

Biodegradability of dissolved organic carbon in permafrost soils and waterways

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Biodegradability of dissolved organic carbon in permafrost soils and waterways: a meta-analysis

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progress. Our results suggest that future, climate warming-induced shifts of continuous permafrost into discontinuous permafrost regions could affect the degradation potential of thaw-released DOC as well as its variability throughout the Arctic summer. We lastly present a recommended standardized BDOC protocol to facilitate the comparison of future work and improve our knowledge of processing and transport of DOC in a changing Arctic.

1 Introduction

Boreal and Arctic ecosystems contain more than half of global terrestrial organic carbon (Tarnocai et al., 2009; Hugelius et al., 2014), much of which will be vulnerable to microbial processing and release to the atmosphere by the end of the century (Slater et al., 2013; Schaefer et al., 2014; IPCC 2013). At high latitudes, ecosystem carbon balance depends largely on aquatic processes (Kling et al., 1992; Striegl et al., 2012; Vonk and Gustafsson, 2013) with lakes, wetlands, rivers, and streams covering more than half of the land surface in many regions (McGuire et al., 2009; Loveland et al., 2000; Lammers et al., 2001; Aufdenkampe et al., 2011; Avis et al., 2011). However, little is known about mechanistic controls on persistence or processing of organic carbon currently flowing through Arctic watersheds (Mann et al., 2012; Wickland et al., 2012), and even less is known about the behavior of permafrost-derived organic carbon that is delivered to arctic freshwater and marine ecosystems (Cory et al., 2013; Vonk and Gustafsson, 2013).

Arctic watersheds transport an average of 34 Tg C yr^{-1} of dissolved organic carbon (DOC) and 6 Tg C yr^{-1} of particulate organic carbon (POC) to the Arctic Ocean (Holmes et al., 2012; McGuire et al., 2009), not including fluxes from coastal erosion. Though no model projections of future circum-arctic hydrologic carbon flux exist, a few recent studies predict that organic carbon loading to the circum-arctic watershed may increase in the future (Abbott et al., 2015; Kicklighter et al., 2013). However, observed patterns of changes in hydrological carbon loading in permafrost regions are inconsistent, with

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effects of bacterial inoculation: (1) no inoculum, (2) 1 % inoculum by volume, (3) 10 % inoculum by volume. Inocula consisted of 1.2 μm filtered water (using pre-combusted (450 $^{\circ}\text{C}$ > 4 h) Whatman GF/C filters, 1.2 μm nominal pore size) that was added to sample waters (filtered at 0.7 μm) to the specified ratio.

We prepared 30 mL aliquots of sample into pre-combusted (550 $^{\circ}\text{C}$ > 4 h) 40 mL glass incubation vials and stored them at 20 $^{\circ}\text{C}$ in the dark, with no nutrient amendment. To ensure oxic conditions we left vial caps loose and shook samples once a day. The incubated samples were re-filtered through 0.7 μm filters to remove flocculation after 0, 2, 7, 14 and 28 days (using separate vials, in triplicate, for each time step). Re-filtration removes the majority of the microbial biomass, resulting in a measured DOC loss including both DOC mineralization and assimilation. Samples were immediately acidified with 30 μL of concentrated HCl (high quality grade; to $\text{pH} \leq 2$). Acidified sample vials were capped and stored refrigerated in the dark until analysis within three months. At the time of analysis, acidified samples were sparged with CO_2 free air for 8 min at 75 mL min^{-1} and run as non-purgable organic carbon (NPOC) on either a Shimadzu TOC-V or TOC-L analyzer. DOC was calculated as the mean of between three and seven injections and the coefficient of variance was always < 2 %. BDOC was calculated as the change in DOC concentration during the 28 day incubation, relative to the initial DOC concentration, and is reported in percent loss.

2.3 Statistical analyses

We combined the literature meta-analysis of 14 papers ($n = 551$) with data from our circum–arctic incubation experiment ($n = 192$). Each of the studies identified used different methods for assessing BDOC, complicating and limiting the analyses available. To examine trends across the total dataset ($n = 743$) we therefore performed categorical principle component analysis (CATPCA) via optimal scaling. This approach allowed us to compare the effect of multiple variables with mixed measurement levels (scalar, nominal, ordinal). After, we performed a standard principle component analysis (PCA) using the optimally-scaled results to aid in data interpretation. Data normality was as-

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sessed using the Shapiro–Wilk test ($p > 0.05$). Separate CATPCA and PCA analyses were performed on the aquatic and soil leachate datasets, as well as for methodological and environmental parameters (Table 1). Validity of each PCA was tested using the Barlett tests of sphericity ($p < 0.001$) and Kaiser–Meyer–Olkin measures of sampling adequacy. Direct oblimin rotation was applied and rotated scores used throughout, allowing for correlation between scores (Manisera et al., 2010). CATPCA runs assigned measures from scalar data (initial DOC, % BDOC, latitude, longitude, Julian day, bottle size, incubation time, and incubation temperature), nominal data (method of C loss, shaking, nutrient addition, inoculum, oxygen availability, location in fluvial network) and ordinal data (filter pore size, and permafrost extent). We considered final rotated PCA correlations of > 0.7 as strong, between 0.5 and 0.7 as moderate, and < 0.5 as weak or absent (Quinn and Keough, 2002). Although this approach was not ideal, in our opinion it proved the best available approach given the diverse dataset which included repeated measures (i.e. multiple time points) of a given parameter (i.e. BDOC; Bradlow et al., 2002). Additionally, we combined data from all studies carried out from 15–25 °C with incubation durations of 28–34 days, which represented the most common temperature and length used, to test for environmental trends (Figs. 3–5). Here we tested for differences among means using analysis of variance (ANOVA). All ANOVA, CATPCA and PCA analyses were conducted in SPSS 22.

