $V_{transp}$, with FIXEDWT, this does not occur. Remarkably, the difference in behaviour of $V_{transp}$ with the water table model is very clear for the land areas and absent for the exposed seafloor areas.
CHAPTER 3. UNCERTAINTIES: THE ROLE OF VEGETATION

Figure 3.2: Increasing the oxidation parameter \( (f_{ox}) \) values results in a strong decrease of the \( \text{CH}_4 \) emissions for the model domain. The decrease is linearly related to \( f_{ox} \).

Figure 3.3: The effects of plant transport factor \( V_{\text{transp}} \) with fixed (FIXEDWT) and modelled (MODELWT) water table values. The plant transport clearly interacts with the water table model applied. For FIXEDWT, an increase in \( \text{CH}_4 \) flux occurs with increasing \( V_{\text{transp}} \), for MODELWT a decrease.
3.5. RESULTS

Figure 3.4: Increasing the maximum depth of the vegetation root system results in a nonlinear decrease of the CH$_4$ fluxes.

Figure 3.5: Fluxes for the wetland vegetation types serving as wetlands vegetation end members, for three modelled climates: MIS3COLD (stadial), MIS3WARM (interstadial), and MODERN (present climate). The horizontal lines in the bars separate the land flux (below the line) and the exposed seafloor flux (above the line) for the MIS3 climates.
In Table 3.4 on page 53, the effect of root exudation as a mass fraction of below-ground labile organic matter substrate for \( \text{CH}_4 \) production is listed. The fluxes increase slightly with higher value because of higher substrate availability for methanogens. However, the increase is less than 5% for a threefold increase of \( f_{ex} \). We tested here also for interaction with the water table model, because the water table also determines how much of the labile organic matter becomes available for \( \text{CH}_4 \) production. However, interaction with the water table model is minor, the increase of the \( \text{CH}_4 \) flux with \( f_{ex} \) is slightly stronger with FIXEDWT, since the water table with MODELWT results in a lower water table for part of the year and less anaerobic decomposition of the exudates.

For the exposed seafloor, the flux with FIXEDWT is slightly higher than that with MODELWT, which is opposite for the land area. The maximum rooting depth \( Z_{\text{root}} \) has a non-linear influence on the \( \text{CH}_4 \) emissions (see Figure 3.4 on page 45). At a larger rooting depth, the flux decreases and this decline is strongest at shallow rooting depths. However, a rooting depth of 0.2 m is shallow for most wetland ecosystems with vascular plants and should be considered as a minimum. In the model, the amount of plant transport at a certain depth is the product of \( V_{\text{transp}} \), the root density and the soil \( \text{CH}_4 \) concentration, which product is in turn is reduced by the oxidated fraction \( f_{ox} \). This results in a larger total fraction of oxidized \( \text{CH}_4 \) with larger rooting depth, in accordance with the large role of rhizosphere oxidation discussed above. The VEGETATION experiment highlights the range of emission values that can be expected assuming changes in (paleo)vegetation of the wetlands. To highlight the effect of each vegetation type, runs have been performed assuming that each of these vegetation types is the only one present (see Figure 3.5 on page 45). Taking the \textit{Sphagnum} type as reference, the \textit{Carex} and Shrub types result in 50% and 42% higher fluxes for the MODERN experiment. For the MIS3COLD experiment, the increase is 77% and 72%; for the MIS3WARM experiment, the increase is 68% and 61%. If we then compare MIS3COLD (Carex type) and MODERN (Sphagnum type), the fluxes from the two climates hardly differ; the MIS3COLD climate has even a slightly higher flux (2.9 vs. 2.8 Gt \( \text{CH}_4 \) yr\(^{-1} \)); the flux of MIS3WARM for the Carex type is conspicuously higher than MODERN with \textit{Sphagnum}, 3.3 Gt \( \text{CH}_4 \) yr\(^{-1} \).

