GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 22, GB2021, doi:10.1029/2007GB002951, 2008

Subglacial methanogenesis: A potential climatic amplifier?

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Received 2 May 2007; revised 11 November 2007; accepted 13 December 2007; published 12 June 2008.

[1] Subglacial environments are a previously neglected component of the Earth's global carbon cycle, a reflection of the view held until recently that they are dominated by abiotic and oxic conditions. Here we provide a realistic assessment of the theory that the basal regions of the ice sheets that formed over North America and Europe during glaciations were host to significant populations of anaerobic microorganisms, including methanogens, able to metabolize organic carbon sequestered during interglacials and overridden during Quaternary glacials. In doing so, we review the current evidence for subglacial methane release during deglaciation, estimate the size of the subglacial reservoir of organic carbon (SOC), and assess the amount of SOC available to subglacial microbes and the likely pathways and rates of carbon turnover. We then discuss the fate of subglacial methane and the potential impact of its release on atmospheric methane concentrations. We calculate that the SOC equates to 418–610 Pg C and includes carbon from terrestrial soils/vegetation, peatlands, lake, and marine sediments. The SOC that is potentially available for microbial conversion to methane is smaller than this estimate due to (1) glacial erosion, (2) accumulation of recalcitrant organic carbon compounds over time, (3) conversion to carbon dioxide by aerobic/anaerobic respiration, and (4) incomplete conversion of labile organic matter to methane. We estimate that the total SOC available for conversion to methane is 63 Pg C. Our estimates of methane production potentials span a wide range because of the current uncertainty surrounding subglacial metabolic rates. We believe, however, that there is a strong likelihood that subglacial microbes could convert 63 Pg of SOC to methane during a glacial cycle. If this were the case, release of this methane from the ice sheet margins during retreat would need to be episodic in order to significantly impact atmospheric methane concentrations. Our findings suggest that it may well be important to consider subglacial environments as active components of the Earth's carbon cycle. Conclusive determination of the potential impact of subglacial methane production on atmospheric methane concentrations during deglaciation, however, awaits more precise determination of the ability of subglacial microbes to degrade organic carbon components and their associated rates of metabolism under in situ conditions.

Citation: Wadham, J. L., M. Tranter, S. Tulaczyk, and M. Sharp (2008), Subglacial methanogenesis: A potential climatic amplifier?, *Global Biogeochem. Cycles*, *22*, GB2021, doi:10.1029/2007GB002951.

1. Introduction

[2] Records of atmospheric methane and carbon dioxide concentrations over the last 400 ka inferred from the gas composition of air bubbles in polar ice cores show significant variations on both long (>10,000 years), millennial and centenary timescales [*Petit et al.*, 1999]. Oceanic processes are thought to drive carbon dioxide variations [*Flückiger et al.*, 2004], but the drive on methane variations is still a matter of conjecture. The expansion and contraction of northern and tropical wetlands may be a key control [*Brook et al.*, 2000; *Delmotte et al.*, 2004; *Flückiger et al.*, 2004; *MacDonald et al.*, 2006], as may the stability of marine and terrestrial clathrates [*MacDonald*, 1983, 1990; *Nisbet*, 1989, 1990; *Paull et al.*, 1991, 1994; *Kennett et al.*, 2003]. There is debate, in particular, regarding the contribution of these sources to the rapid rises in methane observed during deglaciation [*Brook et al.*, 2000]. For example, the change in the δD_{CH4} of atmospheric methane during the periods of rapid warming which follow cold periods such as the Younger Dryas is not consistent with a marine clathrate contribution [*Sowers*, 2006], and it is uncertain whether wetlands alone can explain the variation in atmospheric methane concentrations [*Valdes et al.*, 2005] despite the hypothesized rapid increase in the productivity and area of wetlands during periods of climatic warming [*Kaplan*, 2002; *MacDonald et al.*, 2006]. More recently, several studies have highlighted the potential role of the

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0886-6236/08/2007GB002951$12.00

basal sediments of ice sheets as a potential source of methane during deglaciation [*Zeng*, 2003; *Weitemeyer and Buffett*, 2006].

[3] Subglacial environments are now known to harbor significant numbers of microorganisms (10^6–10^7 cells mL^{-1} including methanogens [*Sharp et al.*, 1999; *Skidmore et al.*, 2000; *Foght et al.*, 2004; *Price and Sowers*, 2004]) and are likely to be anoxic [*Wadham et al.*, 2004; *Tranter et al.*, 2005; *Wynn et al.*, 2006]. There are three important prerequisites for subglacial methane production; that anoxic conditions prevail, that a suitable carbon substrate exists (e.g., overridden soil carbon) and that physical conditions are favorable (e.g., meltwater is present). Sizable reserves of organic carbon (OC) sequestered in forest and tundra environments during interglacials were overridden by Northern Hemisphere ice sheets during successive cycles of Quaternary glaciation [*Simpkins and Parkin*, 1993; *Punkari and Forsström*, 1995]. The fate of the subglacial reservoir of organic carbon (SOC) is uncertain. In models of global carbon cycling and calculations of the global carbon budget at the Last Glacial Maximum (LGM) through to the present-day, the carbon storage under ice sheets is effectively set to zero [*Adams et al.*, 1990; *Van Campo et al.*, 1993; *François et al.*, 1999]. None of these consider that the buried OC is converted to greenhouse gases (methane and carbon dioxide) by subglacial microbial activity during storage in warm-based parts of the ice sheets, where liquid water was present. A considerable proportion (30–60%) of the former ice sheets is believed to have been warm-based during the last glacial [*Kleman and Hättesland*, 1999; *Marshall and Clark*, 2002]. These wet subglacial environments would not be subjected to seasonal freezing and thawing and may in fact have had a greater potential for microbial activity than their precursor nonglacial environments, some of which freeze in winter. These findings, coupled with observations of elevated methane and carbon dioxide concentrations in the basal regions of ice cores [*Tison et al.*, 1998; *Campen et al.*, 2003], and methane release from subglacial samples during incubation [*Skidmore et al.*, 2000], have been used to imply that subglacial environments may be potential sources of methane to the atmosphere. Numerical modeling conducted as part of these investigations has demonstrated that if all subice sheet soil carbon was converted to methane by subglacial microbes in wet-based areas of the Laurentide Ice Sheet and subsequently stored as clathrates at the ice sheet base, clathrate instability triggered by ice retreat could result in the periodic release of methane to the atmosphere [*Weitemeyer and Buffett*, 2006], with the potential to significantly impact global atmospheric methane concentrations. Although these methane release events are short-lived (1 ka), they may account for some aspects of the rapid rises in methane during deglaciation present in some paleorecords [*Kennet et al.*, 2003].

[4] The potential significance of subglacial methane production has been highlighted by *Zeng* [2003] and *Weitemeyer and Buffett* [2006]. We build on these studies in several important ways. First, we attempt to test hypotheses of subglacial methane production against published records of atmospheric methane and methane isotopes, which can be achieved using isotope mass balance arguments. Second, we provide a fully comprehensive estimate of the subglacial carbon reserve (research to date has concentrated on soil and vegetation reserves alone). Third, an assessment of the availability of the SOC to subglacial microbes is made, given rates of glacial erosion of SOC and the accumulation of less bioavailable OC compounds over time. Fourth, we consider in detail the subglacial microbial pathways and rates for SOC degradation. Subglacial microbial consortia include a range of aerobic and anaerobic types, including aerobic heterotrophs, iron reducers, sulphate reducers and methanogens. The gaseous respiratory end product for many of these microbes is carbon dioxide. The balance of carbon dioxide and methane production has not been addressed in papers to date, neither has the possibility that some methane is oxidized to carbon dioxide. In addition, the rates of subglacial microbial metabolism have not yet received consideration, despite their ultimate control upon the amount of SOC that can be converted to methane. In doing so, we aim to provide a critical and comprehensive assessment of the idea that methane production beneath ice sheets and its subsequent release might explain some of the rises in methane concentrations observed during deglaciation.

2. Evidence for Methane Production and Release to the Atmosphere

2.1. Evidence for Methane Production Under Ice

[5] Viable microbes have now been detected in significant concentrations (10^4–10^7cells mL^{-1}) beneath all types of ice mass, including small valley glaciers [*Sharp et al.*, 1999; *Foght et al.*, 2004], polythermal-based glaciers [*Skidmore et al.*, 2000], ice caps [*Gaidos et al.*, 2004], and the Greenland [*Kivimaki*, 2004; *Christner et al.*, 2003; *Miteva et al.*, 2004] and Antarctic ice sheets [*Mikucki et al.*, 2004; *Christner et al.*, 2006]. These viable microbes include methanogens, found in basal ice from Greenland (via GISP2 [*Tung et al.*, 2005]) and John Evans Glacier, Canada [*Skidmore et al.*, 2000]. In the latter case, incubation experiments confirm their ability to release considerable concentrations of methane from subglacial debris. No direct measurements of subglacial biogenic gas release have been made to date, but a number of lines of evidence suggest that subglacial environments may be sources of methane. First, anoxic conditions occur beneath glaciers [*Bottrell and Tranter*, 2002; *Wadham et al.*, 2004; *Wynn et al.*, 2006]. This anoxia is likely to be accentuated still further beneath ice sheets due to the poor hydrological connectivity that is believed to exist under much of the basal warm sector and the consequent prolonged residence times for water in the ice sheet interior. Second, the periodic advance of ice sheets over boreal forest, tundra and other ecosystems provides a labile carbon substrate. This, when combined with anoxia, designates subglacial environments as sites of potentially high methane production. Third, elevated concentrations of methane and carbon dioxide have been reported in the silty basal regions of ice cores from Greenland (GISP2, GRIP and Dye 3 [*Souchez et al.*, 1995, 1998; *Tison et al.*, 1998]) and South America [*Campen et al.*, 2003], which have been

inferred to result from in situ microbial activity [*Tranter*, 2003], and also support the existence of anoxic conditions. Fourth, isotope measurements on methane in GRIP basal ice are consistent with a biogenic origin [*Souchez et al.*, 2006]. Fifth, methane is still produced in North American glacial till, from the remnants of boreal forest overridden by advancing ice circa 16,000 years B.P. [*Simpkins and Parkin*, 1993].

2.2. Evidence for Subglacial Methane Release From Ice

2.2.1. Methane Isotopic Studies

[6] One means of elucidating whether subglacial environments were a significant source of methane during periods of deglaciation is to examine the δD_{CH4} of atmospheric methane preserved in ice cores, in relation to methane produced in freshwater (δD_{CH4} = −400 to −250‰ and $\delta^{13}C$ = −65 to −50‰ [*Whiticar et al.*, 1986]) and marine environments (δD_{CH4} = −250 to −170‰ and $\delta^{13}C$ = −110 to −60‰ [*Whiticar et al.*, 1986]). In the former case, methane generation takes place primarily by acetate fermentation (equation (1)) and in the latter case, by CO_2 reduction (equation (2)). The GISP2 record of δD_{CH4} shows that during deglaciation, periods of rapid methane increase (e.g., the Younger Dryas/Preboreal and the Older Dryas/Bølling transitions) are accompanied by no significant change or a slight decrease in the δD_{CH4} [*Sowers*, 2006]. In order to explain these variations, the δD_{CH4} of methane released at these times must be isotopically light, pointing toward a freshwater, rather than a marine clathrate, source for the methane [*Sowers*, 2006]:

$$CH_3COOH \Rightarrow CH_4 + CO_2 \quad (1)$$

$$CO_2 + 4H_2 \Rightarrow CH_4 + 2H_2O \quad (2)$$

The δD_{CH4} of methane produced under ice is poorly constrained and will vary depending on the nature of the carbon substrate overridden, and the subglacial geochemical environment that evolves subsequently. It might be expected that most methane produced under ice would have carbon substrates and microbes that originate from terrestrial rather than marine ecosystems, and so the isotopic composition of the methane would be more likely to align with isotopically light terrestrial freshwater values [*Whiticar et al.*, 1986]. We might also expect that as the SOC ages and the extent of microbial degradation increases, the pathway followed by subglacial methanogensis may shift from one of acetate fermentation to CO_2 reduction. This has been observed in bog environments [*Risatti*, 1987]. Consistent with this are isotope measurements on methane produced at present from organic remnants in glacial till of Weichselian age ($\delta^{13}C$ = −68 to −91‰, δD_{CH4} = −214 to −240‰ [*Coleman et al.*, 1988]) and methane, at least 1 Ma in age, trapped in the basal ice sequences of the GRIP ice core, Greenland ($\delta^{13}C$ = −81 to −84‰ [*Souchez et al.*, 2006]). All values suggest a CO_2 reduction pathway for the methane produced [*Whiticar et al.*, 1986]. We do not consider either of these values to be truly representative of methane produced from SOC during ice advance over North America and Europe. GRIP values partially or wholly reflect methane production within the vein system of glacial ice [*Tung et al.*, 2005, 2006] where closed system conditions will quickly lead to SOC substrate exhaustion. The methane in glacial till is also produced in an environment where labile SOC has been exhausted (by degradation to carbon dioxide and methane during 75 ka of glaciation). These studies, therefore, are more likely to give end-member maximum values for methane produced during the final stages of and/or after glaciation, once the SOC has been significantly microbially degraded.

