Ecosystems (2023) 26: 55–71
https://doi.org/10.1007/s10021-022-00741-0
ECOSYSTEMS

Dissolved Organic Carbon Mobilization Across a Climate Transect of Mesic Boreal Forests Is Explained by Air Temperature and Snowpack Duration

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Abstract

The mobilization of soil dissolved organic carbon (DOC) is driven by biogeochemical and hydrological processes operating at different temporal and spatial scales. In seasonally snow-covered ecosystems, the snowpack holds both biogeochemical and hydrological significance as insulator of the soil during winter and reservoir of a large proportion of the annual precipitation that is released during spring melt. This four-year study was conducted within three maritime balsam fir forests spanning 47°N to 53°N where mean annual precipitation (1074 mm to 1340 mm) and mean annual temperature (0 °C to 5 °C) increase with decreasing latitude. All forests are consistently snow-covered throughout winter with snowpack depths sufficient to protect soils from extreme freezing. However, there is a decrease in the amount of snowfall (462 to 393 cm), and a decrease in the length of the snowpack season (160 to 109 days) with decreasing latitude, analogous to the changing winter conditions. Mean annual DOC fluxes decreased with latitude and exhibited no relationship with interannual precipitation, but a positive relationship with interannual air temperature. To interpret this result, a series of additional hydrometeorological indices were ranked. Of these, air temperature and snowpack duration best described interannual variability in DOC flux and were highly correlated. Therefore, air temperature may indirectly affect DOC mobilization through a direct control on snowpack season length. Both warmer years and warmer sites have shorter snowpack seasons and mobilize more soil DOC, suggesting that boreal forest soils are larger sources of DOC to mineral soil and/or aquatic ecosystems under warmer winter temperatures via changes to snowpack dynamics.

Received 24 May 2021; accepted 8 January 2022;
published online 19 February 2022

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-022-00741-0.
Author Contributions: KAE, SAB, and SEZ designed the study with instrumentation input from JW and AS. AS and KAE collected designed and maintained the sampling regime. JW performed laboratory analyses. KLB and KAE analyzed the data, with input from SEZ. YW provided pertinent statistical advice. KLB prepared the manuscript with editing by KAE, SEZ, SAB, and YW.
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Key words: Dissolved organic carbon; Boreal forests; Soil carbon; Snowpack; Climate change; Podzols; Temperature; Precipitation; Organic horizon; Climate transect.

Highlights

- Mean annual soil dissolved organic carbon (DOC) fluxes increased from north to south along a climate transect of wet boreal forests.
- While there was no relationship between annual DOC fluxes and annual precipitation, there was a positive relationship with temperature.
- Air temperature and snowpack duration best described interannual DOC variability, suggesting greater mobilization of soil DOC under warmer winter temperatures

Introduction

The mobilization of soil dissolved organic carbon (DOC) is an important component of the terrestrial to aquatic (T-A) flux of the global carbon (C) cycle. Estimates of the global T-A flux have increased in magnitude through the last two editions of the International Panel on Climate Change (IPCC) report (Ciais and others 2013; Denman and others 2007) and, whereas small in comparison to global gross photosynthesis and respiration rates, the global T-A flux offsets the global net land C sink (Webb and others 2019). A greater mechanistic understanding of this flux is needed to refine calculations both globally and regionally in effort to enable accurate projections of T-A fluxes under future climate conditions. These projections are especially needed in high-latitude ecosystems which are warming faster than the global average (Hoegh-Guldberg and others 2018), and contain approximately half of the global soil organic C pool (Hobbie and others 2000; Tarnocai and others 2009). The mobilization of soil DOC is driven by biogeochemical and hydrological mechanisms but the relative dominance of these mechanisms and their interaction at different temporal and spatial scales is not clear (Jansen and others 2014). A positive relationship between long-term precipitation (that is, 30-year mean annual precipitation; MAP) and DOC fluxes at the continental scale (Michalzik and others 2001) was confirmed at smaller spatial scales by some studies (Schmidt and others 2010), but not by others (Fröberg and others 2006; Lindroos and others 2008; Borken and others 2011). This suggests that a direct control of DOC fluxes by bulk precipitation is not ubiquitous. Many studies agree that soil water fluxes directly control DOC mobilization from O horizons (Tipping and others 1999; Buckingham and others 2008; Wu and others 2014; Bowering and others 2020), however, soil water fluxes can be decoupled from bulk precipitation inputs through canopy and forest floor interception, which is additionally affected by precipitation dynamics, such as event intensity and precipitation type (Van Stan and others 2020). Additionally, long-term precipitation (that is, MAP) is both a representation of the annual water input and a site condition that drives the development of other factors such as vegetation type, and therefore encapsulates congruently operating direct and indirect controls on DOC mobilization that are not well understood.