### 3.6 Discussion

Model reconstructions are fundamental tools whenever proxy data are missing in paleoclimate research, but they are based on assumptions on model structure, parameters and model input. The PEATLAND-VU model is able to simulate the seasonal changes in \( \text{CH}_4 \) flux from a wide range of temperate and arctic wetland sites [284, 206, 283], at the level of individual sites. Van Huissteden et al. [283] have shown that the model is relatively insensitive to the soil definition, while it is strongly sensitive to vegetation parameters, in particular oxidation during plant-mediated transport. The model contains simulation of the soil temperature, including soil freezing and active layer depth and the active layer thickness [206]. Since peat and humic material are explicitly incorporated as organic carbon reservoirs [276], the model can simulate carbon fluxes resulting from decomposition of old carbon in soils. However, this results mostly in higher \( \text{CO}_2 \) fluxes, since old carbon reservoirs generally consist of refractory material that is not easily decomposed by methanogens. As mentioned before, a small contribution from decomposing
peat is included for CH$_4$ formation by assuming a rate constant $R_{0,\text{peat}}$ of $0.01 \times R_0$ for labile organic matter in the model. The low decomposition rate agrees well with the observations on organic matter in Pleistocene successions in northern Europe, which is generally well preserved \[275, 45\]; therefore, large scale decomposition of older organic matter in sediments during rapid climate changes of the LG is unlikely. The thickness of the organic layer in the model soil profile definition (in 3.4.3, Model Runs) also precludes large scale decomposition of old carbon. The CH$_4$ emissions modelled here are largely fluxes generated by decomposition of labile organic matter directly derived from ecosystem NPP.

The delineation of ice cover extent and exposed seafloor areas is also subject to large uncertainties. PEATLAND-VU uses the climate output and boundary conditions from the STAGE 3 Project model. The rather small Scandinavian ice caps assumed in the STAGE 3 project are confirmed by recent data. According to Helmens et al. \[107\], ice-free conditions occurred in northern Finland during MIS3 interstadials. The area of exposed seafloor is based on other models used as boundary conditions for the climate model \[266, 15\].

Our model does not account for permafrost degradation. During MIS3 interstadials, thaw lake formation may have occurred \[275, 215, 45\]. Nonetheless, our values are still consistent with those published by Van Huissteden \[276\] and in line with earlier estimates by Brook et al. \[46\] based on inverse modelling.

Our model shows that vegetation characteristics are a large source of uncertainty. In particular, assumptions on the amount of CH$_4$ oxidation during plant-mediated transport ($f_{ox}$) have a large effect on the results, but to a lesser extent also NPP, maximum rooting depth $Z_{\text{root}}$, and transport parameter $V_{\text{transp}}$. Higher $f_{ox}$ gives a strong decrease of the CH$_4$ fluxes. The production of labile organic matter in the root zone $f_{ex}$ had only a very minor effect. Larger $Z_{\text{root}}$ results in decreasing flux. It influences the emissions from vegetation because of its interaction with $V_{\text{transp}}$ and $f_{ox}$; a larger rooting depth supports more oxidation, which agrees with experimental observations \[247\]. Clearly, oxidation of CH$_4$ in vegetation is a highly important parameter determining the wetland CH$_4$ flux. Changes in the vegetation characteristics that affect oxidation therefore potentially affect CH$_4$ fluxes more strongly than changes in climate affecting water table or soil temperatures. In Figure 3.2 on page 44 a change in $f_{ox}$ from 0.2 to 0.9 results in an 58% decrease of the CH$_4$ flux, while in Figure 3.5 on page 45 the flux decrease between MODERN and ST3COLD climate ranges between 31 and 43%. The transport parameter $V_{\text{transp}}$ clearly interacts with the water table input of the model. When a fixed water level is imposed, the fluxes change in both magnitude and trend. This interaction is driven by the effect of the exponential root distribution in the model on the plant mediated transport. Also for $f_{ex}$ a slight interaction is noted, resulting in a stronger increase of the flux with increasing $f_{ex}$ with FIXEDWT. However, compared to the effect of oxidation, these interaction effects are of minor significance.