[7] We next employ carbon isotope budgeting approaches to estimate the potential methane release from subglacial environments during deglaciation. We assume that the $\delta^{13}C$ for methane produced in glacial till and the basal ice layers of the GRIP core are maximum end-member values for hypothetical methane produced under Northern Hemisphere ice sheets during the last glaciation. We follow the approach of *Maslin and Thomas* [2003], which was designed to estimate a possible marine clathrate contribution to atmospheric methane concentrations during deglaciation. We employ the same values selected by *Maslin and Thomas* [2003] for parameters in the following mass balance equation:

$$\left(C_O \times \Delta\delta^{13}C_O\right) + \left(C_A \times \Delta\delta^{13}C_A\right) + \left(\Delta C_L \times \delta^{13}C_L\right) + \left(\Delta C_{SG} \times \delta^{13}C_{SG}\right) = 0 \quad (3)$$

where C is the total carbon storage at the end of the last glaciation and $\Delta\delta^{13}C$ is the isotopic shift during deglaciation in the ocean (O) and atmosphere (A), respectively. ΔC_L is the change in carbon storage of land biomass (soils and vegetation) during the last deglaciation, and $\delta^{13}C_L$ is the average isotopic composition of land biomass expansion. ΔC_{SG} is the subglacial methane release during the last deglaciation, and $\delta^{13}C_{SG}$ is the isotopic composition of the gas released (68–91‰ [*Coleman et al.*, 1988; *Souchez et al.*, 2006]). Key points to note are that carbon reservoirs in the ocean and atmosphere are assumed constant during deglaciation, and the changes in the isotopic composition of these reservoirs are perturbed by small quantities of carbon from land and subglacial sources with very different $\delta^{13}C$ values to the ocean and atmosphere.

[8] Because of the uncertainly in values for $\Delta\delta^{13}C_O$, ΔC_L, $\delta^{13}C_L$ [*Maslin and Thomas*, 2003] and $\delta^{13}C_{SG}$, it is possible to generate a wide range of estimates for ΔC_{SG}. We estimate most probable, maximum and minimum estimates of ΔC_{SG} using the parameter sets presented in Table 1. These calculations give estimates of ΔC_{SG} of 82, 308 and −48 Pg C, respectively. The observed variability is a result of the sensitivity of the isotope budgeting method to the parameterizations of $\Delta\delta^{13}C_O$, ΔC_L, $\delta^{13}C_L$. Our most probable estimate of subglacial methane release (82 Pg C) is still <10% of the methane increase recorded in ice cores between 18 and 8 ka B.P. (400 ppmv [*Brook et al.*, 2000]), assuming constant residence times for methane in the atmosphere of 11 years [*Chappellaz et al.*, 1993]. This suggests that unless methane release from ice sheets was episodic and focused during short periods of several hundreds of years, the potential to impact atmospheric methane concentrations would be small.

[9] The isotope budget results presented in this section are not inconsistent with a significant subglacial methane contribution to some of the short-lived (10^2 years) atmospheric methane variations recorded during deglaciation. However,

Table 1. A Summary of the Parameters Used in Isotope Mass Balance Arguments to Produce Minimum, Maximum, and Most Probable Estimates of Methane Released From Beneath Ice Sheets (ΔC_{SG}) During the Last Deglaciation

Parameters	Maximum Estimate	Minimum Estimate	Most Probable Estimate
C_O, Pg C	38,000	38,000	38,000
$\Delta\delta^{13}C_O$, ‰	0.3	0.5	0.4
C_A, Pg C	560	560	560
$\Delta\delta^{13}C_A$, ‰	0.3	0.6	0.45
ΔC_L, Pg C	1300	1000	1000
$\delta^{13}C_L$, ‰	−25	−15	−22
$\delta^{13}C_{SG}$, ‰	−68	−91	−81
ΔC_{SG}, PgC	308	−48	82

the uncertainty in parameter values makes it difficult to determine this with certitude. A useful extension to this exercise would be an analysis of the δD_H composition of methane trapped in basal ice samples and a comparison with trends in atmospheric methane δD_{CH4} following cold periods during the last deglaciation, as has been conducted for marine methane clathrates [*Sowers*, 2006].

2.2.2. Modeling Studies

[10] Ice core records from the last glacial cycle reveal several abrupt changes in atmospheric methane concentrations, notably during the last deglaciation at ~11.6 ka B.P. and ~14.7 ka B.P. [*Blunier and Brook*, 2001]. Similar rapid increases in methane are seen at the terminations of the previous three glacial periods [*Delmotte et al.*, 2004]. *Weitemeyer and Buffett* [2006] recently employed a numerical model of the Laurentide-Cordilleran ice sheets to model aerial extent, thickness and thermal conditions at the ice sheet base over the last glacial-interglacial cycle and coupled this model to an inventory of subglacial carbon (derived from inferred distributions of soil and vegetation). They subsequently modeled the spatial distribution of methane clathrate (assuming all soil carbon is converted to methane) over time with ice sheet growth and decay and quantified the timing and amplitude of methane release during ice sheet retreat. They predicted fluctuations in atmospheric methane (80–200 ppbv) of a similar order to those observed in the ice core record (300 ppbv), with the largest releases in methane predicted at 11 and 14.4 ka B.P. The latter increase coincides quite well with the peak in methane in the ice core record at 14.7 ka B.P. The predicted increase at 11 ka B.P. seems to lag the observed increase (11.6 ka B.P.), but may reflect inadequacies in the model. This work clearly shows that there may well be the potential for subglacial methane release to explain some of the more short-lived pulses of atmospheric methane increase observed in the ice core records. Current uncertainties in this hypothesis lie in the size of the carbon reservoir available to microbes (given glacial erosion and the increased abundance in nonlabile OC components over time) and the ability of microbes to degrade this SOC reservoir.

3. An Evaluation of Organic Carbon Supply to the Base of the Northern Hemisphere Ice Sheets

[11] The SOC pool during Quaternary glacials was probably considerably higher than today, as glaciers and ice sheets advanced over boreal and temperate forests or tundra. Some proglacial material is bulldozed into push moraines and thrust ridges during glacial advance, but a significant amount of sediment and vegetation is overridden by advancing ice [*Winkler and Nesje*, 1999; *Motyka and Echelmeyer*, 2003]. In support of this are numerous incidents of fossil carbon found in glacial till [*Simpkins and Parkin*, 1993; *Punkari and Forsström*, 1995; *Wiles et al.*, 1999], and reports of Holocene forests being buried by advancing ice [*Luckman et al.*, 1992, 1993; *Luckman*, 1995; *Motyka and Echelmeyer*, 2003]. *Simpkins and Parkin* [1993] demonstrate that methane continues to be produced in these tills from OC that is 14–17 ka old. Evidence for methane generation in Paleozoic tills and glacial sediments has also been reported [*Coleman et al.*, 1988].

[12] Modern ice masses show evidence of OC sequestration under ice. Elevated concentrations of NH_4^+ and the organic acid, oxalate, in the basal sequences of the GRIP core indicate in situ microbial degradation of organic matter, possibly from paleosols [*Tison et al.*, 1998]. Similar phenomena have been documented in Antarctica. Dissolved OC concentrations of 50 ppm and a fluorescence signature diagnostic of humic material have been detected in basal ice along the Antarctic Ice Sheet margin, which is thought to derive from overridden ice marginal sediments [*Barker et al.*, 2006]. Fluorescence characteristics of runoff from Outre Glacier (Canada), which advanced over temperate rain forest during the Little Ice Age, also show periodic contributions from terrestrially derived fulvic material, consistent with OC supply from overridden paleosols [*Barker et al.*, 2006].

[13] The SOC in the Northern Hemisphere would have included four main OC components: (1) soil and vegetation from a number of ecosystems, including tundra, open boreal woodland, taiga, moist and dry steppe and cool temperate forest (J. M. Adams, Environmental Sciences Division, Oak Ridge National Laboratory, 1995, QEN Web site http://www.esd.ornl.gov/projects/qen, hereinafter referred to as Adams, 1995), (2) peatlands, (3) lake sediments, and (4) marine sediments. Only the soil carbon contribution to SOC has received any attention in the literature to date [*Zeng*, 2003; *Weitemeyer and Buffett*, 2006]. We attempt to calculate the magnitude of each of these carbon reserves, using areas and extents of the former ice sheets in the Northern Hemisphere during the Weichselian glaciation. For these purposes, we include only the Laurentide, Cordilleran and Innuitian ice sheets (LIS/CIS and IIS, respectively) in North America and the European Ice Sheet (EIS). Smaller ice masses are not considered here. We also exclude areas that were already ice covered prior to initiation of the Weichselian glaciation (e.g., Greenland), since the carbon reservoir in these areas is likely to be small in comparison with the other reservoirs.

3.1. Soil and Vegetation

[14] An estimate of the SOC beneath the Laurentide/Cordilleran/Innuitian and European ice sheets during the Weichselian glaciation is given in Tables 2 and 3. Following *Weitemeyer and Buffett* [2006], we take two approaches to calculating soil and vegetation carbon. Scenario A assumes

Table 2. Organic Carbon in Soil and Above Ground Vegetation Overridden by Northern Hemisphere Ice Sheets and Assuming Present Potential Vegetation Limits: Scenario A[a]

Ecosystem Type	Area (10^6 km^2)	Carbon Storage (Soils + Vegetation)[b] (kg m^{-2})	Total SOC (Soils + Vegetation)[b] (Pg C)
		European Ice Sheet	
Southern Taiga	1.93	13.5/14	26/27
Open boreal woodland	0.157	12.9/5	2.03/0.786
Lowland tundra	0.2	21/1	4.13/0.196
Cool temperate forest	0.47	14/16	6.6/7.54
Total (EIS)	2.75	-	38.7/35.5
Total (EIS − peat/lake corrected)			30.5/30.7
		Laurentide/Cordilleran/Innuitian Ice Sheet	
Mid-Taiga	3.0	21.9/8.2	66/24.7
Southern Taiga	2.19	13.5/14	29.6/30.7
Open boreal woodland	0.85	12.9/5	11/4.26
Tundra (50% lowland tundra, 50% montane/dry tundra)	1.83	21/1 (lowland), 5/0.5 (montane/dry)	19.7/1.37
Cool temperate forest	0.982	14	13.7/15.7
Grassland (50% moist, 50% Steppe)	0.85	25/7	13.6/0.68
Total (LIS/CIS/IIS)	9.72.	-	157/77.4
Total (LIS/CIS/IIL − lake/peat corrected)			123/62
Total (peat/lake corrected)			154/92.7

[a] Excluding peatlands that are considered separately.

[b] Soil-derived carbon is presented first, followed by vegetation-derived carbon and separated by slash.

that the distribution of vegetation types was similar to the present-day (corrected for anthropogenic influences) when the ice sheets formed over North America and Europe. Hence, our values are based on present potential vegetation maps for areas of North America and Europe (derived from Adams (1995)). We use estimates of carbon storage (in kg m^{-2}) in soils and above ground vegetation for each ecosystem (after Adams (1995)), together with our calculations of the area of each ecosystem overridden by ice [after *Dyke and Prest*, 1987; *Siegert*, 2001], to generate estimates of overridden carbon. Scenario B assumes that ecosystems responded to climate cooling coincident with ice sheet advance and tundra ecosystems prevailed at the ice sheet margin. In the latter case, we assume that the predominant tundra biome was steppe tundra [*Prentice et al.*, 2000], which displays lower carbon storage values (5.5 kg C m^{-2}) than many of the forest ecosystems (7–25 kg C m^{-2}) (Adams, 1995). We include only soil carbon in this minimum estimate, assuming that vegetation died off prior to ice advance. Since there is sedimentary evidence that ice did override forest both during the last glacial period and the Holocene [*Simpkins and Parkin*, 1993; *Punkari and Forsström*, 1995; *Luckman et al.*, 1992, 1993; *Luckman*, 1995], we do not consider scenario B to be entirely realistic. There is evidence, however, that some vegetation change did take place in North America and Europe as the ice sheets built up, with tundra becoming more abundant [*Prentice et al.*, 2000]. We believe that the most likely scenario lies somewhere between the extreme end-member scenarios. These calculations are based on area estimates of different biomes and therefore automatically include some estimate of carbon storage in peatlands and lakes. Since we consider peatland and lake carbon storage separately (see discussion in sections 3.2 and 3.3, respectively), we subtract from our total soil/vegetation carbon storage values, the product of peatland/lake area (see sections 3.2 and 3.3, respectively) and the mean soil/vegetation carbon storage value for European and North American biomes of 15.4 and 14.8 kg C m^{-2}, respectively. We calculate that 54–246 Pg C was overridden by Northern Hemisphere ice sheets during the last glacial (Table 3).

