

Organic matter content and quality in supraglacial debris across the ablation zone of the Greenland ice sheet

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ABSTRACT. Quantifying the biogeochemical cycling of carbon in glacial ecosystems is of great significance for regional, and potentially global, carbon flow estimations. The concentration and quality of organic carbon (OC) is an important indicator of biogeochemical and physical processes that prevail in an ice-sheet ecosystem. Here we determine the content and quality of OC in debris from the surface of the Greenland ice sheet (GrIS) using microscopic, chromatographic, spectrophotometric and high-temperature combustion techniques. The total OC content in the debris increased with distance from the edge of the ice sheet, from virtually zero to >6% dry weight at 50 km inland, and there was a peak in the carbohydrate proportion and the microbial abundance at ~6 km inland. The highest (galactose + mannose)/(arabinose + xylose) ratios, indicating maximum autochthonous microbial production, were found at >10 km inland. We propose that three key processes influence the carbon cycling on the GrIS: aeolian input of microbial inoculum and nutrients, in situ biological C transformation and the wash-away of supraglacial debris by meltwaters. We show that all these processes have significant spatial variability. While the total OC content of the debris on the ice sheet is probably controlled by the physical processes of wind transport and wash-away by meltwater, the microbial abundance and the quantity of the labile cell-contained OC within the debris is likely to be driven by the balance between the wash-away and the microbial productivity.

INTRODUCTION

Glaciers and ice sheets cover ~10% of the Earth's land surface and represent an important and under-explored part of the Earth system (Hodson and others, 2008). Glacier ecosystems are among the fastest-changing on our planet, and the rapid loss of glacier ice from the Earth's surface, mainly in the Arctic (Zwally and others, 2005), means that there will be a future shift from glacial to proglacial environments where carbon is sequestered and cycled in a different manner to glaciers. Quantifying the biogeochemical cycling of carbon in glacial ecosystems at present is therefore of great significance for carbon flow estimations and predicting future change (Anesio and others, 2009; Hood and others, 2009).

Glacier surfaces receive solar radiation, an essential source of energy for melting as well as for photosynthesis. Aeolian debris and aerosols, which contain microbial cells and other organic and inorganic matter, are also deposited on glaciers (Pearce and others, 2009). Viable microbes that can adapt to such a harsh environment colonize glacier surfaces and usually reside in cryoconite holes, cylindrical water-filled depressions which form on glaciers worldwide when dark debris deposited on the surface melts down into the ice (Wharton and others, 1985). The supraglacial microbial communities consist mainly of heterotrophic bacteria (where organic carbon is the source of energy and carbon for growth) and photoautotrophic bacteria and algae (where light is an energy source and inorganic carbon used for growth) (Margesin and others, 2002; Säwström and others, 2002; Stibal and others, 2006). Therefore, supraglacial environments have the potential to play a significant role in regional, and possibly global, carbon budgets by means of primary production and respiration (Anesio and others, 2009; Hood and others, 2009). However, most

observations to date have been limited to small valley glaciers, and thus have only local significance and a limited applicability for large-scale estimates.

In a large ice-sheet ecosystem, aeolian debris eroded from soils and sediment in deglaciated areas is the principal source of microbes and both labile and recalcitrant organic matter to the ice surface (Bøggild and others, 2010). This organic carbon (OC) may be transformed by microbial processes such as respiration and secondary production, with new OC being produced within the system by conversion of inorganic carbon (CO₂) from the atmosphere via photosynthesis. Organic matter is usually attached to mineral debris on the glacier surface and may be transported with the debris down-glacier and/or washed into moulins and crevasses, and so exported from the system (Stibal and others, 2008a). Organic matter that remains on the surface is likely to decay and become less labile over time. The OC content and quality may therefore be an important indicator of biogeochemical and physical processes that prevail in an ice-sheet ecosystem.

Various methods have been used to assess the quality of glacial OC, including spectrofluorometric analysis that distinguishes between labile and recalcitrant C and may reveal the possible origin of the organic matter present (Dubnick and others, 2010) and nuclear magnetic resonance (NMR) techniques revealing the composition and provenance of OC (Xu and others, 2010). A more quantitative indicator of active biogeochemical processes is the concentration and quality of carbohydrates and their proportion in the organic matter. Carbohydrates represent an important component of the OC pool owing to high concentrations of storage polysaccharides and glucose in microbial exopolymers (Biersmith and Benner, 1998). The abundance and range of carbohydrates in particulate organic matter has