Exposed seafloor areas not only contribute to the MIS3 CH$_4$ fluxes, they also interact with some of the vegetation parameters and the water table model, notably for $V_{\text{transp}}$. $V_{\text{transp}}$ interacts strongly with the water table model for the land areas but not for the seafloor areas. An explanation for this interaction is the difference in elevation distribution between the land areas and the exposed seafloor areas. The latter have a much smaller range in elevation. The climate model grid cells are small enough to resolve regional relief in Europe and the model can therefore simulate the effects of topography on
CHAPTER 3. UNCERTAINTIES: THE ROLE OF VEGETATION

regional climate. The resulting regional differences in precipitation and temperature in turn affect the modelled water table in the MODELWT experiments (not in FIXEDWT which assumes a constant water table at the surface throughout the year). Consequently, the difference in elevation distributions of land and seafloor areas also affect vegetation parameters that strongly interact with the water table and with the way it is modelled. For the exposed seafloor areas, this results in a much smaller spatial variability of the water table. This is combined with a weaker seasonality of the precipitation distribution in generally maritime climate conditions, resulting also in less temporal variability of the water table; hence, the MODELWT water tables will also be more constant and similar to FIXEDWT. However, since the exposed seafloor areas are small relative to land area, this has only a minor effect on the total flux.

Interaction between the vegetation parameters are difficult to test in our modelling setup, because the number of model runs to be performed increases rapidly with the number of parameters. Van Huissteden et al. [283] tested the PEATLAND-VU model on the scale of observation sites using monte-carlo methods. This showed the presence of interaction between $f_{ox}$, $V_{transp}$ and microbial CH$_4$ production rate $R_0$; a higher $V_{transp}$ and $R_0$ can for instance compensate for a higher $f_{ox}$. In the case of paleo-wetland fluxes, vegetation parameters need to agree with paleobotanical reconstructions. However, species cover percentages are difficult to derive from paleobotanical data (e.g. [124]). Moreover, wetland vegetation tends to have a mosaic-like pattern. Ran [214] could determine vegetation communities based on detailed macro-remain analysis. Her MIS3 stadial and interstadial wetland vegetation in the eastern Netherlands consisted of a pattern of treeless vegetation communities dominated by Cyperaceae and Juncaceae, with varying amounts of non- Sphagnum bryophytes and a water table generally close to or above the soil surface. Carex roots dominated the organic matter of the silt and peat beds deposited in these wetlands. Areal percentages of vegetation communities could not be determined, however. By comparison, a present-day Siberian tundra site consist of a mosaic of vegetation dominated by either Carex species (or Sphagnum in the parts with high water table, and Betula nana or Eriophorum tussocks in the drier parts. The Carex-dominated areas occupy up to 20% of the area, Sphagnum-dominated vegetation up to 45%, drier vegetation types vary between 35 and 90% [271]. The sphagnum mosses are important in the present-day CH$_4$ cycle, but their contribution may have been much smaller in glacial paleo-climates as is shown by the paleobotanical record. Conversely, Carex spp. and graminoid vegetation in general provide the most effective pathway to transport CH$_4$ from soil into the atmosphere [120]. Low transport, high oxidation vegetation (Sphagnum-type) produces much lower fluxes than high transport rate, low oxidation vegetation (Carex-type), with Shrubs intermediate as summarized in Figure 3.5 on page 45. Our model shows that for the colder glacial climates, the dominance of Carex-type vegetations may have resulted in CH$_4$ fluxes of similar or even higher magnitude, as those for the modern climate with largely sphagnum-dominated vegetation in wetlands, despite the colder climate which should have reduced methanogenesis. Of course, we used end members for the wetland vegetation in our model experiments which exacerbates the differences, and in present-day wetlands large areas are covered with Carex-type vegetation as well. Nonetheless, it indicates that glacial wetland CH$_4$ fluxes should have been relatively high compared with those of present-day wetlands because of the differences in vegetation-related oxidation and transport of CH$_4$. In present-day northern wetland environments, thawing permafrost or an increase of the active layer thickness is often accompanied by a change from a
Sphagnum-dominated vegetation towards a vegetation cover with predominant Carex and Eriophorum spp., leading to increased CH$_4$ emissions [63, 282]. Our results show that such an increase in Carex-dominated wetland ecosystems may result in a considerable rise of CH$_4$ fluxes, although this may also be compensated by a larger rate of CO$_2$ uptake [263]. Conversely, for the early Holocene, the decreasing trend of CH$_4$ [17, 229] may also be caused by the gradual expansion of Sphagnum-dominated wetlands at the expense of other wetland types.