3.2. Peatlands

[15] Up to 40% of some parts of Canada and Fennoscandia are covered by wetland ecosystems, within which organic detritus accumulates due to waterlogged, anoxic and cool conditions. These wetland environments accumulate sediments with an organic carbon content of 51.7% on average [*Gorham*, 1991]. This, together with peat depths in excess of the typical soil depth of 1 m (mean global peatland depth of 2.3 m [*Gorham*, 1991]), designates these ecosystems as significant sinks for atmospheric carbon. Although there is some ambiguity as to where the category of “peat” ends and “soil” begins, the majority of the ecosystem soil carbon storage assessments presented in Tables 2 and 3 do not include carbon stored in peat (Adams, 1995). We use data for present peatland areas in Canada (1.19×10^6 km^2) and Fennoscandia (0.289×10^6 km^2) to give minimum estimates for the area overridden by the LIS/CIS/IIC and EIS, respectively. We employ values for mean peat depth of 2.2 and 1.1 m, respectively; typical organic carbon contents of 51.7%; and a mean bulk density of 112 g L^{-1} [*Gorham*, 1991]. Using these values, we calculate that 170 Pg C (Table 4) derived from peat may have been overridden by the Laurentide/Cordilleran/Innuitian and European ice sheets.

3.3. Lakes

[16] Another potentially significant source of OC to advancing ice sheets is lake sediments. Lakes account for ~9% of the areas of Canada and Fennoscandia at present. Calculated over the terrestrial parts of the former Laurentide/Cordilleran/Innuitian and Fennoscandian ice sheets, this gives areas of 0.87 and 0.25×10^6 km^2, respectively.

Table 3. Organic Carbon in Soil Overridden by Northern Hemisphere Ice Sheets Assuming That Ecosystems Respond to Climate Change as the Northern Hemisphere Ice Sheets Advance: Scenario B[a]

Ecosystem Type	Area (10^6 km^2)	Carbon Storage (kg m^{-2})	Total SOC (Pg C)
European Ice Sheet			
Steppe-tundra	2.75	5.5	15.1
Laurentide/Cordilleran/Innuitian Ice Sheet			
Steppe-tundra	9.72	5.5	53.5
Total			68.6
Total (peat/lake corrected)			54.3

[a] Excluding peatlands that are considered separately.

If we take a typical organic carbon content for Holocene lakes sediments in North America of 20 mg cm^{-3} (~3–5% [*Dean and Gorham*, 1998]) and values for lake sediment depth of 5 m for Fennoscandian Lakes and 8 m for North American lakes (during the Holocene, North American, and European lakes accumulated 8 m and 5–6 m of sediments, respectively [*Dean and Gorham*, 1998]), we generate estimates of 140 and 25 Pg C for lake carbon overridden by the Laurentide/Cordilleran/Innuitian and European ice sheets, respectively (Table 4), giving an overall total of 165 Pg C.

3.4. Marine Sediments

[17] Portions of the Laurentide/Cordilleran/Innuitian and European ice sheets, were marine-based. For example, a substantial ice sheet formed over most of the Kara and Barents seas during the major periods of ice build up during the Weichselian glaciation at 90, 60, and 30 ka B.P. [*Siegert*, 2001], with the entire Barents and Kara seas being covered by grounded ice by 30 ka B.P. In North America, ice sheets also formed over Hudson Bay and the Canadian Arctic Islands and coastal parts of the Pacific bordering the Cordilleran Ice Sheet. Evidence for ice streaming in both the Kara/Barents Sea area [*Siegert*, 2001] and in the Hudson Strait in North America [*Andrews et al.*, 1985] also indicate that at least parts of the bed of this marine-based ice were warm. We have calculated the amount of SOC in marine sediments, using an estimate of the area of marine-based ice for the Laurentide/Cordilleran/Innuitian and European ice sheets, an estimated marine sediment depth of 5 m, bulk density values of 2 g cm^{-3} and organic carbon contents of 0.5%. These are typical values recorded for marine sediments deposited during the Holocene in the Barents/Kara seas and on the Labrador Shelf, North America [*Levitan et al.*, 2000; *Gataullin et al.*, 2001; *Andrews et al.*, 1999]. The total marine SOC for both ice sheet complexes is 29 Pg C, with 19.4 Pg of this derived from the European Ice Sheet (Table 4).

[18] In summary, our estimates of SOC in North America and Europe during the last glaciation are 54–246 Pg C for terrestrial soil and vegetation carbon, 170 Pg C for peatlands, 165 Pg C for lake sediments, and 29 Pg C for marine sediments. This gives an overall total of ~418–610 Pg C. Three of these reservoirs (peat, lake and marine sediments) have not been estimated before, but make significant contributions to the SOC. Our values compare with present total global carbon pools for soil, vegetation, and the atmosphere of 2011, 466, and 785 Pg C, respectively [*Janzen*, 2004]. Hence the pool of carbon that is buried beneath ice sheets is a significant global reservoir. The total SOC depends significantly upon which of Scenarios A and B is more realistic for terrestrial soil/vegetation OC. Given that neither scenario is likely to be completely accurate, it is probable that a SOC reservoir somewhere between the values estimated. In sections 4–8, we employ a mean value of ~514 Pg C to represent amount of OC sequestered beneath Northern Hemisphere ice sheets during the last glacial. The potential conversion of the SOC to methane depends on (1) the availability of this carbon to subglacial microbes, which in turn depends upon the residence time of soil and lake carbon under the ice sheets, given the dynamics of ice advance and retreat, thermal conditions at the ice sheet base, and the quality of the SOC, and (2) pathways and rates of organic carbon turnover to include aerobic/anaerobic respiration and methanogenesis. These conditions will be explored in sections 4 and 5.

4. Availability of SOC to Subglacial Microorganisms

4.1. Residence Times of Carbon Under Ice

[19] The residence time of soil and lake carbon under the ice sheet will be a function of (1) rates of sediment erosion and entrainment at the ice sheet base and (2) rates of horizontal sediment transport from the ice sheet interior to the margins.

[20] The SOC will be progressively depleted due to erosion and transport of subglacial material to the ice sheet margin. Unfortunately, there is considerable uncertainty with regard to long-term rates of subglacial erosion beneath ice sheets (review by *Hildes et al.* [2004]). Glacial erosion rates may reach ~1 m a^{-1} [*Hallet et al.*, 1996], but it is also known that some parts of Scandinavia preserved Tertiary landscapes and weathering profiles despite multiple Quaternary glaciations [*Lidmar-Bergström*, 1997]. Here, we use existing geological constraints and simple modeling of glacial erosion to argue that a large fraction of SOC material may still be in the subglacial environment by the onset of deglaciation, ~75 ka after glaciation begins. We propose that retention of SOC in the subglacial environment is mainly due to low rates of sediment transport, rather than

Table 4. Organic Carbon Preserved in Peatlands, Lake, and Marine Sediments Overridden by Northern Hemisphere Ice Sheets

Ecosystem Type	Area (10^6 km^2)	Carbon Storage (kg m^{-2})	Total Carbon Storage (Pg C)
European Ice Sheet			
Peat [after *Gorham*, 1991]	0.289	64	18.4
Lake sediments	0.25	100	24.8
Marine sediments	3.9	5	19.4
Laurentide/Cordilleran/Innuitian			
Peat [after *Gorham*, 1991]	1.19	127	152
Lake sediments	0.87	160	140
Marine sediments	1.9	5	9.3
Total Peat	1.479	-	170.4
Total Lake sediments	1.12	-	165
Total Marine sediments	5.8	-	28.7

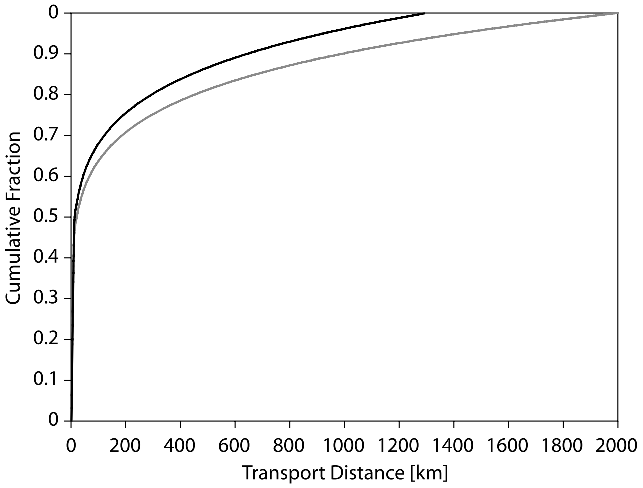

Figure 1. Cumulative fraction of sediments arriving at the ice margin (x = 0 km) as a function of sediment transport distance (equation (4)) for the case of a flow line within the Laurentide ice sheet (thin line, L = 2000 km) and within the European ice sheet (thick line, L = 1300 km).

low rates of erosion. In other words, the erosion of SOC, which we assume resides in a 1-m-thick layer of soil or sediment, may be relatively quick but its transport to the edge of the ice sheet is inefficient. Overall, our estimate of residence time may be low since peat, lake and marine SOC may extend to depths of up to 5 m, as described in sections 3.2–3.4.

[21] Our argument rests on the observation that subglacial tills in North America and Europe consist predominantly of local material, transported over just tens of kilometers [*Shilts*, 1984; *Clark*, 1987; *Kjaer et al.*, 2003]. To quantify this effect, we use *Boulton*'s [1984] model of till generation for a flow line running from the ice divide to the margin of the European ice sheet. Examination of his results indicates that the cumulative along-flow fractional contribution, *f*, to the composition of till deposited at the ice sheet margin can be approximated by the following function:

$$f = \left(\frac{x}{L}\right)^n \tag{4}$$

where *x* is along-flow coordinate (*x* = 0 at the margin), L is flow line length, and *n* is empirical exponent. We choose the numerical value of *n* (∼0.15) by assuming that *f* = 0.5 at the average half distance of 14.3 km from the margin, as calculated from Table 1 of *Clark* [1987]. The cumulative fraction of sediment arriving at the margin of the Laurentide and European ice sheets according to equation (4) is presented in Figure 1.

[22] If all locations along a flow line were contributing equally to the marginal till composition, the eroded fraction, F_o, of SOC could be simply expressed as

$$\mathrm{F_o} = \frac{\mathrm{qT}}{\mathrm{HL}} \tag{5}$$

where *q* is marginal flux of subglacial sediment per unit width of the margin [$m^2\ a^{-1}$], T is time period of glaciation [years], and H is thickness of SOC [m]. However, given the decreasing contribution of upstream areas encapsulated in equation (4), the expression for the eroded fraction of SOC becomes

$$\mathrm{F} = \mathrm{F_o}\left[1 - (1-\mathrm{n})(\mathrm{F_o n})^{\mathrm{n}/1-\mathrm{n}}\right] \tag{6}$$

Note that we have implicitly assumed that the porosity of glacial till is the same as the porosity of the eroded material (we assume a value of ∼30%) in both equations (5) and (6). This assumption is likely to hold well for erosion of the SOC, but the equations would have to be modified if conversion of low-porosity bedrock into till was considered.

[23] Since the marginal flux of subglacial material, *q*, is the least constrained quantity, in Figure 2 we plot the eroded fraction of F as a function of q (assuming T = 75 ka, H = 1 m, and L = 2000 and 1300 km for the flow line length with the Laurentide and European ice sheets, respectively) for our two models of SOC removal encapsulated in equations (5) and (6). Comparison between the solid (differential contribution; equation (6)) and dashed lines (equal contribution, equation (5)) in Figure 2 shows how important it is to consider more realistic models of SOC removal. If one assumes that all locations along a flow line contribute equally to the accumulation of ice marginal subglacial sediments (equation (5)), then even relatively low debris fluxes of ∼10 $m^2\ a^{-1}$ lead to a complete removal of SOC if sustained over 75 ka. In the case of equation (6), marginal fluxes have to be about an order of magnitude higher to achieve a complete removal of the 1-m-thick SOC.

[24] Several published studies have estimated or modeled till fluxes along parts of the southern Laurentide ice sheet for the time period of its maximum extent. The published values cover a wide range from 10 to 50 $m^2\ a^{-1}$ [*Cutler et al.*, 2001] to 100–400 $m^2\ a^{-1}$ [*Alley*, 1991; *Johnson et al.*, 1991; *Jenson et al.*, 1995]. It does not appear likely that the upper range of values could be sustained throughout a

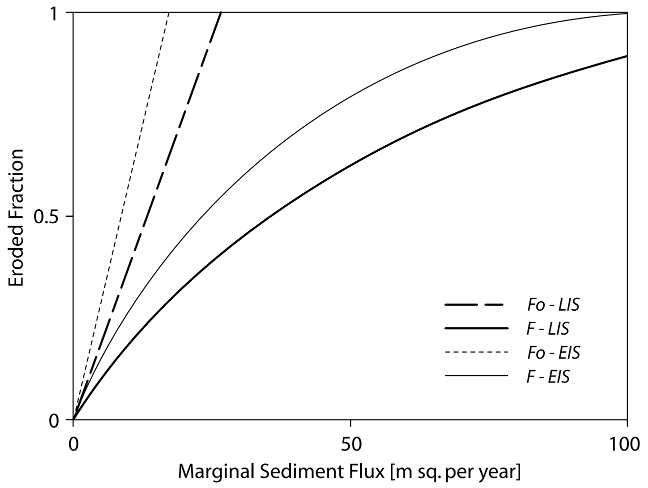

Figure 2. Eroded fraction of SOC (Fo, equation (5), dashed lines; and F, equation (6), solid lines) as a function of marginal sediment flux for the case of LIS (thick lines) and FIS (thin lines).

whole glaciation and may be simply representative of high fluxes during ice sheet decay, when abundant basal meltwater may promote high rates of ice sliding and, thus, sediment transport [*Marshall and Clark*, 2002]. For instance, if 400 m^2 a^{-1} flux out were sustained for 75 ka that would imply erosion of $\sim$2–4 m of material even in the deep interior part of the LIS (estimated from equation (6), using all other values as described in the previous paragraph). However, *Hay* [1998] assessed that total, glacial and nonglacial denudation of the Canadian Shield during the last 3 Ma on the basis of marine records amounted to $\sim$16 m. Hence, we choose the upper value from the modeling study of *Cutler et al.* [2001], 50 m^2 a^{-1}, as being more likely to represent the long-term subglacial debris fluxes along an ice sheet margin. Under such an assumption, about 30–40% of the SOC is still present in the subglacial zone of FIS and LIS after 75 ka. This is not to say that 30–40% of SOC material remained in its original position. Rather, the material can be thought of as en route to the ice sheet margin by the deglacial retreat of the margin.