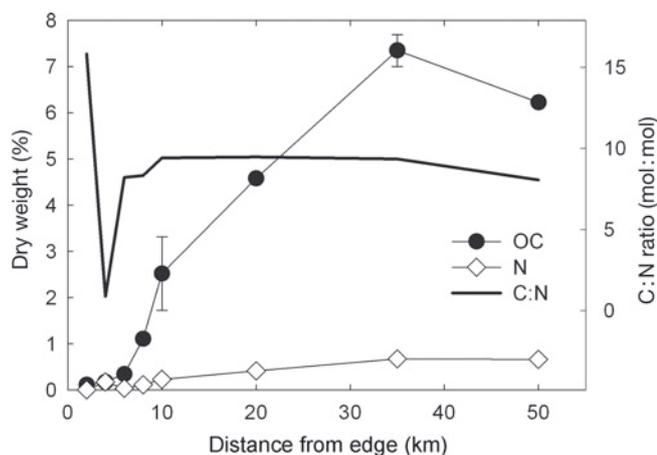


Fig. 1. Total organic carbon and total nitrogen in the cryoconite debris samples collected along the transect.

been investigated in various environments, including Antarctic sea ice, by detecting the monosaccharides liberated after acid hydrolysis (Mopper and others, 1992; Herborg and others, 2001; Pusceddu and others, 2009). However, biochemical analysis of organic matter is scarce in cryospheric research, partly owing to analytical limitations in detecting and quantifying trace-level analytes.

Here we present the first study to determine the content and quality of OC within the debris on the surface of an ice sheet using microscopic, chromatographic, spectrophotometric and high-temperature combustion techniques. Glacier surface debris (cryoconite) was sampled along a transect across the entire ablation zone of the Greenland ice sheet (GrIS). On the basis of the results, we propose the key processes that govern the distribution and quality of organic matter within debris on the surface of the ice sheet.

MATERIALS AND METHODS

Field site and sampling

The GrIS is the second largest body of ice on Earth. Its area is $\sim 1\,700\,000\text{ km}^2$ (>10% of the world's ice surface), and its ablation zone stretches up to 100 km inland, comprising all 'glacier ecological zones', i.e. large areas of barren ice, slush and wet snow (Hodson and others, 2010a). Samples of

surface debris (cryoconite) were collected between 1 and 15 August 2009 in the southwest part of the GrIS, along a transect across the entire ablation zone of the ice sheet. The transect consisted of 11 points beginning at the terminus of Leverett Glacier and finishing $\sim 100\text{ km}$ inland (Table 1; Fig. 1). Cryoconite samples were collected in sterile 0.5 L Whirl-Pak bags (Nasco, Fort Atkinson, WI, USA) with a sterile 50 mL syringe and frozen immediately after return to the field camp by Leverett Glacier. Samples remained frozen at -20°C prior to analysis, whereby they were slowly thawed in the laboratory. The coverage of surface debris was estimated at each sampling point using the quadrant method (Stibal and others, 2008a).

Organic carbon analysis

The total carbon (TC) and nitrogen (TN) contents of the debris were determined using a EuroVector EA3000 Elemental Analyser (EuroVector, Milan, Italy). Inorganic carbon was measured on a Ströhlein Coulomat 702 analyser (Ströhlein Instruments, Kaarst, Germany) adapted for this purpose. Both analysers were calibrated using certified standards. Detection limits were 10 ppm for both elements, and the precision of determinations was 0.3%. The total OC content was calculated as the difference between TC and inorganic carbon content.

Carbohydrate concentrations in the debris samples were analysed by ion chromatography with pulsed amperometric detection. This followed an acid-extraction protocol, involving hydrolysis, neutralization and desalting, to convert any polysaccharides and sugar derivatives to lower molecular weight components (mono- and disaccharides) for ion chromatography determination (Jensen and others, 2005). Briefly, 250 mg of wet debris was weighed into 8 mL glass screw-cap serum vials and fitted with Teflon cap liners. 5 mL of 1 M H_2SO_4 was added and the vial sealed. Samples were hydrolysed at 110°C for 24 hours. After cooling, they were shaken for 30 min and centrifuged. The supernatant was then neutralized to pH 4–5 by the addition of NaOH and an aliquot diluted for analysis and stored in sterile polypropylene tubes. Samples were stored at -20°C until analysis. Each extraction procedure was conducted in triplicate, and blanks run to assess possible contamination during the procedure. In addition, carbohydrate standards were subject to the same extraction procedure to determine the loss of mono- and disaccharides during the hydrolysis step. Losses

Table 1. Sampling points along the transect across the ablation zone of the GrIS and the presence of meltwater and surface debris (cryoconite) during sampling in August 2009. Distance is from the terminus of Leverett Glacier. +, present; –, absent

Distance	Altitude m a.s.l.	Lat. (N)	Long. (W)	Supraglacial meltwater	Supraglacial debris
0	248	67°03'36.7"	50°10'25.6"	+	+
2	410	67°04'07.3"	50°07'59.0"	+	+
4	494	67°04'28.4"	50°05'21.6"	+	+
6	546	67°04'59.7"	50°02'56.4"	+	+
8	591	67°05'37.0"	50°00'37.4"	+	+
10	649	67°05'56.1"	49°57'56.4"	+	+
20	761	67°06'15.4"	49°48'26.6"	–	+
35	1022	67°06'56.7"	49°24'05.2"	–	+
50	1186	67°07'36.4"	49°00'36.0"	–	+
70	1446	67°09'10.8"	48°22'14.6"	–	–
100	1682	67°09'45.3"	47°32'57.2"	–	–

ranged from 53% to 97%, with fructose and sucrose destroyed entirely, in line with losses observed elsewhere (Borch and Kirchman, 1997). Hence, the concentrations of carbohydrates present in sediment samples represent minimum estimates.