3 Results

3.1 Literature synthesis

The 14 literature studies comprised a total of 551 data points of which 418 were aquatic. Most studies were located in North America (242 in Alaska, USA and 227 in Canada; Fig. 1), 234 were from regions without permafrost, and 230 were from regions with continuous permafrost (Fig. 2e). The most common incubation temperatures were 17.5 or 20 °C (41 and 36 % of the data, respectively). The majority of studies (60 %

3.2.2 Soil leachate BDOC

Three principle components explained 72 % of the variance across all soil incubation samples (PC1 = 34 %, PC2 = 21 %, PC3 = 16 %; Table 2). Component 1 was strongly correlated with BDOC loss ($r = 0.75$), as well as the availability of oxygen in incubations ($r = 0.94$), the method used to measure carbon loss ($r = 0.87$) and whether samples were shaken during incubation ($r = 0.73$). Neither component 2 nor 3 closely correlated with BDOC, but component 2 correlated positively with incubation time ($r = 0.88$), filter pore size ($r = 0.74$) and temperature ($r = 0.54$), and component 3 was positively correlated to bottle size ($r = 0.74$), and inoculum ($r = 0.57$) and negatively related to temperature ($r = -0.66$) and shaking ($r = -0.57$).

3.3 Environmental factors affecting BDOC

Similar to Sect. 3.2, here we present the statistical results of the combined literature synthesis and circum–arctic incubation experiments concentrating on how environmental variables co-vary with BDOC losses.

3.3.1 Aquatic BDOC

Three components explained 82 % of the total variance among environmental parameters from all aquatic incubations (PC1 = 52 %, PC2 = 18 %, PC3 = 13 %; Table 3). The first component was moderately correlated with BDOC ($r = 0.51$) and strongly correlated with location within the fluvial network ($r = 0.95$), dominant permafrost type ($r = 0.94$; greater BDOC in continuous permafrost regions, see also Fig. 3a), sample latitude ($r = 0.93$), and initial DOC ($r = -0.70$). The second component was strongly negatively correlated with BDOC ($r = -0.71$), and was explained by sample longitude ($r = 0.78$). The third component did not correlate to BDOC but showed a strong correlation with sampling period (Julian day; $r = 0.95$).

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3.3.2 Soil leachate BDOC

Two components explained 77% of the variance in environmental parameters across soil leachate incubations (PC1 = 55%, PC2 = 22%; Table 3). BDOC was most closely correlated to component 1 ($r = 0.81$), which was associated with latitude ($r = 0.97$) and dominant permafrost type ($r = 0.96$; greater BDOC in continuous permafrost regions; see also Fig. 3b), and initial DOC ($r = -0.83$). The second component did not correlate with BDOC but was positively correlated to longitude ($r = 0.79$) and sampling period (Julian day; $r = 0.78$).

4 Discussion

4.1 Methodological factors influencing BDOC

Aquatic BDOC losses were most strongly influenced by incubation time, with higher total BDOC observed in longer experiments. Despite total DOC loss increasing with longer incubation time, the fraction of BDOC removed over time likely decreases. These are two perspectives to look at the same process, but we want to briefly re-stress our usage of the term BDOC as a proxy for the potential of DOC to degrade in a specific environment.

Soil leachate BDOC was not clearly affected by incubation time across experiments. We suggest that the effects of incubation time may have been masked by multiple additional methodological factors significantly influencing particularly soil BDOC experiments. For example, the presence of O_2 within incubations or regular bottle shaking appeared to play a crucial role in soil BDOC losses. As soil extractions typically have higher initial DOC concentrations (despite some degree of dilution applied in the experiment), they may be more susceptible to oxygen drawdown, increasing the importance of regular bottle shaking. Also, the method of assessing carbon loss appeared to play a critical role in the amount of BDOC measured during soil incubations, but not so

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and Canada was on average higher than in Eastern Siberia. This could be related to a combination of the spatial spread in our dataset with the distribution of yedoma. Yedoma is Pleistocene-aged permafrost (Zimov et al., 2006) predominantly present in northeast Siberia that releases extremely biolabile DOC upon thaw (BDOC between 40–65 % after 30–40 days of incubation, Vonk et al., 2013b; Abbott et al., 2014). In our meta-analysis, most of the aquatic BDOC incubations with yedoma-derived DOC are located in Alaska, which could explain the longitudinal pattern.