The hydrology and C balance of boreal forests is strongly dependent on the structure and composition of the forest floor. Boreal forest transect studies in Alaska show that organic horizon depths increase from warmer sites to cooler sites, with effects on soil water storage (Kane and Vogel 2009). Moss interception can be 23% of canopy interception (Price and others 1997), and the latitudinal distribution of moss suggests that moss abundance is determined by temperature at large spatial scales (Berdugo and others 2018). Therefore, the effect of increasing precipitation on DOC mobilization across boreal forest sites can be modulated by the proportion of precipitation that is intercepted by the forest floor; a factor dependent on the temperature sensitive thickness of the organic horizon and the abundance of moss cover.

Critically, a significant proportion of annual precipitation is received as snow in the boreal ecozone. In forests, the tree canopy intercepts more precipitation falling as snow than as rain (Starr and Ukonmaanaho 2003). The amount of water that reaches the forest floor is therefore influenced by the interaction between stand density and precipitation type. Furthermore, significant processing of soil organic matter occurs underneath the snowpack of seasonally snow-covered environments (Brooks and others 2011), which can affect the chemical character of DOC mobilized during snowmelt (Bowering and others *unpublished manuscript*). Increased soil freezing is expected in some snow-covered systems as warmer winter air temperatures alter the amount and timing of snow accumulation, resulting in decreasing soil temperature (Groffman and others 2001). Under extreme freezing conditions, (that is, < -5 °C) this can increase DOC production in soils and consequently, DOC concentrations in streams (Haei and others 2010). Both laboratory and field studies, however, suggest that milder soil freezing (0 – 5 °C) does not affect soil DOC concentrations (Bombonato and Gerdol 2011; Campbell and others 2014). Therefore, in forest systems where the changing snowpack may continue to sufficiently insulate the soil, or result in only mild freezing, increased variation in snowfall amount, timing of snowpack formation, snowpack depth, and increased frequency of midwinter melting may result in more meaningful consequences on soil hydrology and DOC mobilization. At the watershed scale, spring snowmelt is usually the dominant hydrological event in seasonally snow-covered environments (Schelker and others 2013) that has also been shown to be a *hot moment* (Berhardt and others 2017) of soil DOC export to streams (Finlay and others 2006). Reductions in the magnitude of spring snowmelt is reducing the magnitude of spring export of soil DOC to aquatic systems, with midwinter snowmelt and DOC export events becoming more frequent (Laudon and others 2013). The effect of changing soil temperatures, hydrology, snow cover, and their combined influence is an important knowledge gap preventing our ability to predict DOC export to streams in a changing climate (Campbell and Laudon 2019).

To better understand the effects of temperature, precipitation, and the interaction between the two factors on soil DOC mobilization in boreal forests at both annual and climatic scales, we conducted a study across forest sites experiencing different historical climates and collected data interannually for four years. Our objectives were to (1) evaluate the relationship between DOC mobilization and temporal and spatial variations in precipitation and temperature; and (2) evaluate the relative influences of interannual temperature, precipitation and hydrometerological indices on temporal variations in DOC mobilization relative to spatial variations. The hydrometeorological indices included here capture variations in specific attributes of temperature, such as growing degree days, and specific attributes of precipitation, such as event size. Some indices capture interactions between temperature and precipitation, such as precipitation type and snowpack duration (Figure 1). In doing so, this study provides insights into the mechanistic role of temperature and precipitation on DOC mobilization in maritime boreal forests, the response of soil DOC mobilization to future increases in temperature and precipitation, and the powerful influence of winter conditions on soil C transformations and losses.