Chromatographic analyses were performed by an ICS-3000 dual-analysis Reagent-Free Ion Chromatography system (Dionex, Camberley, UK), equipped with Chromeleon 6.8 software. Carbohydrates were separated isocratically by a CarboPac PA20 column (3 × 150 mm), with in-line CarboPac PA20 guard column (3 × 30 mm), and detected by a Dionex ED40 electrochemical detector operating in a pulsed amperometric mode and using non-disposable electrodes. The mobile phase consisted of degassed 15 mM NaOH flowing at 0.35 mL min⁻¹. During initial runs, xylose and mannose tended to co-elute due to similar retention times. However, separation was deemed necessary for subsequent interpretations of the origin of the bulk carbohydrate component (e.g. xylose indicates decomposition of plant residues, whereas mannose suggests the accumulation of microbial metabolites). Separation was achieved during a 30 min run, using a degassed 3 mM NaOH mobile phase and 0.4 mL min⁻¹ flow rate. The retention times of the compounds of interest were determined by running mixed standard solutions, and concentrations of individual compounds were obtained by directly interpolating the peak area in respect to the corresponding regression equation, supplied by the standard calibration. Calibrations were linear, based on a minimum of five standards, prepared daily from aqueous serial dilutions of a 1 mg L⁻¹ intermediate stock standard (prepared weekly). Analytical blanks were run in parallel. Drift was determined by running a 100 µg L⁻¹ standard after every ten samples. The column was regenerated every 2–3 days by washing with 200 mM NaOH for 45 min, and re-equilibrating with 15 mM NaOH for a further 45 min, which removed carbonates and other contaminants from the column. Detection limits, calculated as 3 × signal-to-noise ratio, were close to 0.5 µg L⁻¹ for all carbohydrates. Relative standard deviations for individual carbohydrate concentrations ranged from 0.9% to 45.7%

Chlorophyll extraction

Chlorophyll was extracted from 1 g of wet cryoconite debris in clean 15 mL centrifuge tubes by adding 10 mL 96% ethanol, shaking on a reciprocating shaker for 30 min at 200 rpm and leaving at 4°C in the dark for 24 hours. The tubes were then shaken again for 30 min at 200 rpm and centrifuged at 2600 rpm for 12 min. The extracts were analysed using a Shimadzu UV-Mini 1240 spectrophotometer (Shimadzu, Kyoto, Japan) at wavelengths of 665 and 750 nm. Calibration was conducted using chlorophyll-*a* standards (1–10 000 µg L⁻¹). Procedural blanks containing no cryoconite debris were also analysed.

Microbial abundance

10 mg of freshly melted wet cryoconite debris and 1 mL of pre-sterilized deionized water was placed in a sterile Eppendorf tube and mixed by vortexing for 30 s. In order to fix the sample, 0.2 µm filter-sterilized 37% formaldehyde (final concentration 1%) was added to the tube, followed by a brief vortexing. The suspension was then filtered onto a sterile 0.2 µm Anodisc filter (Whatman, Maidstone, UK). Dried filters were placed onto 100 µL drops of 2 × SYBR Gold (Invitrogen, Eugene, OR, USA) for 15 min, dried and

mounted on microscopic slides with the anti-fade agent Citifluor AF2 (Citifluor, Leicester, UK). More than 300 SYBR Gold stained cells were enumerated on each slide with an Olympus BX41 epifluorescence microscope (Olympus Optical, Tokyo, Japan) using the filter block U-N31001 (excitation 480 nm, emission 535 nm; Chroma Technology, Rockingham, VT, USA). Cells showing red chlorophyll autofluorescence were enumerated using the filter block U-MWU2 (excitation 330–385 nm, emission 420+; Olympus Optical, Tokyo, Japan). Two slides per sample were counted. A procedural blank with no cryoconite sediment was counted in parallel and the average blank counts were then subtracted from the experimental sample counts.

RESULTS

The distribution of cryoconite debris changed markedly with increased distance away from the ice-sheet margin, i.e. the terminus of Leverett Glacier. The amount of supraglacial water present at the monitoring sites decreased inland, with virtually no small surface-melt features (e.g. cryoconite holes, melt pools) observed on the surface of the study sites further than 10 km inland (Table 1).