4.2.2 Patterns within the fluvial network

In continuous permafrost regions, aquatic BDOC decreases within the fluvial network (Fig. 4). Here, large rivers (defined as watersheds larger than 500 000 km²) showed significantly lower BDOC than streams, large streams, rivers and large rivers. We should note here that streams (< 250 km², *n* = 149) and large rivers (> 500 000 km², *n* = 60) are overrepresented in the continuous permafrost dataset, when compared to large streams (250–25 000 km², *n* = 46) and rivers (25 000–500 000 km², *n* = 18). Nevertheless, this suggests that continuous permafrost regions release DOC that degrades more rapidly in the fluvial network and that these sources may be absent in regions with discontinuous or no permafrost. Pleistocene yedoma could be such a source, as its strong degradation potential (Vonk et al., 2013a, b; Abbott et al., 2014) leads to preferential utilization in headwater streams (Mann et al., 2015; Spencer et al., 2015).

4.2.3 Seasonality

BDOC decreased with Julian day for rivers and large streams in both continuous and discontinuous permafrost regions, whereas streams (Fig. 5b) and soil leachates (Fig. 5c) showed no seasonal pattern. This pattern may be associated to shifts in carbon source (winter and spring DOC in large Arctic rivers is more biolabile than summer DOC; Wickland et al., 2012; Mann et al., 2012; Holmes et al., 2008) but it is likely more related to a changing hydrologic residence time. In boreal and Arctic systems

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soil thaw-depth increases throughout the summer, resulting in longer water residence times in soils and headwater streams (Harms and Jones, 2012; Jones and Rinehart, 2010; Koch et al., 2013). This allows more time for biodegradable carbon compounds to be mineralized before reaching the river late in the season, effectively reducing measured BDOC in higher-order streams and rivers later in the season. Increasing water temperature through the season could magnify this effect with little mineralization early in the year when soils and streams are cold but accelerating biolabile carbon removal in summer. Hydrologic connectivity between soils and surface waters is generally weaker later in summer (Striegl et al., 2005; Spencer et al., 2008; Koch et al., 2013), which could explain the decoupling in seasonal trends. Furthermore, soil core leachates from a near-surface core that developed fresh plant growth during the growing season showed higher BDOC than cores without fresh plant growth (Fig. 6). These local plant growth-induced spikes in BDOC, likely induced by root exudates (Marscher and Kalbitz, 2003) could also mask seasonal trends in soil leachate BDOC and instead highlight spatial variability.

4.2.4 Other factors affecting BDOC

There are multiple factors that affect BDOC that neither we nor the investigated literature studies have considered. One of these factors is the effect of light. Photochemical processes can lead to rapid DOC losses (up to 30% in 14 days; Mann et al., 2012) and may alter the DOC composition so that it is more susceptible to microbial degradation (Cory et al., 2013). Furthermore, the presence of POC also serves as an important catalyst in DOC biolability (Battin et al., 2008). In this study we do not investigate any potential co-metabolizing effects of POC degradation, or for the biodegradability of POC itself, which could be substantial (Sánchez-García et al., 2011; Richardson et al., 2013).

Something we could not directly address in our synthesis was the effect of DOM composition which can be related to the depth of the active layer and the associated retention of (certain fractions of) the DOC pool. For example, sugars and microbially-

derived organic matter appear more biolabile than plant-derived organic matter (Balcarczyk et al., 2009; Mann et al., 2012). Also, permafrost DOM appears to be enriched in hydrogen-rich, aliphatic compounds that are preferentially degraded in incubation experiments (Spencer et al., 2015). The preferential degradation of biolabile components of the bulk DOC results in an enrichment of more recalcitrant components in soil pore waters (Wickland et al., 2007) and in larger rivers downstream (Spencer et al., 2015).

Another factor that could affect BDOC is leaching of nitrogen stocks in permafrost (Harden et al., 2012) with increased thaw depth (Keuper et al., 2012). Higher concentrations of inorganic nitrogen have been shown in some studies to increase BDOC in the receiving ecosystems (Holmes et al., 2008; Wickland et al., 2012), even though we do not find a strong correlation in our meta-analysis and other studies show little response of BDOC to inorganic nutrient additions (Mann et al., 2015).

4.3 Circumarctic patterns in BDOC

4.3.1 Geographical and seasonal patterns in BDOC

We identified distinct large-scale patterns in the biodegradability of DOC, which we illustrate in a conceptual diagram (Fig. 7). The percentage BDOC in both soil and aquatic systems increased from regions without permafrost to regions with continuous permafrost. We attribute this increase to better preservation of DOC in permafrost regions where frozen storage has limited processing of the soil organic matter. Furthermore, within aquatic networks, BDOC was lower in large river systems compared with small streams, and this pattern was most obvious in continuous permafrost regions. This suggests that continuous permafrost regions release DOC sources that degrade rapidly in the fluvial network such as Pleistocene yedoma (Vonk et al., 2013b; Abbott et al., 2014; Mann et al., 2015; Spencer et al., 2015).

Aquatic BDOC in large streams and rivers decreased as the Arctic summer progressed. This pattern was absent for soils and small streams. This could be related

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values for each permafrost zone (20, 15 and 8 % BDOC for continuous, discontinuous and no permafrost regions, respectively; mean values from Fig. 3b) we can calculate the permafrost-normalized average soil BDOC, to be 16 %. Inclusion of DOC processing within soils is likely to significantly raise the 2.3 Tg C yr⁻¹ estimate for aquatic networks alone (Wickland et al., 2012). However, questions about the linkages between soil and stream BDOC with deepening active layer depths remain. Changes in hydrological flow paths associated with deepening active layers could reduce the inputs of DOC due to mineral sorption and additional processing during transport (MacLean et al., 1999; Striegl et al., 2005; O'Donnell et al., 2010) but the net effects of permafrost thaw on BDOC inputs to streams are not yet well characterized.