Materials and Methods

Site Description

The study was conducted as part of the greater Newfoundland and Labrador Boreal Ecosystem Latitudinal Transect (NLBELT) project taking place within forested regions spanning 47°N to 53°N: south (Grand Codroy: GC), intermediate (Salmon River: SR) and north (Eagle River: ER). The southern and intermediate regions are located on the western portion of the island of Newfoundland, and the northern region is located in southeastern Labrador, Canada. Although three forest sites per region exist across NLBELT, only one forest site per region was selected for this study (ER- Muddy Pond, SR-Hare Bay, GC-O'Regans; Figure 2) due to the destructive nature and labor involved in installing and sampling the pan lysimeters. Previous studies demonstrate regional differences, but similarities in relevant soil and other ecosystem properties among the three forest sites of each region (Laganiere and others 2015; Philben and others 2016; Ziegler and others 2017). This helps support the use of one of three forest sites per region for this lysimeter study, however, we acknowledge the limitation this imposes (see statistical approach below).

Climate indices were derived from weather stations representative of each region (Environment and Climate Change Canada 30-year means, 1980–2010). Where there were multiple stations per region, the representative climate station was chosen based on the availability of precipitation data measured as both snowfall and rainfall. As a result, climate stations employed during this study differ from prior NLBELT studies (for example, Ziegler and others 2017). Station information and climate data can be found in Table 1A.

Mean annual temperature (MAT) and mean annual precipitation (MAP) refer to the 30-year means of annual temperature and precipitation. There is an increase in MAP (1074 mm to 1340 mm) and an increase in MAT (0 °C to 5 °C) with decreasing latitude (Table 1A), analogous to predicted climate change by the end of the century in Newfoundland and Labrador (Finnis and Daraio 2018). All three regions are consistently snow-covered throughout winter. However, there is an increase in the amount of snowfall (393 to 462 cm), and an increase in the proportion of precipitation received as snowfall from south to