Figure 1 shows the total organic carbon (TOC) and TN contents, and the molar ratios of TOC and TN, within the supraglacial debris samples. Both OC and N increased with distance from the edge of the ice sheet, from virtually zero to >6% dry weight (dw) of OC and >0.6% dw of N at 35 and 50 km inland. The C:N molar ratio was around 8–9 in most samples. The total amount of carbohydrates extracted from the debris showed a similar trend to that of total OC and N, with some divergence at 4, 6 and 8 km (Fig. 2a). No significant differences were found in the proportion of the different carbohydrate compounds between the samples, with glucose and galactose being the dominant carbohydrates throughout. The ratio of (galactose + mannose)/(arabinose + xylose) exceeded 1 at all sites, reaching a maximum of 3.9 at 10 km (Fig. 2b).

A different trend became apparent when the amount of carbohydrates was related to the total OC content within the debris. There is a peak in the carbohydrate proportion at 6 km inland, and this trend is almost identical to the independently determined numbers of microbial cells associated with the debris, with a peak of $\sim 1.5 \times 10^8$ cells per gram of wet weight debris at 6 km inland (Fig. 3a).

The numbers of photoautotrophic cells (cyanobacteria and algae) were very variable and ranged from 0.1 to 11×10^6 cells per gram of wet weight debris (Fig. 3b). Due to the high variability, an apparent local peak at 6 km corresponding to the peak in the total microbial abundance (Fig. 3a) is not significant. Most phototrophs were present in the form of tight clusters of filaments, and so were very difficult or, in the case of the sample from 50 km inland, impossible to enumerate. Low concentrations of chlorophyll were detected in the debris, ranging from ~ 0.3 to ~ 3.8 µg chlorophyll g⁻¹ (Fig. 3c).

DISCUSSION

Distribution of cryoconite debris on the ice sheet

Close to the margin (point 0 km), large amounts of debris were scattered in a thin layer covering much of the ice surface (Fig. 4a). This debris was different from that in

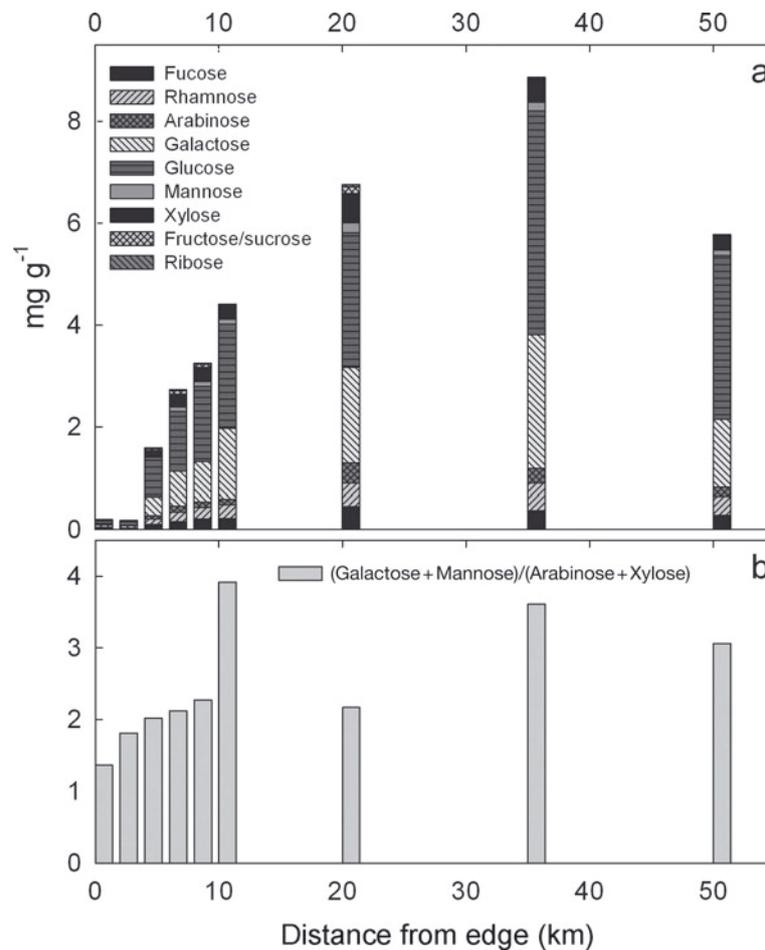


Fig. 2. (a) Carbohydrates extracted from the cryoconite debris and (b) the (galactose + mannose)/(arabinose + xylose) ratios in the samples collected along the transect.

cryoconite holes further up-glacier in being much coarser and lighter in colour. It is likely to have partly originated from pressure ridges (Fig. 4a), and so to have been of subglacial origin (Hodson and others, 2010a). More than 2 km inland, cryoconite debris was present on the surface (Fig. 4b), covering up to 10% of the surface, and increasing in its per cent areal coverage from 2 to 10 km. From 10 to 50 km the amount of visible surface debris decreased again, with most covered by a layer of firn or ice (Fig. 4c and d). No cryoconite was found at 70 and 100 km inland. Since most microbial activity and organic matter is associated with the debris in glacier surface environments (S awstr om and others, 2002; Hodson and others, 2007), this variation in debris distribution may be a key factor in determining the spatial distribution of productivity in the ecosystem.