4.4 Method considerations and recommendations

In order to compare BDOC losses across Arctic, and alternate systems, it is crucial to standardize the methods with which biodegradability is assessed. Our meta-analysis highlighted the significant variability in incubation design across the currently available literature making robust comparisons of BDOC across studies challenging. We suggest the following DOC incubation method, which is intentionally kept simple to be feasible at more remote field sites (a more detailed protocol is available in the Supplement). Additionally, we suggest a few optional protocol steps that could be used to assess further environmental controls on BDOC.

Standardized incubation protocol

- As soon as possible after collection, filter water samples through pre-combusted (450 °C > 4 h) 0.7 µm glass fiber filters and chill (ca. 4 °C) until ready to incubate.
 - Rapid incubation setup is strongly recommended since many biolabile DOC compounds have turnover times of hours. We advocate against freezing samples due to DOC flocculation, compositional and structural changes in the DOC, and bacterial viability (Fellman et al., 2008).

- Decant filtrate into triplicate sets of 40 mL pre-combusted (550 °C > 4 h) glass vials, and fill each vial with 30 mL filtrate. Use a triplicate glass vial set for each time point in your incubation. We recommend five time points at which one triplicate set will be consecutively removed from incubation: $T = 0$, $T = 2$, $T = 7$, $T = 14$ and $T = 28$ days. Use caps with silicone or teflon septa (avoid rubber which can leach DOC).
- Our reason for recommending 40 mL glass vials are multiple; they are commonly available, can be cleaned through pre-ashing, the required total volume per incubation is relatively small but sufficient for analysis, and our analyses suggest that variation in bottle size may affect BDOC results.
- Inoculation of samples is not needed as filtration through 0.7 μm allows for a sufficient amount of bacteria to pass the filter.
- Incubate the vials in the dark (to avoid autotrophic respiration and photodegradation), with loose caps and shake regularly to avoid oxygen-depletion.
- We recommend performing sample incubation at room temperature (20 °C), as this is most common and relatively easy to maintain. Document the temperature throughout the experiment precisely.
- If possible, the incubations should be carried out at a stable temperature for example by using an oven or incubator.
- Re-filter the incubated samples through pre-combusted (450 °C > 4 h) 0.7 μm filters (to avoid problems with flocculation and remove microbial biomass) for each time step. Store the filtered samples in pre-combusted (550 °C > 4 h) 40 mL glass vials, acidify to pH 2 with 30 μL concentrated HCl. Cap tightly and store dark and chilled until analysis.
- For logistical reasons, we recommend assessment of BDOC through DOC loss.
- For details regarding DOC analysis, see the Supplement.

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include optical properties (specific ultraviolet absorbance, fluorescence excitation emission matrices), and compound-specific analyses (carbohydrates, amino acids, lignin phenols, Fourier transform ion cyclotron resonance mass spectrometry, etc.).

5 Conclusions

Half of the global belowground soil OC pool is stored in circum-arctic permafrost but little is known about the processes controlling transport and degradation of DOC, the key regulator of the rate of permafrost carbon release from the Arctic watershed to the atmosphere. We synthesized results from 14 BDOC studies from the permafrost region and complemented this with novel BDOC data from across the Arctic. We observed a large variability in soil and aquatic BDOC, even under standardized conditions. Nonetheless, we found that both soil and aquatic DOC is more labile in regions with continuous permafrost compared to regions without permafrost. Within continuous permafrost regions, the degradability of DOC decreased from headwater streams to larger river systems, suggesting that permafrost DOC is preferentially utilized within the network. Furthermore, we discovered that aquatic BDOC in large streams and rivers decreased as the Arctic summer progressed, whereas this pattern was absent for soils and small streams.

Based on the findings of our synthesis of BDOC studies and additional measurements, we predict that slow future transformation of continuous permafrost into discontinuous permafrost regions could release a first, relatively short-term, pulse of biodegradable DOC but would on longer timescales possibly lead to the release of DOC that is more recalcitrant. The total gaseous watershed C flux could however increase as more DOC could be processed within soils prior to release into aquatic networks, due to deeper thaw depths and increasing residence time (Striegl et al., 2005).

The Arctic is changing, and so is the coupling between its carbon and hydrologic cycles. There still are large uncertainties related to processing and transport of DOC,

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and little data are available from northern Canada and Russia, from discontinuous permafrost regions, and across all seasons. We strongly recommend that future studies of DOC degradability assess BDOC by means of our standardized BDOC protocol, to facilitate optimal use and integration of future datasets with existing knowledge.