### 3.7 Conclusions

The emissions of CH$_4$ from wetland soils to the atmosphere are not only a matter of hydrology and wetland area, but also depend on a more complicated balance between all the sinks and sources of CH$_4$ within the soil-vegetation-atmosphere continuum, including all methanotrophic and methanogenic bacteria involved in such reactions. Our model experiments show that in Pleistocene climates CH$_4$, fluxes are sensitive to wetland vegetation characteristics: oxidation during soil-vegetation-atmosphere exchange, NPP, rooting depth and plant-mediated transport rate. Oxidation proves to be a major parameter which effectively modifies fluxes. Particularly, flux differences between Carex-dominated and Sphagnum-dominated wetlands may be large, 50% to 78% relative to sphagnum. We have shown that vegetation characteristics cannot be neglected when paleo-wetland fluxes are modelled, and therefore paleobotanical information is crucial to estimate past CH$_4$ emissions. Our experiments show that changes in wetland vegetation may alter CH$_4$ fluxes drastically. This pertains to past Pleistocene as well as future Anthropocene wetland CH$_4$ fluxes. Because of differences in vegetation derived from the paleobotanical record, the glacial wetlands in Europe may have had similar or even higher fluxes than the present-day wetlands.

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<table>
<thead>
<tr>
<th>Wetland Description</th>
<th>Transport</th>
<th>Oxidation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carex type</td>
<td>Rapid</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
<tr>
<td>Sphagnum type</td>
<td>Minimal</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
<tr>
<td>Ombrotrophic bogs,</td>
<td>Intermediate</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
<tr>
<td>Riparian, Fens, Lawns</td>
<td>Intermediate</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
<tr>
<td>Hummocks and pools</td>
<td>Intermediate</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
<tr>
<td>Carex type</td>
<td>Rapid</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
<tr>
<td>Sphagnum type</td>
<td>Minimal</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
<tr>
<td>Ombrotrophic bogs,</td>
<td>Intermediate</td>
<td>In Rhizosphere, Lawns</td>
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<tr>
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<td>Intermediate</td>
<td>In Rhizosphere, Lawns</td>
<td>Low, Riparian, Ombrotrophic bogs</td>
</tr>
</tbody>
</table>

**Table 3.1:** Wetland plant functional types and their main characteristics as used in the model experiments.
Table 3.2: Vegetation and microbial population parameters used in PEATLAND-VU and the model experiments described in 3.4.3. If no units are given in column Units/range, the parameter is dimensionless. Column Symb: symbols used for the parameters; Column Ref: literature references; W-H is Walter and Heimann [302]; S is Shaver et al. [245]; H is van Huissenden et al. [283].