[25] Our 514 Pg C estimate of SOC is reduced to 154 Pg C, if we take 30% as a reasonable minimum estimate of the proportion of SOC that is retained under the EIS and LIS for the whole of the last glacial (75 ka). We make the approximation that of the remaining 70% ($\sim$360 Pg C), $\sim$50% (180 Pg C) remained under the ice sheets for about half of the last glacial ($\sim$38 ka). If we assume that rates of microbial metabolism were sufficient to degrade SOC completely in 38–75 ka, the SOC available for microbial degradation would be $\sim$334 Pg C, assuming there was no limitation on the availability of liquid water or the quality of the SOC. These latter constraints are considered next.

4.2. Thermal Conditions at the Ice Sheet Base

[26] The availability of liquid water at the base of the Laurentide and European ice sheets is one of the fundamental determinants of the rate of microbial conversion of SOC to carbon dioxide or methane since it will affect (1) the physical characteristics of the microbial habitat (e.g., liquid water veins in ice versus pore waters in a water saturated sediment layer) and hence, the ability of microorganisms to move and grow, (2) the exchange of dissolved organic carbon, and other metabolites between different parts of the ice sheet base and between anoxic/oxic microenvironments, and (3) the rates of microbial respiratory processes via the effect of temperature. Our current understanding of the thermal conditions at the base of former ice sheets is based entirely on indirect lines of evidence (e.g., geomorphological observations and numerical modeling studies) and comparisons with the hydrologies of contemporary ice sheets.

[27] There are significant differences in basal temperatures generated by numerical models of the Laurentide Ice Sheet, because of the poor constraint on parameters such as paleoclimate and snowfall distribution [*Marshall et al.*, 2000]. These models are also unable at present to include processes such as ice streaming, which undoubtedly occurred in sectors of the Laurentide and European ice sheets [*Dowdeswell and Siegert*, 1999; *Stokes and Clark*, 2003; *Christoffersen and Tulaczyk*, 2003], and would influence temperatures at the ice sheet base. *Marshall and Clark* [2002] simulate three-dimensional ice temperature fields beneath the Laurentide Ice Sheet during the last glacial cycle and indicate that 60–80% of the bed was frozen at the LGM, rising to 10–20% by 8 ka B.P., although sensitivity model runs indicate considerable variation in the warm-based ice (e.g., 8–42% for the LGM) depending on climate input parameters. Geomorphological assessments of the thermal conditions of the Fennoscandian and European ice sheets at the LGM, based on the areal distribution of ribbed moraine indicative of frozen bed conditions, also suggest that significant proportions ($\sim$50%) of the European and Laurentide ice sheets were cold-based at the LGM [*Kleman and Hättesland*, 1999]. This compares well with modeling investigations and inferences made from deep borehole temperatures (*Rolandone et al.*, 2003). Where warm based, rates of basal melting are estimated at 5–7 mm a^{-1} due to basal melting alone [*Kump and Alley*, 1994; *Breemer et al.*, 2002; *Clarke et al.*, 2005]. This value was probably exceeded in ice marginal areas where there was surface melt supply to the bed and a greater degree of frictional melting associated with ice streaming [*Breemer et al.*, 2002].

4.3. Quality of SOC

[28] Only a proportion of subglacial organic carbon will be labile, and SOC quality will alter over time. For example, it is well known that soil organic matter (SOM) consists of at least three pools, including first, relatively simple soluble organic molecules and second, relatively labile polymers such as hemicellulose and non lignified cellulose (which are anaerobically degradable, albeit more slowly). The third, lignin and lignified cellulose, is the least degradable substrate [*Miyajima et al.*, 1997]. These pools have characteristic turnover times of <1 year, years to decades and hundreds to thousands of years, respectively [*Trumbore*, 2000]. Boreal forest, one such ecosystem that would have been overridden by ice sheets during the last glaciation, has a labile fraction of $\sim$38% of the total SOM pool, and a turnover time of <60 years [*Trumbore*, 2000]. The remaining recalcitrant humic and mineral fractions ($\sim$50% of the OM pool in boreal and tundra ecosystems [*Trumbore*, 2000; *Weintraub and Schimmel*, 2003]) turnover in 1000–1500 years [*Trumbore and Harden*, 1997]. A 1000 year time interval for carbon turnover is relatively short compared to the 85 ka of ice sheet occupation of North America and Europe, indicating that, theoretically, the SOC carbon could be metabolized within a glacial/interglacial period. There are two complications to this scenario, however.

[29] First, the quantity of labile SOC will decrease over time in the absence of primary productivity, leaving an increasing proportion of recalcitrant organic matter. Early work suggested that recalcitrant OC was not degradable under anaerobic conditions [*Zeikus et al.*, 1982], but more recent research [*Benner et al.*, 1984] has demonstrated that some more complex compounds can be degraded to methane under anoxic conditions. Indeed, 5–10% of cellulose is degraded anaerobically in soils and sediments [*Leschine*, 1995]. Degradation of lignocellulose components, however, can be 10–30 times slower than aerobic mineralization rates

[*Benner and Hodson*, 1985] and research on lake sediments shows very long timescales for lignin degradation (half lives for lignin in lake sediments have been calculated as 400 ka) [*Ishiwatari and Uzaki*, 1987]. The production of methane from fossil carbon buried in tills in the present-day [*Simpkins and Parkin*, 1993] and observations that microbes in recently deglaciated terrain use ancient carbon [*Bardgett et al.*, 2007] support the degradation of recalcitrant OC. Decomposition rates under persistent cold temperatures, however, will be slower [*Hobbie et al.*, 2000]. We adopt a conservative approach due to uncertainty in this area and assume that the lignin/cellulose component of the SOM does not degrade over the 75 ka glacial-interglacial cycle time period. Of the component of SOC that remains beneath the ice sheets for 38–75 ka despite glacial erosion (334 Pg C), we estimate that 50% (167 Pg C) does not derive from nonbiodegradable lignin-cellulose (as in boreal and tundra systems) and could be potentially degraded by subglacial microbes.

[30] Second, the maximum turnover times of 1000 years in boreal forest reflect relatively high rates of microbial metabolism (e.g., 10^2–10^3 g C (g cell C)$^{-1}$ a^{-1} [*Fang et al.*, 2005] compared with rates for 10^{-2} for microbes in glacial ice [*Price and Sowers*, 2000]). It is probable that the low temperatures under ice sheets will result in slower rates of microbial metabolism and hence, longer OC turnover times. This issue is addressed in section 5.2, where we attempt to construct envelopes of potential subglacial methane production.

5. Potential Pathways and Rates of Subglacial Organic Carbon Turnover

5.1. Pathways for Organic Carbon Turnover

[31] A number of functional microbial types have been identified in subglacial microbial consortia, including aerobic heterotrophs [*Skidmore et al.*, 2000], nitrate reducers [*Skidmore et al.*, 2000; *Kivimaki*, 2004], sulphate reducers [*Skidmore et al.*, 2000; *Kivimaki*, 2004], Fe(III) reducers [*Tung et al.*, 2006] and methanogens [*Skidmore et al.*, 2000; *Tung et al.*, 2006]. The production of methane from these consortia [*Skidmore et al.*, 2000; *Tung et al.*, 2006] also implies that syntrophic bacteria are present, since these function in concert with methanogens to produce methane. Methanogenesis represents the last step for organic matter degradation, and takes place in the most anoxic environments once oxygen, nitrate, sulphate and Fe(III) have been removed by reduction.

[32] Redox reactions in glacial environments can take a number of different pathways, with the reaction products of one set of reactions often being used in other reactions, so driving Eh down. For example, oxygen is often used to oxidize sulphides in glacial environments at relatively high Eh, and the reaction product, sulphate, can be used to oxidize organic matter in the absence of oxygen at lower Eh. Ultimately, organic matter is oxidized, to a degree that is controlled by the initial concentration of oxygen. We estimate how much organic carbon may be oxidized in subglacial environments during aerobic and anaerobic respiration by assuming that the different terminal electron acceptors directly oxidize organic matter (rather than react with bedrock components, so producing compounds which, in turn, may oxidize organic matter).

Table 5. A Summary of the Amount of Organic Carbon Degradation That Takes Place Aerobically and Anaerobically at the Ice Sheet Base and, by Extension, the Amount of Carbon Dioxide Produced[a]

	OCD (g C m^{-2} ka^{-1})	OCD (Pg OC Pg C as CO$_2^{-1}$) (LIS/EIS)[b]
Aerobic respiration	67.8	35
Anaerobic respiration		
Nitrate	0.063–0.101	0.11–0.18
Sulphate	0.072	0.18
Fe(III)	0.006	6.5
Total	-	42

[a] OCD, organic carbon degradation.

[b] Total organic carbon degradation/carbon dioxide production is calculated over the areas of the Laurentide/Innuitian/Cordilleran and European ice sheets for 75 ka of glaciation (warm based area of 30%) and 10 ka of deglaciation (warm based area of 60%).

[33] First, we calculate the amount of organic carbon degradation (OCD) in the SOC that would occur (equation (7)) assuming (1) that the only oxygen supply to the bed is from geothermal melting of basal ice and (2) that the oxidation of organic carbon is the first sink for this oxygen (as opposed to other reactions that consume atmospheric oxygen, such as sulphide oxidation). The rate of organic carbon degradation and carbon dioxide production (in moles) is equal to the rate of oxygen liberated from ice melt (in moles):

$$\mathrm{CH_2O} + \mathrm{O_2} \Rightarrow \mathrm{CO_2} + \mathrm{H_2O} \tag{7}$$

The rate of oxygen production, OP (in mol m^{-2} ka^{-1}), can be calculated as follows:

$$\mathrm{OP} = (\mathrm{VM^*\,GC})^*\,\mathrm{F}^*\,\frac{1}{\mathrm{G}} \tag{8}$$

where VM is the volume of meltwater produced by geothermal heating of basal ice (in m^3 m^{-2} ka^{-1}), GC is the typical gas content of basal ice (0.1 mol m^{-2} ka^{-1}; derived from gas concentrations of 0.1 cm^3 g^{-1} [*Souchez et al.*, 2003]), F is the fractional percentage of oxygen present in the atmosphere, and G is the universal gas constant (22.4 L mol^{-1}).

[34] The amount of oxygen liberated by the melting of basal ice is dependant on the basal melt rate. Melt rates of 5–6 mm a^{-1} are typically used as representative values for the rate of basal melting beneath the Northern Hemisphere ice sheets [*Breemer et al.*, 2002], although lower area averaged values have been computed (2–4 mm a^{-1} [*Clarke et al.*, 2005]). These values compare well with maximum contemporary rates for the Greenland Ice Sheet (7 mm a^{-1} [*North Greenland Ice Core Project Members*, 2004]). We use the upper of these values (6 mm a^{-1}) in our calculation. Melt rates of 6 mm a^{-1} give values of OCD values of 67.8 g C m^{-2} ka^{-1}. Calculated over the areas of the Laurentide/Innuitian/Cordilleran and European ice sheets over 75 ka of glaciation (warm-based area of 30%)

and 10 ka of deglaciation (warm-based area of 60%), we derive a value of 35 Pg C for potential OCD by aerobic microbial respiration during the last glacial cycle (Table 5).

[35] The full utilization of oxygen during the respiration of organic carbon promotes anaerobic respiration, when compounds such as nitrate, sulphate and Fe(III) are reduced. These compounds can arise from ice melt and glacial flour. Ice melt is a source of sulphate and nitrate, with concentrations typically of the order of ~1.0 μeq L^{-1} [*Röthlisberger et al.*, 2002; *Herron and Langway*, 1985]. Nitrate may be reduced during denitrification or nitrate reduction (equations (7) and (8), respectively):

$$\frac{1}{4}CH_2O(s) + \frac{1}{5}NO_3^-(aq) + \frac{1}{5}H^+(aq) \rightarrow \frac{1}{4}CO_2(aq) + \frac{1}{10}N_2(aq) + \frac{7}{20}H_2O(aq) \quad (9)$$

$$\frac{1}{4}CH_2O(s) + \frac{1}{8}NO_3^-(aq) + \frac{1}{4}H^+(aq) \rightarrow \frac{1}{4}CO_2(aq) + \frac{1}{8}NH_4^+(aq) + \frac{1}{8}H_2O(aq) \quad (10)$$

Sulphate is reduced according to equation (11), in which 2 mol of organic carbon are oxidized for each mole of sulphate reduced:

$$\frac{1}{4}CH_2O(s) + \frac{1}{8}SO_4^{2-}(aq) + \frac{1}{8}H^+(aq) \rightarrow \frac{1}{4}CO_2(aq) + \frac{1}{8}HS^-(aq) + \frac{1}{4}H_2O(aq) \quad (11)$$

The amount of organic carbon degraded anaerobically (OCD_{AN}) during sulphate/nitrate reduction is calculated as follows:

$$OCD_{AN} = [VM{*}R{*}(C{*}12g)]{*}A{*}t \quad (12)$$

where VM is the volume of meltwater produced by geothermal heating of basal ice (in m^3 m^{-2} ka^{-1} and assuming a basal melt rate of 6 mm a^{-1}), R is the molar ratio of nitrate/sulphate reduced:organic carbon oxidized, C is the concentration of sulphate or nitrate (in mmol m^{-3}), A is the combined area of the Laurentide/Cordilleran/Innuitian and European ice sheets and t is time (ka). We calculate that 0.11–0.18 Pg C and 0.18 Pg C would be oxidized to carbon dioxide during nitrate reduction and sulphate reduction, respectively, under ice sheets during 75 ka of glaciation and 10 ka of deglaciation.