5 **The Supplement related to this article is available online at
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Table 1. List of methodological and environmental parameters we included in our meta-analysis. Variables are classified as scalar (no symbol), nominal (^a) and ordinal (^b). For scalar parameters we have listed the data range, for categorical (nominal and ordinal) data we have listed the number of categories along with their definition. Note that for nominal data (e.g. for location in aquatic network) the parameters lose the directionality of their numeric value.

| Parameter | Unit | Type of data and range or categories | Definition of categories (PCA value assigned) | Comments | |
|--|-------------------|--------------------------------------|---|--|--|
| | | Scalar Data range | Categorical Number of categories | | |
| BDOC | % | 0–67 | | | |
| Methodological | | | | | |
| Nutrients ^a | – | | 2 | No nutrients (1) – nutrients added (2) | |
| Filter pore size ^b | µm | | 3 | 0.7 (1)–0.45 (2)–0.2 (3) | |
| Inoculation ^a | – | | 2 | Not inoculated (1) – inoculated (2) | For experimental data, we identified not inoculated –1% inoculated –10% inoculated |
| Shaking ^a | – | | 2 | No shaking (1) – shaking (2) | |
| Oxygen ^a | – | | 2 | Anoxic (1) – oxic (2) | All aquatic incubations were assumed to be performed under oxic conditions |
| Bottle size | mL | 40–3000 | | | |
| Method of analysis ^a | – | | 2 | DIC production (1) – DOC loss (2) | |
| Incubation temperature | °C | 3.5–25 | | | In the literature synthesis, we assumed "room temperature" was 20 °C. |
| Incubation time | days | 1–97 | | | |
| Environmental | | | | | |
| Permafrost ^b | – | | 3 | No permafrost (1) discontinuous (2) – continuous (3) | Dominant permafrost type in each catchment was used. |
| Location in aquatic network ^a | – | | 6 | Soil leachate (1) – lake (2) – stream (3) – large stream (4) – river (5) – large river (6) | Based on watershed size: streams < 250 km ² ; large streams 250–25 000 km ² ; rivers 25 000–500 000 km ² ; large rivers > 500 000 km ² |
| Soil or aquatic ^a | – | | 2 | Aquatic (1) – soil (2) | |
| Latitude | °N | 55.82–70.33 | | | |
| Longitude | °E | –162.88–161.45 | | | *W is given as negative °E degrees |
| Julian day | – | 12–288 | | | |
| Initial DOC | mgL ⁻¹ | 1.9–155 | | | |

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Table 2. Correlations between methodological variables and BDOC for each principle component axis (1, 2, 3) in a structure matrix for aquatic incubations (530 data points) and soil incubations (202 data points). Correlations above 0.7 (in bold) are considered strong, and correlations above 0.5 (italic) as moderate. All aquatic samples were incubated under oxic conditions and so this was excluded from the PCA. Similarly, none of the soil incubations were nutrient-amended so this was excluded from PCA. The parameters are ordered based upon their importance to explaining axis 1. Variables are classified as scalar (no symbol), nominal (^a) and ordinal (^b).

| | Aquatic | | |
|--------------------------------|--------------|-------------|--------------|
| | 1 | 2 | 3 |
| Shaking ^a | 0.97 | 0.07 | −0.46 |
| Method C loss ^a | 0.91 | 0.09 | −0.30 |
| Temperature | 0.84 | 0.11 | −0.18 |
| Bottle size | −0.77 | 0.08 | <i>0.54</i> |
| Filter pore size ^b | 0.34 | 0.90 | −0.44 |
| Nutrient addition ^a | 0.37 | 0.90 | −0.45 |
| Inoculum ^a | <i>−0.51</i> | <i>0.64</i> | 0.32 |
| Incubation time | 0.34 | 0.12 | −0.85 |
| BDOC | 0.23 | 0.26 | −0.83 |
| % variance explained | 46 | 23 | 12 |

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Table 2. Continued.

| | Soil | | |
|--|-------------|-------------|--------------|
| | 1 | 2 | 3 |
| O ₂ availability ^a | 0.94 | −0.16 | −0.06 |
| Method C loss ^a | 0.87 | −0.30 | 0.02 |
| BDOC | 0.75 | 0.37 | −0.02 |
| Shaking ^a | 0.73 | −0.05 | −0.57 |
| Incubation time | 0.06 | 0.88 | −0.13 |
| Filter pore size ^b | −0.25 | 0.74 | 0.25 |
| Bottle size | 0.06 | 0.10 | 0.74 |
| Temperature | −0.05 | 0.54 | −0.66 |
| Inoculum ^a | −0.44 | 0.08 | 0.57 |
| % variance explained | 34 | 21 | 16 |

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Table 3. Correlations between environmental variables and BDOC for each principle component axis in a structural matrix for aquatic incubations (505 data points) and soil incubations (165 data points). Correlations above 0.7 (in bold) are considered strong, and correlations above 0.5 (italic) as moderate. The parameters are ordered based upon their importance to explaining factor 1. Variables are classified as scalar (no symbol), nominal (^a) and ordinal (^b). Location in stream network, i.e. streams, large streams, rivers and large rivers, is indicated as “network”.

| | Aquatic | | |
|-------------------------|--------------|--------------|-------------|
| | 1 | 2 | 3 |
| Network ^a | 0.95 | −0.05 | −0.21 |
| Permafrost ^b | 0.94 | 0.05 | −0.06 |
| Latitude | 0.93 | 0.06 | −0.07 |
| DOC initial | −0.70 | −0.11 | 0.47 |
| Longitude | 0.41 | 0.78 | 0.12 |
| BDOC | <i>0.51</i> | −0.71 | −0.05 |
| Julian day | −0.14 | 0.11 | 0.95 |
| % variance explained | 52 | 18 | 13 |