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symb.</th>
<th>Description</th>
<th>Units/range</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant transport factor</td>
<td>$V_{transp}$</td>
<td>Vegetation type factor for gas transport by plants</td>
<td></td>
<td>W-H</td>
</tr>
<tr>
<td>Oxidation fraction</td>
<td>$f_{ox}$</td>
<td>Fraction of methane oxidized during transport by plants</td>
<td>01</td>
<td>W-H</td>
</tr>
<tr>
<td>Maximum net primary</td>
<td>$P_{max}$</td>
<td>Maximum daily NPP at optimum productivity temperature conditions</td>
<td>kg $Cm^{-2}$ day$^{-1}$</td>
<td>S</td>
</tr>
<tr>
<td>Shoots factor</td>
<td>$f_{shoots}$</td>
<td>Mass factor of NPP that consists of shoots, the remainder is root growth</td>
<td>0.20.8</td>
<td>S</td>
</tr>
<tr>
<td>Exudate factor</td>
<td>$f_{ex}$</td>
<td>Mass factor of below-ground production turned into root exudates</td>
<td>0.10.3</td>
<td>H</td>
</tr>
<tr>
<td>Rooting depth</td>
<td>$Z_{root}$</td>
<td>Maximum rooting depth</td>
<td>0.2-0.5</td>
<td>H</td>
</tr>
<tr>
<td>CH$_4$ production</td>
<td>$R_0$</td>
<td>Production rate factor for CH$_4$ production from labile organic carbon</td>
<td>$\mu m h^{-1}$</td>
<td>W-H</td>
</tr>
<tr>
<td>Temperature sensitivity CH$_4$</td>
<td>$Q_{10}$</td>
<td>$Q_{10}$ correction for temperature sensitivity of CH$_4$ production</td>
<td>1.716</td>
<td>W-H</td>
</tr>
</tbody>
</table>
**Table 3.3:** Standard and PFT adapted values for vegetation parameters. The standard parameter values are used for runs when no vegetation distinction is made, as in Berrittella and Van Huissteden [31]. Parameter symbols as in Table 3.2 on page 51. Wetland PFTs as in Table 3.1 on page 50.

<table>
<thead>
<tr>
<th>Wetland vegetation type</th>
<th>$R_0$</th>
<th>$f_{ox}$</th>
<th>$f_{shoot}$</th>
<th>$Z_{root}$</th>
<th>$V_{transp}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard value</td>
<td>0.4</td>
<td>0.2</td>
<td>0.7</td>
<td>0.3</td>
<td>12</td>
</tr>
<tr>
<td><em>Carex</em> type</td>
<td>0.4</td>
<td>0.2</td>
<td>0.5</td>
<td>0.4</td>
<td>12</td>
</tr>
<tr>
<td><em>Sphagnum</em> type</td>
<td>0.2</td>
<td>0.9</td>
<td>0.8</td>
<td>0.1</td>
<td>4</td>
</tr>
<tr>
<td>Shrubs</td>
<td>0.3</td>
<td>0.1</td>
<td>0.6</td>
<td>0.4</td>
<td>10</td>
</tr>
</tbody>
</table>
Table 3.4: Experimental results for parameter with a linear relation between parameter value and model output: oxidation fraction \( (f_{ox}) \), vegetation net primary production (NPP, parameter symbol \( P_{max} \)), and root exudation rate \( (f_{ex}) \). The numbers in the last three columns contain the modelled flux (Gt\(CH_4\) yr\(^{-1}\)) at lower end of the modelled parameter range and the percentage increase (+) or decrease (-) at the higher end.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Parameter range</th>
<th>Maximum model output change %</th>
<th>Land</th>
<th>Seafloor</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oxidation fraction</td>
<td>( f_{ox} )</td>
<td>0.2-0.9</td>
<td></td>
<td>5.10-60.3%</td>
<td>4.05-47.6%</td>
<td>1.05-57.7%</td>
</tr>
<tr>
<td>Maximum net primary productivity</td>
<td>( P_{max} )</td>
<td>0.003-0.009 kg Cm(^{-2}) day(^{-1})</td>
<td></td>
<td>4.77 + 9.7%</td>
<td>3.81 + 12.5%</td>
<td>0.97 + 10.3%</td>
</tr>
<tr>
<td>Exudate factor MODELWT</td>
<td>( f_{ex} )</td>
<td>0.1-0.3</td>
<td></td>
<td>7.25 + 3.6%</td>
<td>6.18 + 3.6%</td>
<td>1.09 + 3.6%</td>
</tr>
<tr>
<td>Exudate factor FIXEDWT</td>
<td>( f_{ex} )</td>
<td>0.1-0.3</td>
<td></td>
<td>6.35 + 4.7%</td>
<td>5.15 + 4.5%</td>
<td>1.29 + 4.6%</td>
</tr>
</tbody>
</table>