[36] The primary source of Fe(III) is glacial flour. Fe(III) can be used to oxidize organic matter, as the following equation shows (equation (13) [after *Stumm and Morgan*, 1996])

$$4FeOOH + CH_2O + 4HCO_3^- + 4H^+ \leftrightarrow 4FeCO_3 + 7H_2O + CO_2 \quad (13)$$

The average ratio of Fe_2O_3:FeO in crustal rocks is ~1:1 by weight, ranging from 1:1.1 for igneous rocks to 1: 0.7 for shales [*Garrels and Mackenzie*, 1971]. The ratio of Fe(III):Fe(II) in crustal rocks is ~1:1.1, and so the ratio of Fe(III) to total Fe is ~1:2.1. Let us assume that there is a 1m thick subglacial debris layer, and that this debris layer has a porosity of ~30%. The density of siliclastic material is ~2700 kg m^{-3}, and hence the mass of siliclastic material in the layer is 1890 kg m^{-2}. The mass of bioavailable Fe in glacial debris is 0.93% by weight (R. Raiswell, personal communication, 2007), and hence the mass of bioavailable Fe in the siliclastic debris is 17.6 kg m^{-2} and the mass of bioavailable Fe(III) is ~8.4 kg m^{-2}. According to equation (12), 4 mol (223.4 g) of Fe(III) oxidizes 1 mol (12 g) of organic C, and so 8.4 kg m^{-2} of Fe(III) will oxidize 0.45 kg m^{-2} of organic C during the last glacial cycle. Calculated over the areas of the Laurentide/Cordilleran/Innuitian and European ice sheets, this gives 6.5 Pg OC oxidized by Fe(III) during 75 ka of glaciation and 10 ka of deglaciation.

[37] A summary of the amount of organic carbon degraded aerobically and anaeobically, and by implication the amount of carbon dioxide produced, is presented in Table 6. The total amount of OC degraded by these means is equal to ~42 Pg C, producing an equivalent amount of CO_2 (in Pg C). These results produce higher estimates of aerobic organic decomposition than similar calculations performed by *Skidmore et al.* [2000], who estimated that 8.1 Pg C would be converted to CO_2 over a glacial cycle. If this latter estimate if the more correct of the two, the potential for conversion to methane only increases. We also produce much lower estimates of anaerobic degradation of organic carbon compared to *Skidmore et al.* [2000] (up to ~8000 Pg C over a glacial cycle), since we do not base our calculations on rates of sulphate reduction in marine sediments, where there is a plentiful supply of sulphate.

[38] The total amount of noneroded, bioavailable SOC that remains under the ice sheets for 38–75 ka and is available to methanogenesis is 125 Pg (167 Pg C – 42 Pg C degraded by aerobic/anaerobic respiration). A maximum of 50% of the 125 Pg C can be converted to methane according to the stoichiometry of methanogenesis by acetate reduction (equations (1)) and carbon dioxide reduction (equation (2)), in the latter case due to the limitation on hydrogen supply from fermentation (equation (14)):

$$CH_2O + H_2O \Rightarrow H_2 + CO_2 \quad (14)$$

These arguments suggest that 63 Pg C could potentially be converted to methane.

5.2. Rates of Carbon Turnover

[39] An implicit assumption of the reasoning in sections 5.1 and 5.2 is that the metabolic rates of subglacial microbes are consistent with them being able to turn over ~63 Pg C to methane and 42 Pg C to carbon dioxide during a period of 38–75 ka. The following discussion explores this assumption, through a careful analysis of potential rates of subglacial microbial metabolism.

[40] The metabolic rate of microbes depends on a number of factors, to include carbon/nutrient supply, water and substrate availability and temperature. While at the pressure melting point and underlain by soil or till, the subglacial

Table 6. Estimates of Potential Subglacial Biogenic Gas Emission From the Laurentide and European Ice Sheets Over the Last Glacial/Interglacial Cycle[a]

	Metabolic Rate ($g\ C\ g\ C^{-1}\ a^{-1}$)	Subglacial Cell Concentration ($cells\ g^{-1}$)	Total C (CO_2/CH_4) Production (Pg C −85 ka)[b]
Upper estimate	10^2	10^7	4680
	[*Price and Sowers*, 2004; after *Jakosky et al.*, 2003]		(2360/2320) (A)
			(2170/2500) (B)
			(4200/480) (C)
Lower estimate	10^{-2}	10^7	22
	[*Christner et al.*, 2003; *Karl et al.*, 1999; *Parkes et al.*, 1990]		(42/−1) (A)
			(10/11) (B)
			(19/2) (C)

[a]Assumptions are as follows: (1) Biogenic gas production can only occur in warm-based areas of the LIS and FIS. (2) Thirty percent of the LIS was warm-based on average for the first 75 ka of the last glacial; between the LGM (20 ka B.P.) and 8 ka B.P., this proportion rose to an average of 60% [*Kleman and Hättesland*, 1999; *Marshall and Clark*, 2002]; most ice had gone by 8 ka B.P. [*Dyke and Prest*, 1987; *Kleman et al.*, 1997]; we assume that the EIS displayed similar basal thermal conditions to the LIS, as indicated at the LGM by geomorphological data [*Kleman and Hättesland*, 1999]). (3) A sediment layer of 1 m thickness overlay bedrock beneath the LIS and EIS and was the habitat for subglacial microbes [*Alley et al.*, 1997]. (4) This sediment layer had a density typical of that of subglacial till, taken to be 2 g cm^{-3} [*Truffer et al.*, 2000]. (5) There was no limitation on the supply of OC available for microbial conversion. (6) The carbon content of a typical subglacial cell is 19 fg, equal to values derived from cells in GISP2 silty ice [*Tung et al.*, 2006].

[b]Note that the total quantity of gas produced (in Pg C) is partitioned into CH_4 and CO_2 by, for case A, CO_2 production is estimated using calculations in this paper for aerobic/anaerobic respiration (42 Pg C CO_2, Table 5). CH_4 is the residual quantity of gas; case B uses CH_4/CO_2 ratios in incubations of subglacial debris in the presence of media [*Skidmore et al.*, 2000]. Case C uses CH_4/CO_2 ratios found in basal ice from the GISP2 ice core [*Souchez et al.*, 2006].

hydrology of the Laurentide and European ice sheets would comprise water flow through porous sediments [*Walder and Fowler*, 1994]. In sedimentary basins, recharge by glacial meltwaters would have also stimulated the development of deeper and continental-scale groundwater reservoirs [*Boulton et al.*, 1995; *Breemer et al.*, 2002; *Person et al.*, 2007]. Thus microbes would be free to move and grow and there would be exchange of nutrients and organic carbon between different components of the subice sheet hydrological system. During the initial phases of glaciation, we believe that recent sequestration of organic carbon would result in a relatively well nourished microbial ecosystem with rates of metabolic activity depressed only by the low in situ temperatures. Rates of microbial metabolism would be expected to decrease over time as labile organic carbon compounds become depleted.

[41] No published rates of in situ microbial activity exist for subglacial environments. We draw upon rates derived for microbes in analogous environments, in the absence of direct measurements of subglacial microbial metabolic rates. None of these give a true indication of rates in the subglacial environment, since nutrient/carbon supply and moisture conditions are slightly different. Using this approach, however, it is possible to produce an envelope of metabolic rates within which we believe subglacial microbial activity would fall.

[42] During the initial phases of glaciation, and while relatively labile organic compounds are present, rates of microbial metabolism might be consistent with those observed in other nutrient/carbon rich "hydrologically open" environments. Examples of such environments might include the permafrost active layer, polar snow and firn. Carbon turnover rates of $10–10^2$ $g\ C\ g\ C^{-1}\ a^{-1}$ at 0°C [*Price and Sowers*, 2004] are found in such systems. There are no ideal analog environments for subglacial microbial activity once the organic carbon substrate has been significantly degraded. As a minimum estimate, we might consider deep ocean environments where limited carbon supply results in low rates of carbon turnover (10^{-6} $g\ C\ g\ C^{-1}\ a^{-1}$ [*Price and Sowers*, 2004]). Although there are several rates now published for microbial metabolism in glacial ice, to include accretion ice of Lake Vostok, silty basal ice of the GRIP and GISP2 ice cores and other polar ice cores [*Price and Sowers*, 2004], we do not consider these as representative of the wet-based parts of the Laurentide and European ice sheets. Microbes inhabiting liquid water veins in ice have very low inferred rates of microbial activity (10^{-6} to 10^{-9} $g\ C\ g\ C^{-1}\ a^{-1}$ [*Price and Sowers*, 2004]), indicating the metabolism of immobile, probably dormant communities or at best, metabolism of communities with low nutrient/carbon levels. These low rates of metabolic activity are in part a reflection of the fact that microbes have no or low mobility, which limits growth and metabolism [*Price and Sowers*, 2004; *Tung et al.*, 2006]. This is not a constraint for microbes inhabiting a till layer beneath an ice sheet, which would have water saturated debris, an initially high carbon/nutrient supply and opportunities for renewal of small amounts of nutrients and carbon from basal ice melt thereafter.

[43] We produce first-order upper and lower estimates of potential methane and carbon dioxide production from subglacial environments beneath the North American and European ice sheets over the last glacial/interglacial cycle (75 ka of glacial conditions and 10 ka of interglacial conditions) using some of the metabolic rates presented above for analog environments. Calculations are given in Appendix A and results of the total mass of C produced as CH_4 in Table 6. Assumptions made in these calculations are also presented in Table 6. These calculations are performed as follows,

[44] 1. For the upper estimate, we assume that subglacial microbes (concentrations of 10^7 mL^{-1} [*Sharp et al.*, 1999; *Price and Sowers*, 2004]) are able to metabolize carbon at rates similar to those displayed by permafrost microbes at 0°C when provided with a suitable carbon substrate.

[45] 2. For the lower estimate, we assume that subglacial microbes have rates of metabolism in line with other parts

of the deep cold biosphere (e.g., deep ocean sediments, Lake Vostok accretion ice and polar ice cores; 10^{-6} g C g $C^{-1}a^{-1}$) at 0°C and are present in concentrations of 10^7 cells mL^{-1}. We emphasize that this estimate is unrealistic since advancing ice sheets will have much higher concentrations of labile subglacial organic carbon than those found in deep ocean environments and do not have the physical constraints on growth observed in liquid water veins in ice. We include this rate, however, for comparative purposes, and in acknowledgment that there are currently no measurements of the rate of subglacial carbon turnover under in situ conditions.

[46] These calculations give total estimates of carbon turnover (and gas production as CO_2 and CH_4). We subsequently partition the total carbon turnover estimates into the CO_2 and CH_4 components using three different methods. These methods are as follows:

[47] In method 1 we subtract our estimate of total CO_2 production by aerobic/anaerobic respiration (42 Pg C) from the total carbon turnover (in Pg C). The remaining quantity is reduced by 50% in order to account for the incomplete conversion of SOC to methane either by acetate or CO_2 reduction (equations (1), (2), and (14)). We assume that any OC not converted to CO_2 is converted to CH_4.

[48] In method 2 we employ a mass fraction of CH_4:(CH_4 + CO_2), equivalent to that produced in incubation experiments by *Skidmore et al.* [2000] (ratio of 0.54), to partition our total carbon turnover estimates.

[49] In method 3 we use a mass fraction for CH_4:(CH_4 + CO_2), equal to that observed in the basal sections of the GISP2 ice core [*Souchez et al.*, 2006] (ratio of 0.1), to separate the total carbon turnover estimates.

[50] We consider methods 1 and 2 as the most likely scenarios, since method 3 is based upon the ratios of carbon dioxide and methane produced in ice veins, where carbon supply and physical space for microbial growth/movement are not an appropriate analog for a water saturated till layer beneath an ice sheet. Methods 1 and 2 give very similar values for methane production (2320 and 2500 Pg C, respectively).