Quantity and quality of organic carbon on the ice sheet

The TOC and TN contents found in the debris on the GrIS are within the range reported from smaller glaciers (Takeuchi, 2002; Stibal and others, 2008a). The C : N molar ratio of 8–9, determined in most samples, is typical of values found in soils (Cleveland and Liptzin, 2007) and slightly lower than that found in cryoconite on other Arctic and alpine glaciers (Takeuchi, 2002; Stibal and others, 2008b), and suggests some biological control in the system. The C : N ratio in the sample from 4 km is very low due to the very high N content determined in the sample.

The fraction of carbohydrates within the debris OC pool is relatively small at most sites (1–16%), similar to the lower range of values found in ocean surface sediments (Cowie and others, 1992; Kerherv e and others, 2002). In samples from the 4–8 km band, there is a significant increase in the contribution of carbohydrates (29–79%), suggesting an abundance of fresh biogenic organic matter (Yamaoka, 1983; Kerherv e and others, 2002), for example, glucose and galactose, two hexoses well known to be labile and utilized by various heterotrophic organisms (Hernes and others, 1996). This suggests both efficient OC production by primary producers and the provision of a bioavailable OC substrate for heterotrophic metabolism.

Further insight into the OC source material and biochemical transformations can be derived from the distribution of carbohydrates. Compositional spectra dominated by galactose, rhamnose and fucose have been linked with macroalgae, macrophytobenthos and bacteria, respectively (Liebezeit, 1988). Xylose is indicative of angiosperms (Opsahl and Benner, 1999) and a useful biomarker for plant residues within the sediment. Several ratios of carbohydrates have been employed to interpret OC data (Biersmith and Benner, 1998; Khodse and others, 2008). We use the ratio of (galactose + mannose)/(arabinose + xylose) to provide an indication of the origin of the monosaccharides since arabinose and xylose are usually not synthesized by microorganisms and so originate mostly in plant materials (Turchenek and Oades, 1979). The determined ratios (>1) in

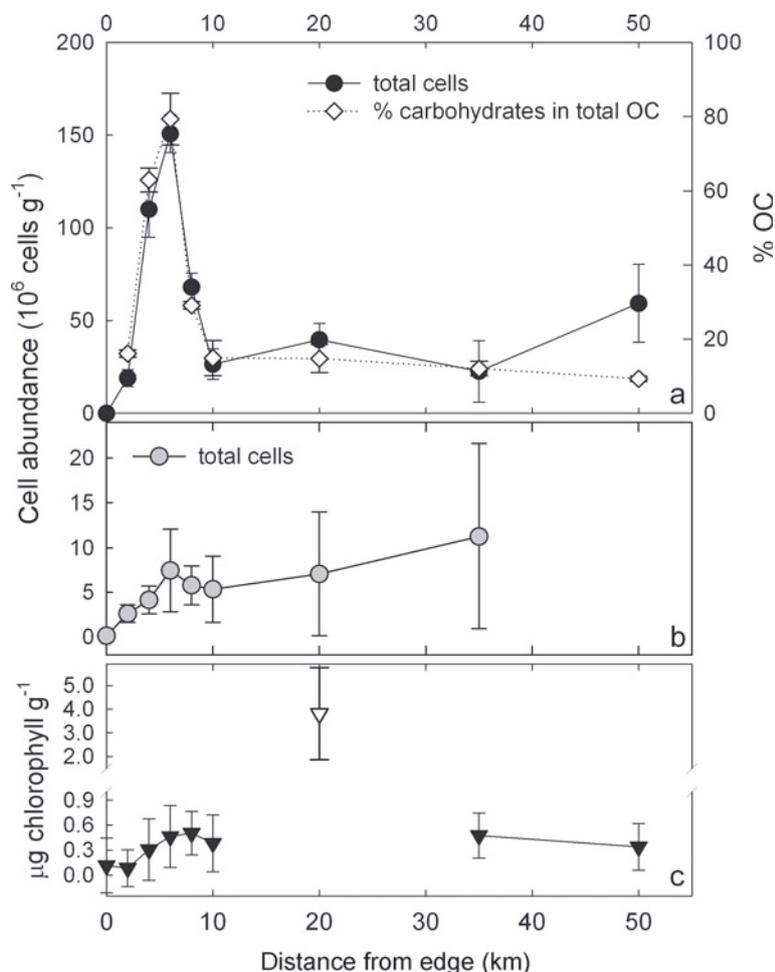


Fig. 3. (a) Microbial abundance and the proportion of carbohydrates in TOC exhibit a very similar trend along the transect across the ablation zone of the GrIS. (b) Abundance of photoautotrophic microbes (cyanobacteria and algae) and (c) chlorophyll concentration in the debris are low, and possible trends are obscured by the high standard deviations, and an outlier at 20 km (white triangle).

our samples from all sites suggest an accumulation of microbial metabolites (i.e. autochthonous OC), with some input of allochthonous terrestrial carbohydrates from plant material. The highest (galactose + mannose)/(arabinose + xylose) ratio was found at the 10 km site (Fig. 2b), and the 35 and 50 km sites also had high ratios. This suggests that microbial production is dominant over allochthonous organic matter input higher up on the ice sheet.