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Table 3. Continued.

| | Soil | |
|-------------------------|--------------|-------------|
| | 1 | 2 |
| Latitude | 0.97 | −0.08 |
| Permafrost ^b | 0.96 | −0.13 |
| DOC initial | −0.83 | 0.30 |
| BDOC | 0.81 | 0.15 |
| Longitude | −0.22 | 0.79 |
| Julian day | 0.06 | 0.78 |
| % variance explained | 55 | 22 |

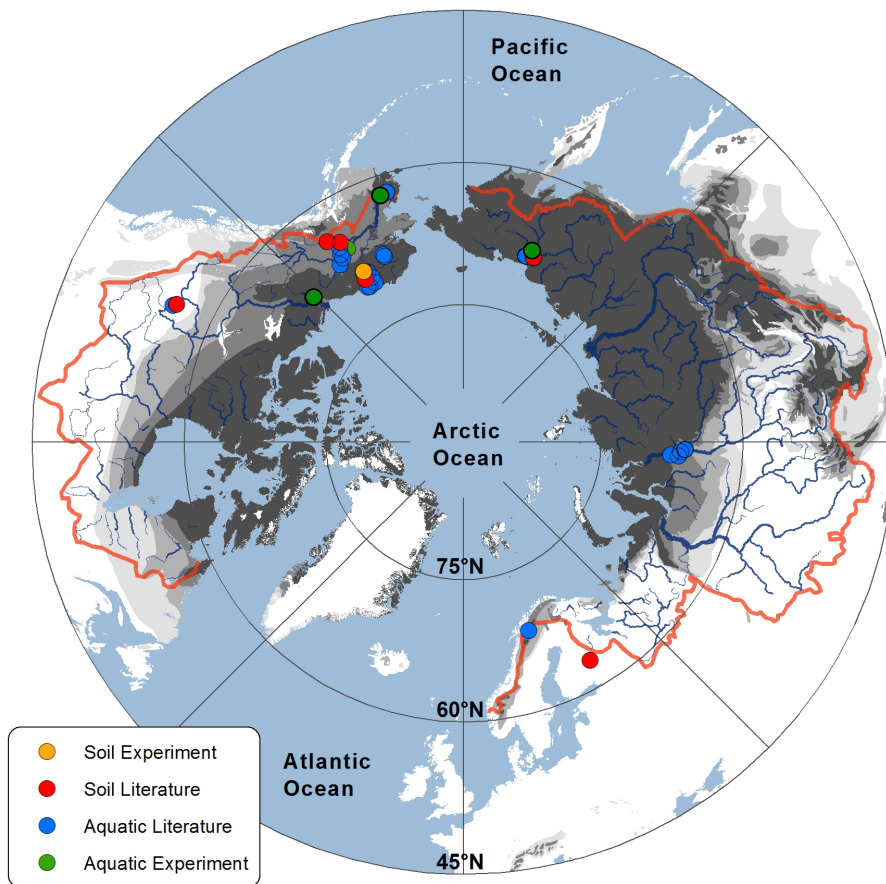


Figure 1. Map of the hydrological network (blue) in the Arctic Ocean watershed (boundary in red) with points showing literature data (blue for aquatic, red for soil) and experimental data (green for aquatic, orange for soil).

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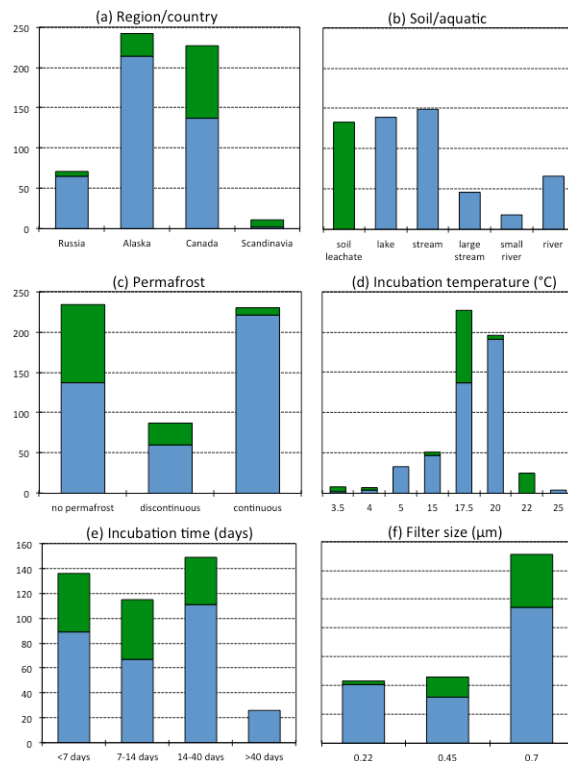


Figure 2. Histograms of environmental and methodological variety reported in the synthesized literature ($n = 426$, see Sect. 2.3), with **(a)** region/country, **(b)** soil leachate and type of aquatic study (categorized as streams ($< 250 \text{ km}^2$), large streams ($> 250 \text{ km}^2$ and $< 25\,000 \text{ km}^2$), rivers ($> 25\,000 \text{ km}^2$ and $< 500\,000 \text{ km}^2$) and large rivers ($> 500\,000 \text{ km}^2$)), **(c)** permafrost zonation, **(d)** incubation temperature in $^{\circ}\text{C}$, **(e)** incubation time (categorized in < 7 , $7\text{--}14$, $14\text{--}40$ days, and > 40 days), and **(f)** filtration pore size (μm). Green represents soil leachate data, blue represents aquatic data. The y axis shows number of data points.