[51] These calculations give a broad spectrum of organic carbon turnover estimates, ranging from a total of 22–4680 Pg C, a reflection in itself on the uncertainty in rates of subglacial microbial metabolism and the partitioning of total carbon fluxes as gas into methane and carbon dioxide. We believe that the most realistic carbon turnover value for a wet-based ice sheet would lie somewhere between these two estimates, being of the order of 10^2 Pg C. We might expect $10-10^2$ Pg C of methane production during the last glacial cycle depending upon which partitioning method we use for carbon dioxide and methane. Our estimate of SOC available for conversion to methane over 38–75 ka (63 Pg C) falls toward the low end of this estimate, suggesting that such a conversion might not be limited by subglacial microbial metabolic rates.

[52] This discussion highlights very clearly that detailed studies of in situ rates of subglacial microbiological activity are required in order to evaluate whether subglacial production of methane could be significant. Until the rates and pathways of subglacial microbial carbon cycling are better constrained, it is difficult to make firm conclusions regarding the potential for subglacial methanogenesis.

6. Summary and Evaluation of the SOC Available for Degradation to Methane in Subglacial Environments

[53] The discussion in section 3 suggests that significant reserves of organic carbon (514 Pg C) may have been buried by Northern Hemisphere ice sheets during the last glacial cycle. We estimate that ~70% of this could have been removed by glacial erosion, giving 334 Pg C that remains under the ice for an average of 75 ka. There are uncertainties regarding the degree to which the noneroded SOC might be degraded. Although there is abundant evidence from other extreme environments that recalcitrant organic carbon compounds can be utilized by microorganisms (marine, proglacial, soils [*Bardgett et al.*, 2007; *Leschine*, 1995; *Ishiwatari and Uzaki*, 1987]), these data are lacking from subglacial ecosystems. As a result, we conservatively estimate that 50% of the SOC that is not eroded (167 Pg C) is available to subglacial microbes. We calculate that, of this bioavailable SOC reserve, 42 Pg C might be converted to carbon dioxide during aerobic and anaerobic respiration, given a supply of oxygen and other electron acceptors (nitrate and sulphate) from melting basal ice and a supply of Fe(III) from glacial flour. Our estimate of the final quantity remaining for conversion to methane is 63 Pg C, with an equivalent quantity producing carbon dioxide either via fermentation (equation (14)) or acetate reduction (equation (1)). A summary of the fate of SOC sequestered by the Northern Hemisphere ice sheets during the last glacial cycle can be found in Table 7.

[54] If our analysis of potential subglacial metabolic rates is correct and the most probable estimate of carbon turnover during the last glacial cycle falls somewhere between our upper (4680 Pg C) and lower (22 Pg C) estimates, there is a strong likelihood that subglacial microbes could convert 63 Pg of SOC to methane. Taking an assumption that 63 Pg C is converted to methane under Northern Hemisphere ice sheets, we next evaluate the fate of the methane and its potential impact on atmospheric methane concentrations during deglaciation.

7. Fate of Subglacial Methane and Potential Impact on Atmospheric Methane Concentrations During Deglaciation

[55] Methane generated at the ice sheet base in excess of the water solubility will be stored as clathrate, provided ice thicknesses are greater than a few hundred meters [*MacDonald*, 1990; *Weitemeyer and Buffett*, 2006]. These clathrates will remain stable provided the pressure is not reduced below the critical limits for stability and the equilibrium between methane in solution and clathrate methane is not perturbed. Local depressurization occurs in areas where surface meltwater accesses the bed and clathrates may be destabilized. This, however, is likely to be a localized phenomenon that occurs close to the ice margins. The fate of

Table 7. Summary of the Fate of SOC Sequestered by Northern Hemisphere Ice Sheets During the Last Glaciation and the Amount of OC Available to Methanogens Over the Same Time Period

Fate of SOC	Total Amount of Loss/ Degradation (Pg C)
Total SOC under LIS/EIS	514
Removal by erosion (<38 ka)	180
Aerobic/anaerobic respiration	
Dissolved oxygen	35
Nitrate	0.11–0.18
Sulphate	0.18
Fe(III)	6.5
Nonbioavailable	167
Total SOC available to methanogens over 38 ka	125
SOC potentially degradable to methane	63
SOC potentially degradable to carbon dioxide (aerobic/anaerobic respiration + methanogenesis)	105

subglacial methane released will depend on (1) methane oxidation rates and (2) ice margin retreat during deglaciation

7.1. Methane Oxidation

[56] A potentially important control on the net release of methane from all anoxic Earth systems is methane oxidation. Since there have been no measurements made of methane oxidation in subglacial environments and methanotrophic bacteria have yet to be identified, we can only judge the significance of this process by comparison with analogous environments. We refer to other wetland environments, such as the permafrost active layer and peat bogs, as the best analogy. Calculations of the balance between methane production and oxidation in these environments give widely ranging estimates, largely a reflection of variations in oxygen availability. *Whalen and Reeburgh* [2000] calculate that about 50% of methane is oxidized in their Alaskan peat bog, but compare this value with much higher estimates of 70–90% of methane oxidized in other wetland environments. *Wagner et al.* [2003] calculate the relative magnitudes of methane production versus methane oxidation for a Siberian peat bog and note that this balance evolves from <5% in the early melt season when the active layer is waterlogged to 100% by the late melt season when the active layer is more aerated. Since subglacial environments will receive a smaller oxygen supply than any of these bog environments, with oxygen supplied at a very slow rate by basal ice melting over much of the ice sheet area, we can only suggest that the methane oxidation: methane production would be smaller than that observed in the aerated wetland environments and at most, align with values reported for the more waterlogged wetlands (e.g., 5%) [*Wagner et al.*, 2003]. Since this value is relatively small compared to net methane production, we assume that methane oxidation is negligible in the anoxic subglacial environment. It is, of course, possible that some methane oxidation takes place during gas release at the margins, but this will depend on rates of release and the microbiology of marginal sediments, both of which are poorly constrained at present. A fuller understanding of subglacial rates of anaerobic methane oxidation awaits experimental investigation.

7.2. Ice Margin Retreat During Deglaciation

[57] We make the assumption that all of the 63 Pg C of SOC can be converted to methane over a glacial cycle, as our metabolic rate estimates tend to suggest, in order to produce the following estimate of the annual gas release from subglacial environments during deglaciation. If we assume that the release of methane from subglacial environments took place at a constant rate over 8 ka of deglaciation (spanning the period 18–10 ka B.P., when the majority of ice sheet retreat took place [*Dyke and Prest*, 1987]), then the rate of methane release calculated from the 63 Pg C SOC estimate is 0.0078 Pg C a^{-1}. This compares with annual atmospheric turnover rates for methane of 0.132 Pg C a^{-1}. The latter is calculated, assuming that (1) the postglacial concentration of methane in the atmosphere is 1.46 Pg C and (2) the residence time for methane in the atmosphere is 11 years [*Chappellaz et al.*, 1993]. This comparison indicates that there is little potential to significantly alter atmospheric methane concentrations during deglaciation if release is constant over 8000 ka. This is consistent with carbon isotope mass balance calculations presented in section 2.2.1. In reality, however, methane is likely to be released episodically when methane clathrates under the ice are destabilized by ice thinning, ice margin retreat and coincident subglacial pressure decrease [*Weitemeyer and Buffett*, 2006]. *Weitemeyer and Buffett* [2006] showed potential maximum methane release rates during deglaciation of 0.017–0.048 Pg C a^{-1} of methane, from 18 to 40 Pg C of clathrate formed under the Laurentide Ice Sheet during 75 ka of glacial burial. We would expect higher estimates of methane release during episodic events from our own findings, since we estimate greater quantities of carbon burial.

8. Summary and Conclusions

[58] The existence of microorganisms in subglacial environments is now well established. Many of these are anaerobic, and there is evidence to suggest that methane producing Archaea are present among the subglacial microbial community. It is probable that similar consortia of metabolizing microbes were present under Northern Hemisphere ice sheets during previous glaciations. We present estimates of potential carbon sequestration under advancing ice sheets during the last glacial period that include carbon held in terrestrial soils, peatlands, lake and marine sediments. These estimates range from 418 to 610 Pg C (mean of 514 Pg C) and represent a large reservoir of carbon for microbial utilization. In reality, we estimate that 62.5 (12.5%) of this carbon pool is potentially convertible to methane due to (1) erosion of the SOC by glacial flow, (2) the presence recalcitrant organic carbon components (we conservatively assume that these account for 50% of the OC pool and cannot be degraded), (3) oxidation of organic carbon to carbon dioxide during aerobic and anaerobic respiration, and (4) incomplete conversion of the remaining SOC to methane. We appreciate that there is a considerable uncertainty in these estimates since our knowledge of glacial erosion rates is incomplete and it is possible that some recalcitrant OC compounds can be degraded by subglacial microbes, as they are in other environments. As such they

form minimum estimates of the SOC convertible to methane. We subsequently produce upper and lower estimates for subglacial methane produced (4680 and 22 Pg C, respectively) during the last glacial cycle. We believe that the most probable estimate of carbon turnover during the last glacial cycle would fall somewhere between these two estimates. Thus, there is a strong likelihood that subglacial microbes could convert 63 Pg of SOC to methane during a glacial cycle. Making the assumption that all of the 63 Pg C was converted to methane, there is only the potential to impact atmospheric methane concentrations if release takes place episodically, as opposed to at a constant rate over 8000 years of deglaciation. This is consistent with previous modeling work [*Weitemeyer and Buffett*, 2006] and with ^{13}C isotope mass balance calculations presented here.

[59] This research suggests that it may well be important to consider ice sheets as active components of the Earth-atmosphere system in studies of global carbon cycling, but that this is difficult to do with certitude until we have a better knowledge and understanding of (1) the ability of subglacial microbial communities to utilize less labile carbon fractions, (2) in situ rates and pathways of subglacial microbial activity, including the potential for methane oxidation, and (3) the coupling between glaciological processes (erosional removal of SOC, subice sheet hydrology and ice sheet retreat) and the microbial production and ice marginal release of subglacial methane.

Appendix A: Calculations of Potential Carbon Turnover Rate for Subglacial Microbes

[60]

$$\mathrm{R} - \mathrm{CO_2/CH_4} = \left[\mathrm{AH}\rho \mathrm{nn_j R(T)}\right] 75\ \mathrm{ka}$$

where R – CO_2/CH_4 is the rate of methane or carbon dioxide production, A is the area of the Laurentide/Cordilleran/Innuitian and Fennoscandian ice sheets, respectively (m^2), H is the sediment thickness (m), ρ is the sediment bulk density (g cm^3), n is the concentration of microbial cells in the sediment layer in cells g^{-1}, n_j is the mean carbon mass per cell (in g), and R(T) is the metabolic rate of in situ microbes producing either methane or carbon dioxide at temperature T (in g C g C^{-1} a^{-1}), calculated over 75 ka of glaciation.

[61] **Acknowledgments.** This research was funded by NERC grant NE/E004016/1. Slawek Tulaczyk's contributed to this work while in residence at the Bristol Glaciology Centre under the Benjamin Meaker Visiting Professorship Program administered by the Institute for Advanced Studies at the University of Bristol. His contribution was also partly supported by a research grant from the National Science Foundation.

References

Adams, J. M., H. Faure, L. Faure-Denard, J. M. McGlade, and F. I. Woodward (1990), Increases in the terrestrial carbon storage from the Last Glacial Maximum to the present, *Nature*, *348*, 711–714, doi:10.1038/348711a0.

Alley, R. B. (1991), Deforming bed origin for southern Laurentide till sheets, *J. Glaciol.*, *37*(125), 67–76.

Alley, R. B., K. M. Cuffey, E. B. Evenson, J. C. Strauser, D. E. Lawson, and G. J. Larson (1997), How glaciers entrain and transport basal sediment physical constraints, *Quat. Sci. Rev.*, *16*, 1017–1038.

Andrews, J. T., J. A. Stravers, and G. H. Miller (1985), Patterns of glacial erosion and deposition around Cumberland Strait, Frobisher Bay and Hudson Strait, and the location of ice streams in the Eastern Canadian Arctic, in *Models in Geomorphology*, edited by M. J. Woldenburg, pp. 93–117, Allen and Unwin, London.

Andrews, J. T., L. Keigwin, F. Hall, and A. E. Jennings (1999), Abrupt deglaciation events and Holocene palaeoceanography from high resolution cores, Cartwright Saddle, Labrador Shelf, Canada, *J. Quat. Sci.*, *14*(5), 383–397, doi:10.1002/(SICI)1099-1417(199908)14:5<383::AID-JQS464>3.0.CO;2-J.

Bardgett, R. D., et al. (2007), Heterotrophic microbial communities use ancient carbon following glacial retreat, *Biol. Lett.*, *3*, 487–490, doi:10.1098/rsbl.2007.0242.

Barker, J., M. J. Sharp, S. J. Fitzsimons, and R. J. Turner (2006), Abundance and dynamics of dissolved organic carbon in glacier systems, *Arct. Antarct. Alp. Res.*, *38*(2), 163–172, doi:10.1657/1523-0430(2006)38[163:AADODO]2.0.CO;2.

Benner, R., and E. Hodson (1985), microbial degradation of the leachable and lignocellulose components of leaves and wood from Rhirhizophora manglein a tropical mangrove swamp, *Mar. Ecol. Prog. Ser.*, *23*, 221–230, :10.3354/meps023221.

Benner, R., A. E. Maccubbin, and R. E. Hodson (1984), Preparation, characterisation, and microbial degradation of specifically labelled 14Clignocellulose from marine and freshwater macrophytes, *Appl. Environ. Microbiol.*, *47*, 998–1004.