The numbers of photoautotrophic cells were within the range found in cryoconite holes on small valley glaciers on Svalbard (Sävström and others, 2002; Stibal and others, 2006; Stibal and Tranter, 2007), although the concentrations of chlorophyll were lower than reported from Svalbard (Stibal and others, 2008a). However, due to the very low and variable cell numbers and chlorophyll concentrations and the resulting relatively high measurement errors, it is difficult to discern a trend in the abundance of photoautotrophs in the debris along the transect. The heterogeneity in their distribution within the debris, consistent with observations from other glaciers, can be attributed to the tendency of the dominant filamentous cyanobacteria to form clusters (Stibal and Tranter, 2007).

The concurrent peaks in the carbohydrate proportion and the numbers of all microbial cells within the debris at ~6 km inland mark a zone where high microbial growth and production coincides with potential in situ accumulation of

organic matter. From this we can develop a concept of what controls the distribution of organic matter on the ice-sheet surface.

Controls of the distribution of organic matter content in debris on the ice sheet

Three key processes are likely to exert a control over the quantity and quality of OC in supraglacial debris on the GrIS. Two simple conceptual models (Fig. 5) present the possible effects of these processes on the OC content within the surface debris. These models are based on the following hypotheses and supported by the OC data shown in Figures 1 (total OC) and 3a (cell-contained OC).

First, the input of aeolian debris, containing microbial cells and other organic matter, to the glacier surface is dependent on the source and size of particles transported (Bøggild and others, 2010). Adjacent deglaciated areas are the most likely source for the majority of cryoconite debris (Stibal and others, 2008b; Bøggild and others, 2010; Xu and others, 2010). It is possible that loose organic matter fragments are transported further than mineral particles due to their lower relative density (Zobeck, 1991), in which case the proportion of OC in the debris could increase inland (Fig. 5b). It is also expected that larger particles of plant residue will only be transported a short distance. Active microbial cells, on the other hand, are usually