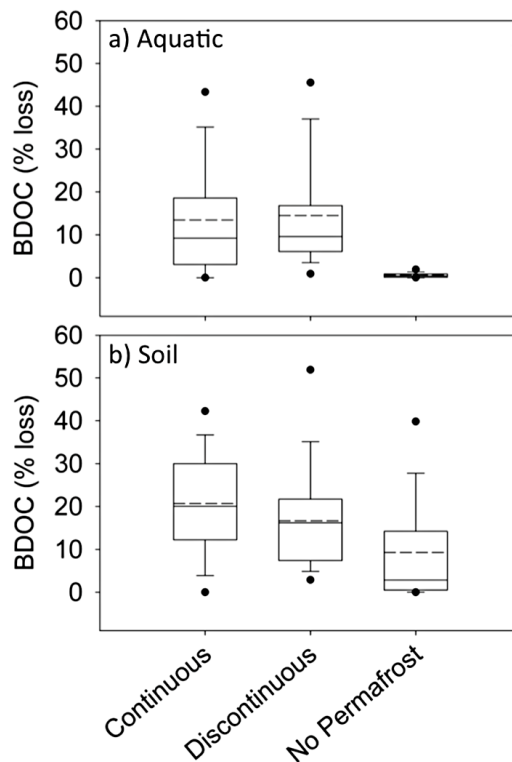


Figure 3. (a) Aquatic and (b) soil leachate BDOC data (15–25 °C, $n = 205$) after 28–34 days incubation across dominant permafrost type from literature-synthesis and our circum–arctic experiment. The data are shown as 5th to 95th percentiles (points), 25th, 50th, and 75th percentiles (lines), median value (bold line) and mean value (dashed line).

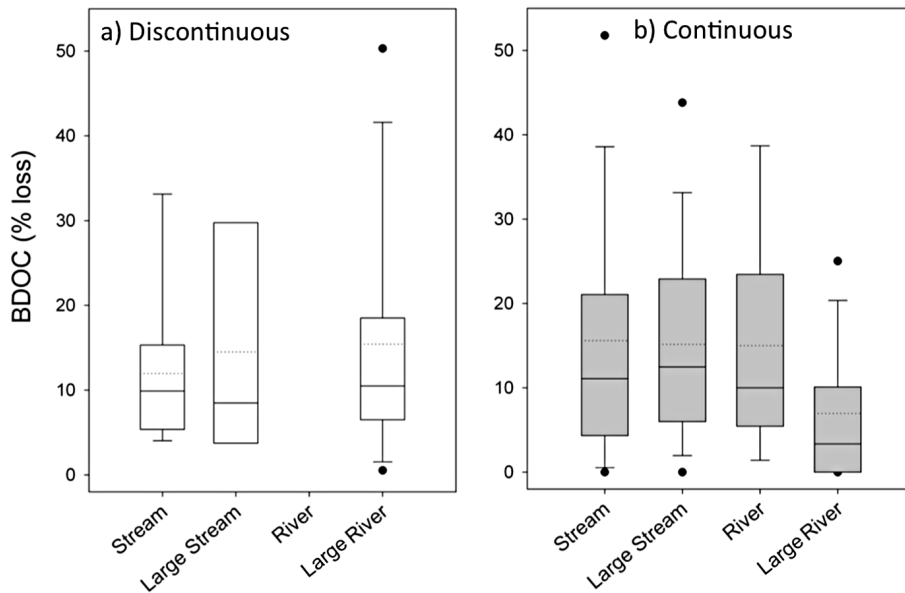


Figure 4. Aquatic BDOC data for 15–25 °C after 28–34 days incubation for streams (< 250 km²), large streams (> 250 km², < 25 000 km²), rivers (> 25 000 km², < 500 000 km²), and large rivers (> 500 000 km²) clustered for **(a)** discontinuous and **(b)** continuous permafrost zones. Symbolology as in Fig. 3. A plot for “no permafrost regions” is not shown as here only BDOC data for rivers were available (median BDOC = 0.44 %, mean BDOC = 0.69 %; *n* = 25).