Blunier, T., and E. Brook (2001), Timing of millennial-scale climate change in Antarctica and Greenland during the last glacial period, *Science*, *291*, 109–112, doi:10.1126/science.291.5501.109.

Bottrell, S. H., and M. Tranter (2002), Sulphide oxidation under partially anoxic conditions at the bed of the Haut Glacier d'Arolla, Switzerland, *Hydrol. Processes*, *16*(12), 2363–2368, doi:10.1002/hyp.1012.

Boulton, G. S. (1984), Development of a theoretical model of sediment dispersal by ice sheets, in *Prospecting in Areas of Glaciated Terrain 1984*, pp. 213–223, Inst. of Min. and Metall., London.

Boulton, G. S., et al. (1995), Groundwater flow beneath ice sheets: part I—Large scale patterns, *Quat. Sci. Rev.*, *14*, 545–562, doi:10.1016/0277-3791(95)00039-R.

Breemer, C. W., P. U. Clark, and R. Haggerty (2002), Modelling the subglacial hydrology of the late Pleistocene Lake Michigan Lobe, Laurentide Ice Sheet, *Geol. Soc. Am. Bull.*, *114*(6), 665–674, doi:10.1130/0016-7606(2002)114<0665:MTSHOT>2.0.CO;2.

Brook, E., S. Harder, J. Severinghaus, E. Steig, and C. Sucher (2000), On the origin and timing of rapid changes in atmospheric methane during the last glacial period, *Global Biogeochem. Cycles*, *14*(2), 559–572, doi:10.1029/1999GB001182.

Campen, R. K., T. Sowers, and R. Alley (2003), Evidence of microbial consortia metabolizing within a low-latitude mountain glacier, *Geology*, *31*, 231–234, doi:10.1130/0091-7613(2003)031<0231:EOMCMW>2.0.CO;2.

Chappellaz, J. A., Y. Fung, and A. M. Thompson (1993), The atmosphere increase since the Last Glacial Maximum, *Tellus, Ser. B*, *45*, 228–241.

Christner, B. C., E. Mosely Thompson, L. G. Thompson, and J. N. Reeve (2003), Bacterial recovery from ancient glacial ice, *Appl. Environ. Microbiol.*, *4*, 433–436.

Christner, B., G. Royston-Bishop, C. M. Foreman, B. R. Arnold, M. Tranter, K. A. Welch, W. B. Lyons, A. I. Tsapin, M. Studinger, and J. C. Priscu (2006), Limnological conditions in Subglacial Lake Vostok, Antarctica, *Limnol. Oceanogr.*, *51*(6), 2485–2501.

Christoffersen, P., and S. Tulaczyk (2003), Signature of paleo-ice stream stagnation: Till consolidation induced by basal freeze-on, *Boreas*, *32*(1), 114–129, doi:10.1080/03009480310001065.

Clark, P. U. (1987), Subglacial sediment dispersal and till composition, *J. Glaciol.*, *95*(4), 527–541.

Clarke, G. K. C., D. W. Leverington, J. T. Tellor, A. S. Dyke, and S. Marshall (2005), Fresh arguments against the Shaw megaflood hypothesis, *Quat. Sci. Rev.*, *24*, 1533–1541, doi:10.1016/j.quascirev.2004.12.003.

Coleman, D. D., C. Lui, and K. M. Riley (1988), Microbial methane in the shallow Palaeozoic sediments and glacial deposits of Illinois, U.S., *Chem. Geol.*, *71*, 23–40, doi:10.1016/0009-2541(88)90103-9.

Cutler, P. I., D. M. Mickelson, P. M. Colgan, D. R. MacAyeal, and B. R. Parizek (2001), Influence of the Great Lakes on the dynamics of the southern Laurentide Ice Sheet: Numerical experiments, *Geology*, *29*(11), 1039–1042, doi:10.1130/0091-7613(2001)029<1039:IOTGLO>2.0.CO;2.

Dean, W., and E. Gorham (1998), Magnitude and significance of carbon burial in lakes, reservoirs and peatlands, *Geology*, *26*, 535–538, doi:10.1130/0091-7613(1998)026<0535:MASOCB>2.3.CO;2.

Delmotte, M., J. Chappellaz, E. Brook, P. Yiou, J. M. Barnola, C. Goujon, D. Raynaud, and V. I. Lipenkov (2004), Atmospheric methane during the last four glacial-interglacial cycles: Rapid changes and their link with Antarctic temperature, *J. Geophys. Res.*, *109*, D12104, doi:10.1029/2003JD004417.

Dowdeswell, J., and M. J. Siegert (1999), Ice sheet numerical modelling and marine geophysical measurements of glacier-derived sedimentation on the Eurasian Arctic continental margins, *Geol. Soc. Am. Bull.*, *111*(7), 1080–1097, doi:10.1130/0016-7606(1999)111<1080:ISNMAM>2.3.CO;2.

Dyke, A. S., and V. K. Prest (1987), The late Wisconsin and Holocene history of the Laurentide ice sheet, *Geogr. Phys. Quat.*, *41*, 237–263.

Fang, C., P. Smith, J. B. Moncrieff, and J. O. Smith (2005), Similar response of labile and resistant soil organic matter to changes in temperature, *Nature*, *433*, 57–59, doi:10.1038/nature03138.

Flückiger, J., T. Blunier, B. Stauffer, J. Chappellaz, R. Spahni, K. Kawamura, J. Schwander, T. F. Stocker, and D. Dahl-Jensen (2004), N_2O and CH_4 variations during the last glacial epoch: Insight into global processes, *Global Biogeochem. Cycles*, *18*, GB1020, doi:10.1029/2003GB002122.

Foght, J., J. Aislabie, S. Turner, C. E. Brown, J. Ryburn, D. J. Saul, and W. Lawson (2004), Culturable bacteria in subglacial sediments and ice from two Southern Hemisphere glaciers, *Microb. Ecol.*, *47*, 329–340, doi:10.1007/s00248-003-1036-5.

François, L. M., Y. Godderis, P. Warnant, G. Ramstein, N. de Noblet, and S. Lorenz (1999), Carbon stocks and isotopic budgets of the terrestrial biosphere at mid-Holocene and the Last Glacial Maximum times, *Chem. Geol.*, *159*, 163–189, doi:10.1016/S0009-2541(99)00039-X.

Gaidos, E., B. Laniol, T. Thorsteinsson, T. Graham, M. Skidmore, S. K. Han, T. Rust, and B. Popp (2004), A viable microbial community in a subglacial volcanic crater lake, Iceland, *Astrobiology*, *4*, 327–334, doi:10.1089/ast.2004.4.327.

Garrels, R. M., and F. T. Mackenzie (1971), *Evolution of Sedimentary Rocks*, 387 pp., Norton, New York.

Gataullin, V., J. Mangerud, and J. Inge-Svendsen (2001), The extent of the late Weichselian ice sheet in the south-eastern Barents Sea, *Global Planet. Change*, *31*, 453–474, doi:10.1016/S0921-8181(01)00135-7.

Gorham, E. (1991), Northern peatlands: Role in the carbon cycle and probable response to climatic warming, *Ecol. Appl.*, *1*(2), 182–195, doi:10.2307/1941811.

Hallet, B. L. H., L. Hunter, and J. Bogen (1996), Rates of erosion and sediment evacuation by glaciers: A review of field data and their implications, *Global Planet. Change*, *12*(1–4), 213–235, doi:10.1016/0921-8181(95)00021-6.

Hay, W. W. (1998), Detrital sediment fluxes from continents to oceans, *Chem. Geol.*, *145*(3–4), 287–323, doi:10.1016/S0009-2541(97)00149-6.

Herron, M. M., and C. C. Langway Jr. (1985), Chloride, nitrate, and sulfate in the dye 3 and Camp Century, Greenland ice cores, in *Greenland Ice Core: Geophysics, Geochemistry, and the Environment*, *Geophys. Monogr. Ser.*, vol. 33, edited by C. C. J. Langway et al., pp. 77–84, AGU, Washington, D. C.

Hildes, D. H. D., G. K. C. Clarke, G. E. Flowers, and S. J. Marshall (2004), Subglacial erosion and englacial sediment transport modelled for North American ice sheets, *Quat. Sci. Rev.*, *23*(3–4), 409–430, doi:10.1016/j.quascirev.2003.06.005.

Hobbie, S., J. P. Schimel, S. E. Trumbore, and J. R. Randersons (2000), Controls over carbon storage and turnover in high-latitude soils, *Global Change Biol.*, *6*, 196–210, doi:10.1046/j.1365-2486.2000.06021.x.

Ishiwatari, R., and M. Uzaki (1987), Diagenetic changes of lignin compounds in a more than 0.6 million year old lacustrine sediment (Lake Biwa, Japan), *Geochim. Cosmochim. Acta*, *51*(2), 321–328, doi:10.1016/0016-7037(87)90244-4.

Jakosky, B. M., K. H. Nealson, C. L. Bakermans, R. E. Ley, and M. T. Mellon (2003), Sub-freezing activity of micro-organisms and the potential habitability of Mars polar regions, *Astrobiology*, *3*, 343–350.

Janzen, H. H. (2004), Carbon cycling in Earth systems: A soils science perspective, *Agric. Ecosyst. Environ.*, *104*, 399–417, doi:10.1016/j.agee.2004.01.040.

Jenson, J. W., P. U. Clark, D. R. MacAyeal, C. Ho, and J. C. Vela (1995), Numerical modeling of advective transport of saturated deforming sediment beneath the Lake Michigan Lobe, Laurentide Ice Sheet, *Geomorphology*, *14*(2), 157–166, doi:10.1016/0169-555X(95)00056-0.

Johnson, W. H., A. K. Hansel, and B. J. Stiff (1991), Glacial transport. rates, late Wisconsinan Lake Michigan lobe in central Illinois: Implication for transport mechanisms and ice dynamics, *Geol. Soc. Am. Abstr. Program*, *23*, A61.

Kaplan, J. O. (2002), Wetlands at the Last Glacial Maximum: Distribution and methane emissions, *Geophys. Res. Lett.*, *29*(6), 1079, doi:10.1029/2001GL013366.

Karl, D. M., D. F. Bird, K. Bjorkman, T. Houlihan, R. Shakelford, and L. Tupas (1999), Microorganisms in the accreted ice of Lake Vostok, *Antarct. Sci.*, *286*, 2144–2147.

Kennet, J. P., K. G. Cannariato, I. L. Hendy, and R. J. Behl (2003), *Methane Hydrates in Quaternary Climate Change: The Clathrate Gun Hypothesis*, *Spec. Publ.*, vol. 54, AGU, Washington, D. C.

Kivimaki, A. L. (2004), Presence and Activity of microbial populations in glaciers and their impact on weathering at glacier beds, Ph.D. thesis, Univ. of Bristol, Bristol, U.K.

Kjaer, K. H., M. Houmark-Nielsen, and N. Richardt (2003), Ice-flow patterns and dispersal of erratics at the southwestern margin of the last Scandinavian Ice Sheet: Signature of palaeo-ice streams, *Boreas*, *32*(1), 130–148, doi:10.1080/03009480310001074.

Kleman, J. C., and C. Hättesland (1999), Frozen bed Fennoscandian and Laurentide ice sheets during the Last Glacial Maximum, *Nature*, *402*, 63–66, doi:10.1038/47005.

Kleman, J. C., C. Hättesland, I. Bergström, and A. Stroeven (1997), Fennoscandian paleoglaciology reconstructed using a glacial-geological inversion model, *J. Glaciol.*, *43*, 283–299.

Kump, L. R., and R. B. Alley (1994), Global chemical weathering on glacial timescales, in *Material Fluxes of the Surface of the Earth*, pp. 46–60, Natl. Acad. Press, Washington, D. C.

Leschine, S. B. (1995), Cellulose degradation in anaerobic environments, *Annu. Rev. Microbiol.*, *49*, 399–426, doi:10.1146/annurev.mi.49.100195.002151.

Levitan, M. A., V. M. Kuptsov, and E. A. Romankevich (2000), Some indication for late Quaternary Pechora River discharge: Results of vibrocore studies in the southeastern Pechora Sea, *Earth Sci.*, *89*, 533–540.

Lidmar-Bergström, K. (1997), A long-term perspective on glacial erosion, *Earth Surf. Processes Landforms*, *22*, 297–306, doi:10.1002/(SICI)1096-9837(199703)22:3<297::AID-ESP758>3.0.CO;2-R.

Luckman, B. H. (1995), Calendar-dated, early Little Ice Age advance at Robson Glacier, British Columbia, Canada, *Holocene*, *5*, 149–159, doi:10.1177/095968369500500203.

Luckman, B. H., M. E. Colenutt, and J. R. Reynolds (1992), Field investigations in the Canadian Rockies in 1991, report, Parks Can., Alberta Parks, and B.C. Parks Serv., Gatineau, Quebec, April.

Luckman, B. H., G. Holdsworth, and G. D. Osborn (1993), Neoglacial glacier fluctuations in the Canadian Rockies, *Quat. Res.*, *39*, 144–155, doi:10.1006/qres.1993.1018.

MacDonald, G. J. (1983), The many origins of natural gas, *J. Pet. Geol.*, *5*, 341–362.