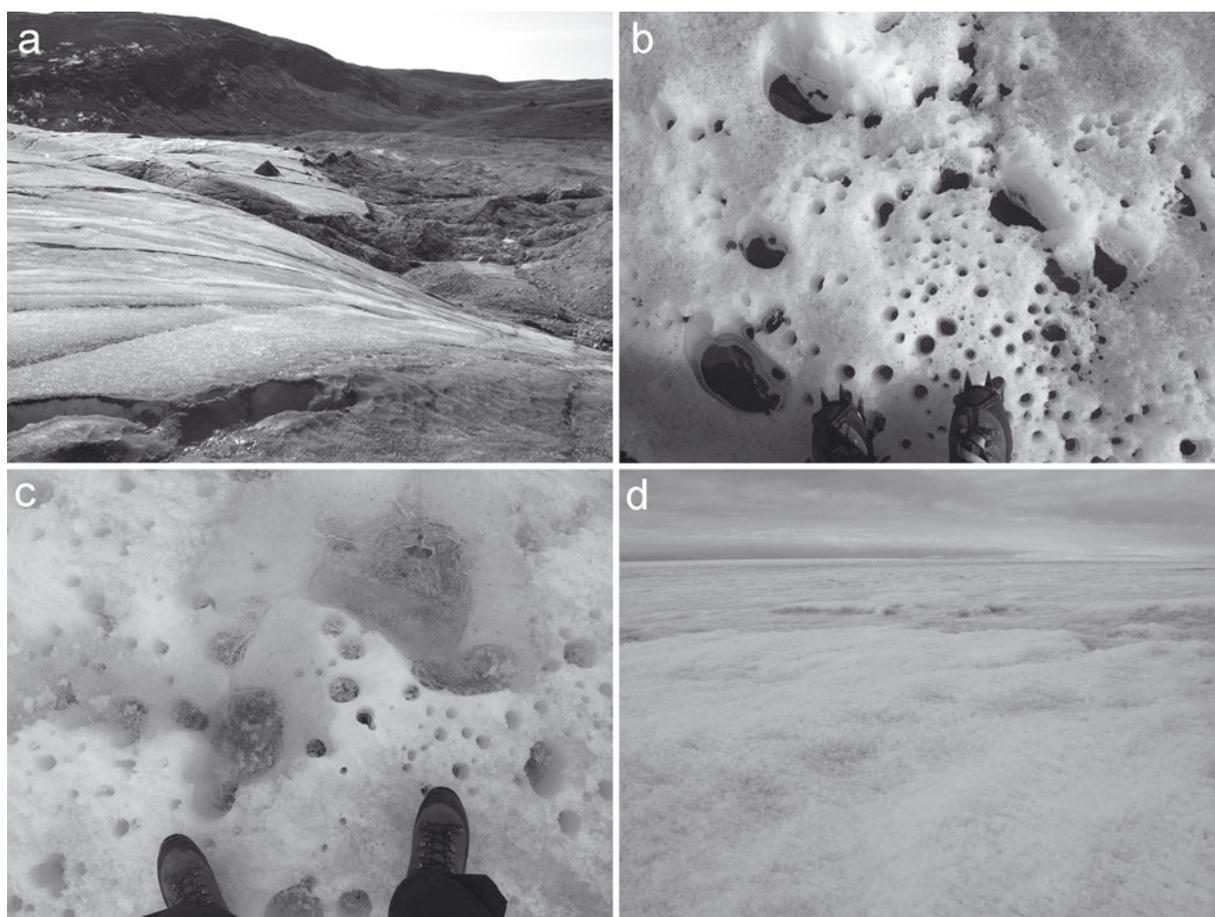


Fig. 4. Surface of the GrIS along the transect. (a) Terminus of Leverett Glacier with pressure ridges and supraglacial kames. (b) Open cryoconite holes and dispersed cryoconite debris at 8 km inland. (c) Ice-lidded cryoconite holes at 20 km inland. (d) At 50 km cryoconite debris is hidden below the ice surface.

attached to mineral particles due to producing exopolymers (Hodson and others, 2010b), and so may be transported with mineral dust particles. In the latter case, the cell-contained OC within the debris would be constant along the transect (Fig. 5a). The role of debris that has melted out of old ice in this scheme is unclear; however, as its origin is likely far from the ice sheet and delivery by long-distance transport mechanisms (Bøggild and others, 2010), no spatial variability of its OC content across the ice sheet would be expected.

Second, biological carbon transformation changes the concentration of OC in the system. Photoautotrophic microbes fix CO_2 from the atmosphere into organic matter, and thus add C to the system. On the other hand, all microbes respire, or 'burn' organic C into CO_2 , back into the atmosphere and so remove C from the system. A wide range of in situ rates of photosynthesis and respiration and their ratios ($P:R$) have been determined on various glaciers to date (Hodson and others, 2007, 2010a,b; Stibal and others, 2008a; Anesio and others, 2009; Telling and others, 2010). This means that there is the potential for glacier surfaces to be net autotrophic (CO_2 sinks; $P:R > 1$) or net heterotrophic (CO_2 sources; $P:R < 1$), and both cases may be of high regional importance (Anesio and others, 2009; Hood and others, 2009). However, it is important to realize that even a balanced $P:R$ does not necessarily imply a constant quantity of the cell-contained OC in the system, since heterotrophic growth can also be sustained by the uptake of allochthonous

OC (Margesin and others, 2002; Anesio and others, 2010). As the presence of liquid water is likely to have a profound effect on all microbial processes on the ice sheet, lower-altitude areas closer to the ice-sheet margin are potentially more productive in terms of cell numbers and the cell-contained OC than more distant, and colder, inland areas.

Third, the wash-away effect of supraglacial meltwater may play an important role in the steep marginal zone of the ice sheet. Organic matter has been shown to be removed from cryoconite debris over time (Stibal and others, 2008a), and the wash-away may result in a decreased content of OC in supraglacial debris in the marginal zones of ice sheets.

Figure 5a is a conceptual model of the three described key environmental effects on the abundance of microbial cells and the cell-contained OC within supraglacial debris on the GrIS. Viable cells are assumed to be transported with dust, so the input of the cell-contained OC is constant across the ablation zone in the model. The productivity component (change in the cell-contained OC in the system) of this model is dependent on the $P:R$ ratio and the heterotrophic activity in the microbial community. We assume the simplest case of a balanced $P:R$, supported by data from Greenland (Hodson and others, 2010a) and Svalbard (Telling and others, 2010), and utilization of both autochthonous and allochthonous OC (Anesio and others, 2010) in the model. The highest productivity is predicted to be related to the extent and duration of melting, so it is negatively correlated with distance from the edge of the ice sheet in the

model. The wash-away effect occurs in the steepest part of the ice sheet, i.e. close to the edge. The combined effect of these processes (dust transport, productivity and wash-away effects) produces a maximum percentage of the cell-contained OC within supraglacial debris that is located at the border between the 'carbon wash-away zone', where rapidly flowing meltwater efficiently removes large amounts of carbon and transports it to subglacial and proglacial ecosystems, and the 'carbon accumulation zone', where the presence of liquid water and inputs of microbes and nutrients via dust transport decrease inland. This is supported by the microbial-abundance and carbohydrate data shown in Figure 3a.