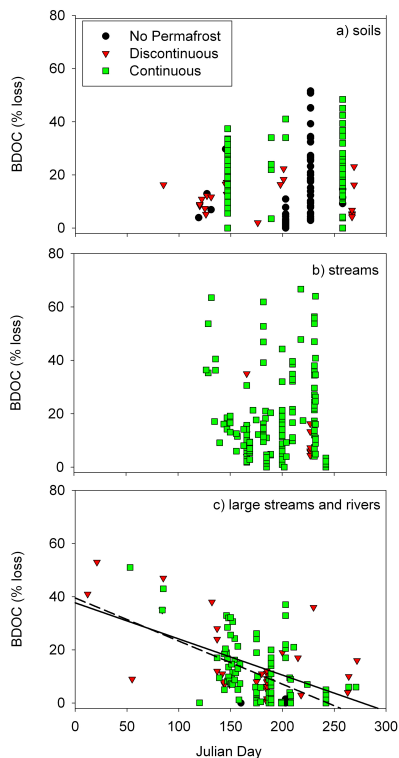


Figure 5. Seasonal BDOC losses (shown against Julian day) at 15–25 °C after 28–34 days incubation for **(a)** soil leachates, **(b)** streams and **(c)** clustered large streams, rivers and large rivers for regions without permafrost, discontinuous permafrost and continuous permafrost. Trend lines denote significant relationships where present. Solid line represents linear fit in discontinuous permafrost ($r^2 = 0.33$, $p = 0.0003$) and dashed line continuous permafrost ($r^2 = 0.29$, $p < 0.0001$).

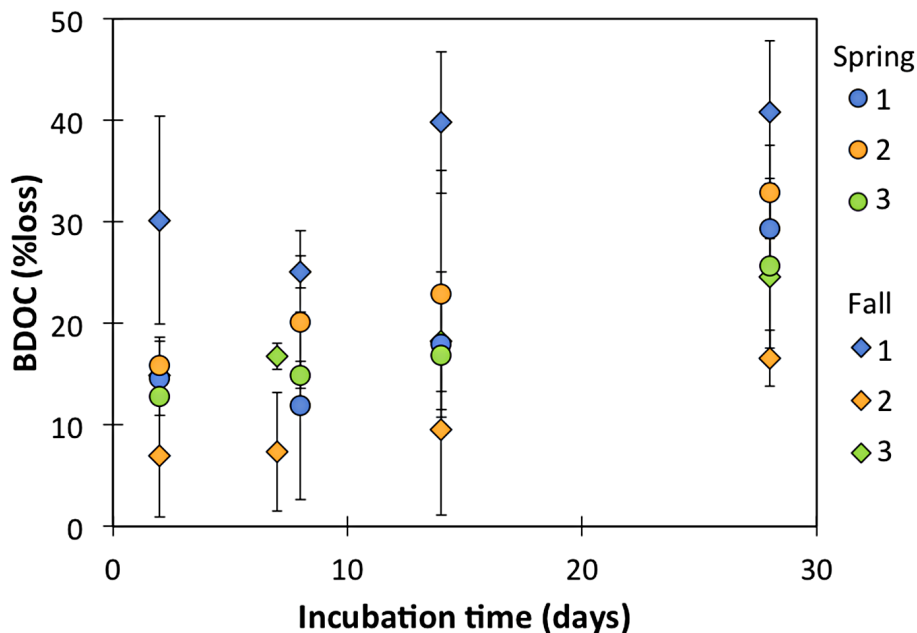
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Figure 6. BDOC losses (at 20 °C) after 28 day incubation for soil leachates from three cores collected near Toolik, Alaska, as part of our circum–arctic incubation experiment (see Sect. 2.1). Soil leachates were collected and incubated both in spring (circles) and fall (diamonds). In core 1 we observed active plant growth during the spring and fall incubations.

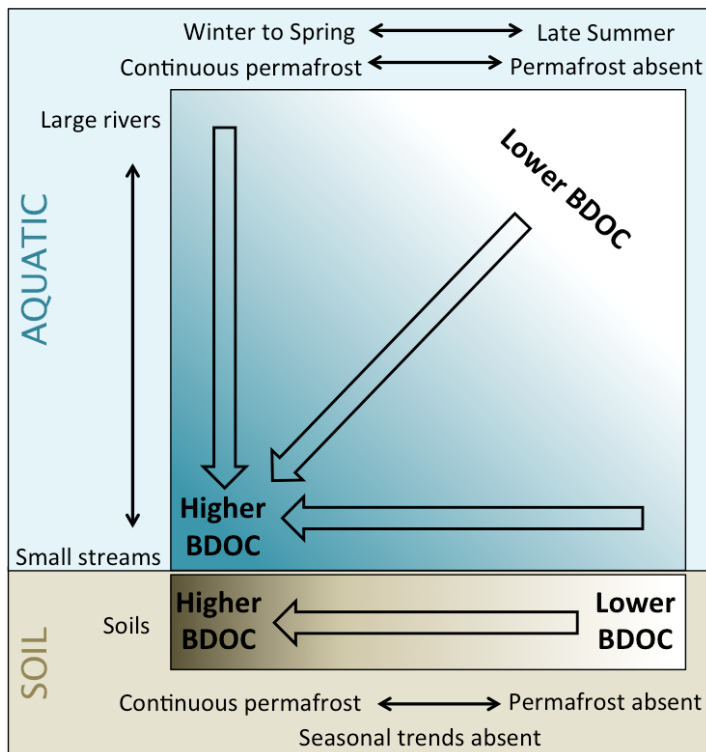


Figure 7. Conceptual graph of landscape-scale and seasonal trends in %BDOC where the upper blue box represents aquatic systems, and the lower brown box represents soils. Aquatic BDOC increases with decreasing catchment area, and aquatic and soil BDOC increase with increasing permafrost extent in the landscape. Aquatic BDOC in watersheds varies temporally, with more BDOC found in winter and spring than late summer.