MacDonald, G. J. (1990), Role of methane clathrates in past and future climates, *Clim. Change*, *16*, 247–281, doi:10.1007/BF00144504.

MacDonald, G. M., D. W. Beilman, K. V. Kremenetski, Y. Sheng, L. C. Smith, and A. A. Velichko (2006), Rapid early development of circumarctic peatlands and atmospheric CH and CO variations, *Science*, *314*, 285–288, doi:10.1126/science.1131722.

Marshall, S. J., and P. U. Clark (2002), Basal temperature evolution of North American ice sheets and implications for the 100-kyr cycle, *Geophys. Res. Lett.*, *29*(24), 2214, doi:10.1029/2002GL015192.

Marshall, S. J., L. Tarasov, G. K. C. Clarke, and W. R. Peltier (2000), Glaciological reconstruction of the Laurentide Ice Sheet: Physical processes and modeling changes, *Can. J. Earth Sci.*, *37*(5), 769–793, doi:10.1139/cjes-37-5-769.

Maslin, M., and E. Thomas (2003), Balancing the deglacial carbon budget: The hydrate factor, *Quat. Sci. Rev.*, *22*, 1729–1736, doi:10.1016/S0277-3791(03)00135-5.

Mikucki, J. A., C. H. Foreman, B. Sattler, W. B. Lyons, and J. A. Priscu (2004), Geomicrobiology of Blood Falls: An iron rich saline discharge at the terminus of Taylor Glacier, Antarctica, *Aquat. Chem.*, *10*, 199–220.

Miteva, V. L., P. P. Sheridan, and J. B. Brenchley (2004), Phylogenetic and physiological diversity of microorganisms isolated from a deep Greenland ice-core, *Appl. Environ. Microbiol.*, *70*, 202–213, doi:10.1128/AEM.70.1.202-213.2004.

Miyajima, T., E. Wada, Y. T. Hanba, and P. Vijarnsorn (1997), Anaerobic mineralisation of indigenous organic matters and methanogenesis in tropical wetland soils, *Geochim. Cosmochim. Acta*, *61*(17), 3739–3751, doi:10.1016/S0016-7037(97)00189-0.

Motyka, R. J., and K. A. Echelmeyer (2003), Taku Glacier (Alaska, USA) on the move again: Active deformation of proglacial sediments, *J. Glaciol.*, *49*(164), 50–58, doi:10.3189/172756503781830962.

Nisbet, E. (1990), Did the release of methane from hydrates accelerate the end of the last ice age?, *Can. J. Earth Sci.*, *27*, 148–157.

North Greenland Ice Core Project Members (2004), High resolution record of northern hemisphere climate extending in to the last interglacial period, *Nature*, *431*, 147–151, doi:10.1038/nature02805.

Nisbet, E. G. (1989), Some northern sources of atmospheric methane: production, history, and future implications, *Can.J. Earth Sci.*, *27*, 148–157.

Parkes, R. J., B. A. Cragg, J. C. Fry, R. A. Herbert, and J. W. T. Wimpenny (1990), Bacterial biomass and activity in deep sediment layers from the Peru margin, *Philos. Trans. R. Soc. London, Ser. A*, *331*, 139–153, doi:10.1098/rsta.1990.0061.

Paull, C. K., W. Ussler, and W. Dillon (1991), Is the extent of glaciation limited by marine gas hydrates?, *Geophys. Res. Lett.*, *18*, 432–434, doi:10.1029/91GL00351.

Paull, C. K., W. Ussler, and W. S. Borowski (1994), Sources of biogenic methane to form marine gas hydrates: In-situ production or upward migration, *Ann. N.Y. Acad. Sci.*, *715*, 392–409, doi:10.1111/j.1749-6632.1994.tb38852.x.

Person, M., J. McIntosh, V. Bense, and V. H. Remenda (2007), Pleistocene hydrology of North America: The role of ice sheets in reorganizing groundwater flow systems, *Rev. Geophys.*, *45*, RG3007, doi:10.1029/2006RG000206.

Petit, J. R., et al. (1999), Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica, *Nature*, *399*, 429–435, doi:10.1038/20859.

Prentice, I. C., D. Jolly, and Biome 6000 Participants (2000), Mid-Holocene and Glacial-Maximum vegetation geography of the Northern Continents and Africa, *J. Biogeogr.*, *27*(3), 507–519, doi:10.1046/j.1365-2699.2000.00425.x.

Price, B. P., and T. Sowers (2004), Temperature dependence for microbial growth, survival and maintenance, *Proc. Natl. Acad. Sci. U. S. A.*, *101*, 4631–4636, doi:10.1073/pnas.0400522101.

Punkari, M., and L. Forsström (1995), Organic remains in Finnish subglacial sediments, *Quat. Res.*, *43*, 414–425, doi:10.1006/qres.1995.1047.

Risatti, J. B. (1987), Biogeochemistry of a temperate zone peat bog, *Geol. Soc. Am. Abstr. Programs*, *19*, 821.

Rolandone, F., J. Mareschal, and C. Jaupart (2003), Temperatures at the base of the Laurentide Ice Sheet inferred from borehole temperature data, *Geophys. Res. Lett.*, *30*(18), 1944, doi:10.1029/2003GL018046.

Röthlisberger, R., et al. (2002), Nitrate in Greenland and Antarctic ice cores: A detailed description of depositional processes, *Ann. Glaciol.*, *35*, 209–216, doi:10.3189/172756402781817220.

Sharp, M. J., J. Parkes, B. Cragg, I. J. Fairchild, H. Lamb, and M. Tranter (1999), Widespread bacterial populations at glacier beds and their relationship to rock weathering and carbon cycling, *Geology*, *27*(2), 107–110, doi:10.1130/0091-7613(1999)027<0107:WBPAGB>2.3.CO;2.

Shilts, W. W. (1984), Till geochemistry in Finland and Canada, *J. Geochem. Explor.*, *21*(1–3), 95–117, doi:10.1016/03750-6742(84)90037-2.

Siegert, M. J. (2001), *Ice Sheets and Late Quaternary Environmental Change*, John Wiley, New York.

Simpkins, W. W., and T. B. Parkin (1993), Hydrogeology and redox chemistry of CH_4 in a late Wisconsinan till and loess sequence in Central Iowa, *Water Resour. Res.*, *29*(11), 3643–3657, doi:10.1029/93WR01687.

Skidmore, M., J. Foght, and M. J. Sharp (2000), Microbial life beneath a High Arctic glacier, *Appl. Environ. Microbiol.*, *66*(8), 3214–3220, doi:10.1128/AEM.66.8.3214-3220.

Souchez, R., M. Janssens, M. Lemmens, and B. Stauffer (1995), Very low oxygen concentration in basal ice from Summit, central Greenland, *Geophys. Res. Lett.*, *22*, 2001–2004, doi:10.1029/95GL01995.

Souchez, R., A. Bouzette, H. B. Clausen, S. B. Johnsen, and J. Jouzel (1998), A stacked mixing sequence at the base of the Dye 3 core, *Geophys. Res. Lett.*, *25*, 1943–1946, doi:10.1029/98GL01411.

Souchez, R., P. Jean-Baptiste, J. R. Petit, V. Y. Lipenkov, and J. Jouzel (2003), What is the deepest part of the Vostok ice core telling us?, *Earth Sci. Rev.*, *60*(1–2), 131–146, doi:10.1016/S0012-8252(02)00090-9.

Souchez, R., J. Jouzel, A. Landais, J. Chappellaz, R. Lorrain, and J.-L. Tison (2006), Gas isotopes in ice reveal a vegetated central Greenland during ice sheet invasion, *Geophys. Res. Lett.*, *33*, L24503, doi:10.1029/2006GL028424.

Sowers, T. (2006), Late Quaternary atmospheric CH_4 isotope record suggests marine clathrates are stable, *Science*, *311*, 838–840, doi:10.1126/science.1121235.

Stokes, C., and C. Clark (2003), Laurentide ice streaming on the Canadian Shield, a conflict with the soft-bedded ice stream paradigm?, *Geology*, *31*(4), 347–350, doi:10.1130/0091-7613(2003)031<0347:LISOTC>2.0.CO;2.

Stumm, W., and J. J. Morgan (1996), *Aquatic Chemistry*, 1022 pp., John Wiley, New York.

Tison, J. L., R. Souchez, E. W. Wolff, J. C. Moore, M. Legrand, and M. de Angelis (1998), Is a periglacial biota responsible for enhanced dielectric response in basal ice from the Greenland Ice Core Project ice core?, *J. Geophys. Res.*, *103*(D15), 18,885–18,894, doi:10.1029/98JD01107.

Tranter, M. (2003), *Geochemical Weathering in Glacial and Proglacial Environments, Treatise Geochem*., vol. 5, edited by J. I. Drever, pp. 189–205, Elsevier, New York.

Tranter, M., M. Skimore, and J. L. Wadham (2005), Hydrological controls on microbial communities in subglacial environments, *Hydrol. Processes*, *19*, 995–998, doi:10.1002/hyp.5854.

Truffer, M., W. D. Harrison, and K. A. Echelmeyer (2000), Glacier motion dominated by processes deep in underlying till, *J. Glaciol.*, *46*, 213–221, doi:10.3189/172756500781832909.

Trumbore, S. E. (2000), Age of soil organic matter and soil respiration: Radiocarbon constraints on below ground C dynamics, *Ecol. Appl.*, *10*(2), 399–411, doi:10.1890/1051-0761(2000)010[0399:AOSOMA]2.0.CO;2.

Trumbore, S. E., and J. W. Harden (1997), Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area, *J. Geophys. Res.*, *102*, 28,817–28,830.

Tung, H. C., N. E. Bramall, and P. B. Price (2005), Microbial origin of excess methane in glacial ice and implications for life on Mars, *Proc. Natl. Acad. Sci. U. S. A.*, *102*(51), 18,292–18,296, doi:10.1073/pnas.0507601102.

Tung, H. C., N. E. Bramall, and G. Vrdoljak (2006), Microorganisms metabolising on clay grains in 3-km-deep Greenland basal ice, *Astrobiology*, *6*(1), 69–86, doi:10.1089/ast.2006.6.69.

Valdes, P. J., D. J. Beerling, and C. E. Johnson (2005), The ice age methane budget, *Geophys. Res. Lett.*, *32*, L02704, doi:10.1029/2004GL021004.

Van Campo, E., J. Guiot, and C. Peng (1993), A data-based reappraisal of the terrestrial carbon budget at the Last Glacial Maximum, *Global Planet. Change*, *8*, 189–201, doi:10.1016/0921-8181(93)90008-C.

Wadham, J. L., S. Bottrell, M. Tranter, and R. Raiswell (2004), Stable isotope evidence for microbial sulphate reduction at the bed of a polythermal high Arctic glacier, *Earth Planet. Sci. Lett.*, *219*, 341–355, doi:10.1016/S0012-821X(03)00683-6.

Wagner, D., S. Kobabe, E.-M. Pfeiffer, and W. H. Hubberten (2003), Microbial controls on methane fluxes from a polygonal tundra of the Lena delta, Siberia, *Permafrost Periglacial Processes*, *14*, 173–185, : 10.1002/ppp.443.

Walder, J. S., and A. Fowler (1994), Channelized subglacial drainage over a deformable bed, *J. Glaciol.*, *40*(134), 3–15.

Weintraub, M. N., and J. P. Schimmel (2003), Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in Arctic tundra soils, *Ecosystems*, *6*(2), 129–143.

Weitemeyer, K., and B. A. Buffett (2006), Accumulation and release of methane from clathrates from below the Laurentide and Cordilleran ice sheets, *Global Planet. Change*, *53*, 176–187, doi:10.1016/j.gloplacha.2006.03.014.

Whalen, S. C., and W. S. Reeburgh (2000), Methane oxidation, production and emission at contrasting sites in a boreal bog, *Geomicrobiol. J.*, *17*, 237–251, doi:10.1080/01490450050121198.

Whiticar, M. J., E. Faber, and M. Schoel (1986), Biogenic methane formation in marine and freshwater environments, CO_2 reduction vs. acetate fermentation—Isotope evidence, *Geochim. Cosmochim. Acta*, *50*, 693–709, doi:10.1016/0016-7037(86)90346-7.

Wiles, G. C., D. J. Barclay, and P. E. Calkin (1999), Tree-ring-dated "Little Ice Age" histories of maritime glaciers from western Prince William Sound, Alaska, *Holocene*, *9*, 163–173, doi:10.1191/095968399671927145.

Winkler, S., and A. Nesje (1999), Moraine formation at an advancing temperate glacier: Brigdalsbreen, western Norway, *Geograf. Ann.*, *81A*, 17–30.

Wynn, P., A. Hodson, and T. Heaton (2006), Chemical and isotopic switching within the subglacial environment of a high Arctic glacier, *Biogeochemistry*, *78*(2), 173–193, doi:10.1007/s10533-005-3832-0.

Zeng, N. (2003), Glacial-interglacial atmospheric CO_2 change—The glacial burial hypothesis, *Adv. Atmos. Sci.*, *20*(5), 677–693.

Zeikus, J. G., A. L. Wellstein, and T. K. Kirk (1982), Molecular basis for the biodegradative recalcitrance of lignin in anaerobic environments, *FEMS Microbiol. Lett.*, *15*(3), 193–197.

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