Another scenario is suggested for the TOC content in the debris (Fig. 5b). Here the easier atmospheric transportability of loose organic matter compared to mineral dust is accounted for, and results in a proportional increase in the OC content of supraglacial debris with increased distance inland. The productivity component (change in the TOC in the system) of this model is only dependent on the *P*:*R* ratio in the microbial community, again assumed to be balanced (Hodson and others, 2010a,b), and not on secondary production that only recycles OC in the system. The wash-away effect of meltwater is identical to that in the previous model. The resulting percentage of the TOC within cryoconite debris then increases from the edge of the ice sheet inland, although the total amount of OC on the surface can actually decrease. This is supported by the TOC and TN contents shown in Figure 1.

These models are very simple and only show the environmental effects on the percentage of OC in surface debris, rather than on the amount of OC per unit area, which is more important for a global picture of supraglacial productivity. It is also possible that the *P*:*R* ratios will be significantly different from balance at various sites. However, the models demonstrate how simple physical and biogeochemical processes may control C cycling in large ice-sheet ecosystems.

CONCLUSIONS AND OUTLOOK

It is now appreciated that supraglacial environments may play an important role in regional carbon cycling given their large area and productivity, and there is an increasing need to estimate the contribution of glacial ecosystems to regional and global carbon flows. We propose that three key processes influence the productivity and carbon cycling on the surface of ice sheets: (1) aeolian input of microbial inoculum and nutrients, (2) biological C transformation on the ice, mostly in cryoconite holes, and (3) the wash-away of supraglacial debris by meltwaters to subglacial and proglacial environments. Using the OC content and quality analysis of supraglacial debris from a transect across the ablation zone of the GrIS, we show here that all these processes have significant spatial variability. While the amount of TOC in supraglacial debris on the ice sheet is probably controlled by the physical processes of wind transport and wash-away by meltwater, the microbial abundance and the quantity of the labile cell-contained OC in the debris is likely to be driven by the balance between the wash-away and the microbial productivity.

Therefore, in order to quantify the productivity and carbon cycling in large glacial ecosystems and to be able to scale up and implement the results into biogeochemical

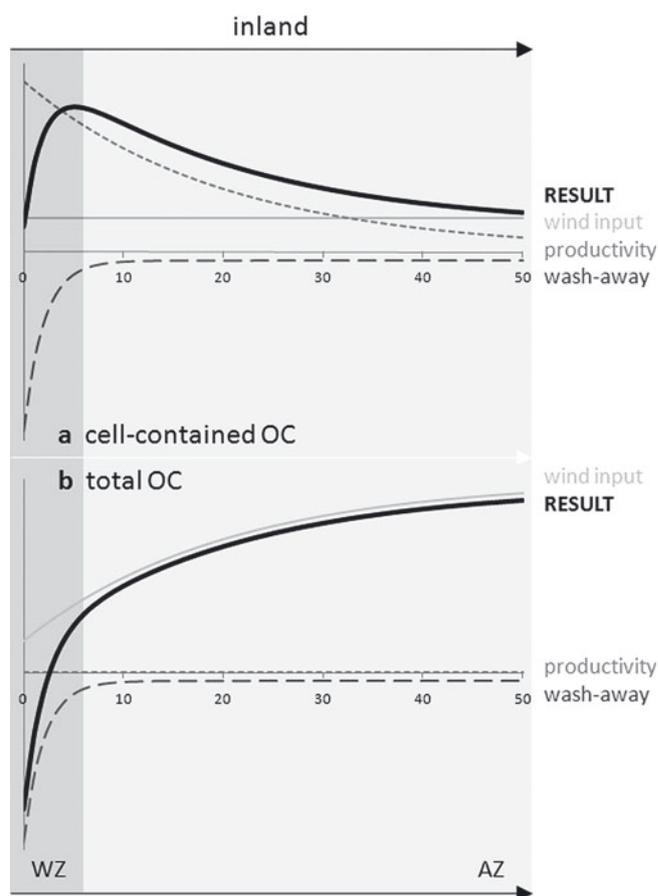


Fig. 5. Conceptual models of the OC distribution across the ablation zone of the GrIS. (a) Microbial abundance and the cell-contained OC (cf. Fig. 3a). (b) TOC (cf. Fig. 1). WZ–OC: wash-away zone; AZ–OC: accumulation zone.

models, it is essential that we account for the spatial variability and the limiting factors of biological activity on glacier and ice sheets. Quantifying aeolian debris deposited on the ice surface, spatial assessment of microbial productivity and linking supraglacial systems with downstream ecosystems via meltwater runoff are the obvious next steps to a better understanding of C cycling in the cryosphere.

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