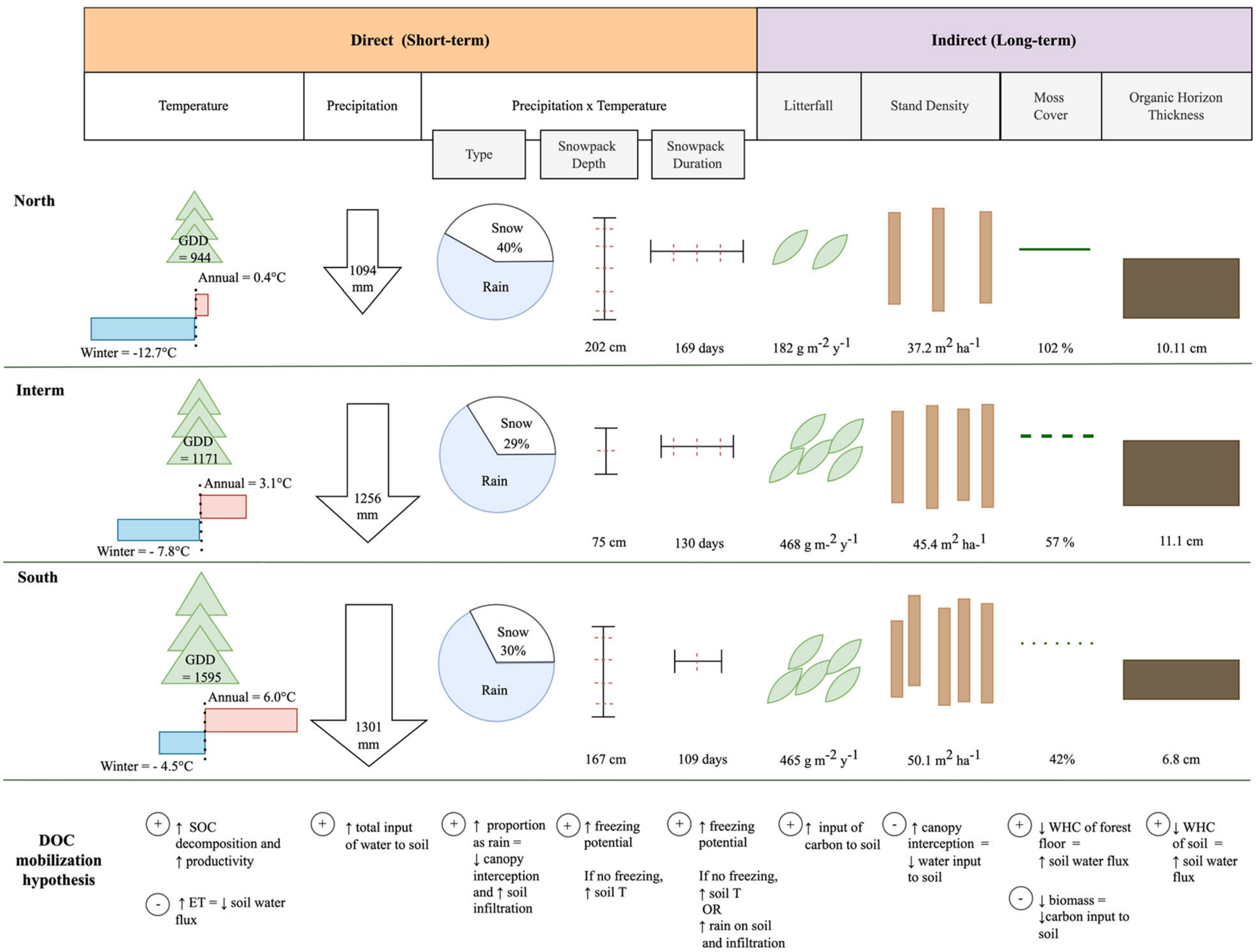

Figure 1. Observed climate trends across NLBELT and hypothesized effect on dissolved organic carbon mobilization. Climate parameters were measured at each site and organized into direct or indirect effects on dissolved organic carbon (DOC) mobilization. Within each parameter, the size, length, or quantity of symbols indicates the relative quantity of that parameter across the three sites: north, intermediate (intermed), and south. Below, the hypothesized positive (+) or negative (−) effect of each climate trend (from north to south) on DOC mobilization is shown and explained by mechanisms that increase (↑) or decrease (↓) hydrologic flow or DOC production (see Table 2 for more details). GDD = cumulative growing degree days above 5 °C, T = temperature, ET = evapotranspiration, WHC = water holding capacity, mobilization refers to movement or transport from soil, and production refers to the creation of DOC from soil.

north (0.29 to 0.43). Air temperature is consistently colder each month from south to north (Figure 3A), and that difference is enhanced during winter months (DJF; 7.2 °C difference between northern and southern sites) compared to summer months (JJA; 3.9 °C difference). The snowpack develops earlier and melts later in the northern site and is generally deeper (maximum snow depth: 157 cm in March; Table 1A, Figure 3B). Total precipitation is evenly distributed throughout all months of the year with slightly drier conditions in all sites in March and April (for example, south site range 80–130 mm month^{-1}; Figure 3C). All forest sites are dominated by balsam fir (*Abies balsamea*) underlain by humo-ferric podzol soils. The southern and intermediate sites receive 60% more tree litterfall than the northern site, and have O horizons with a greater C stock, and less moss coverage. The northern and intermediate sites have thicker O horizons than the southern site. Detailed forest and organic horizon characteristics of these sites are summarized in Table 1B,C. Extreme wind events at the intermediate site (data not shown) impacted litterfall during the study period.

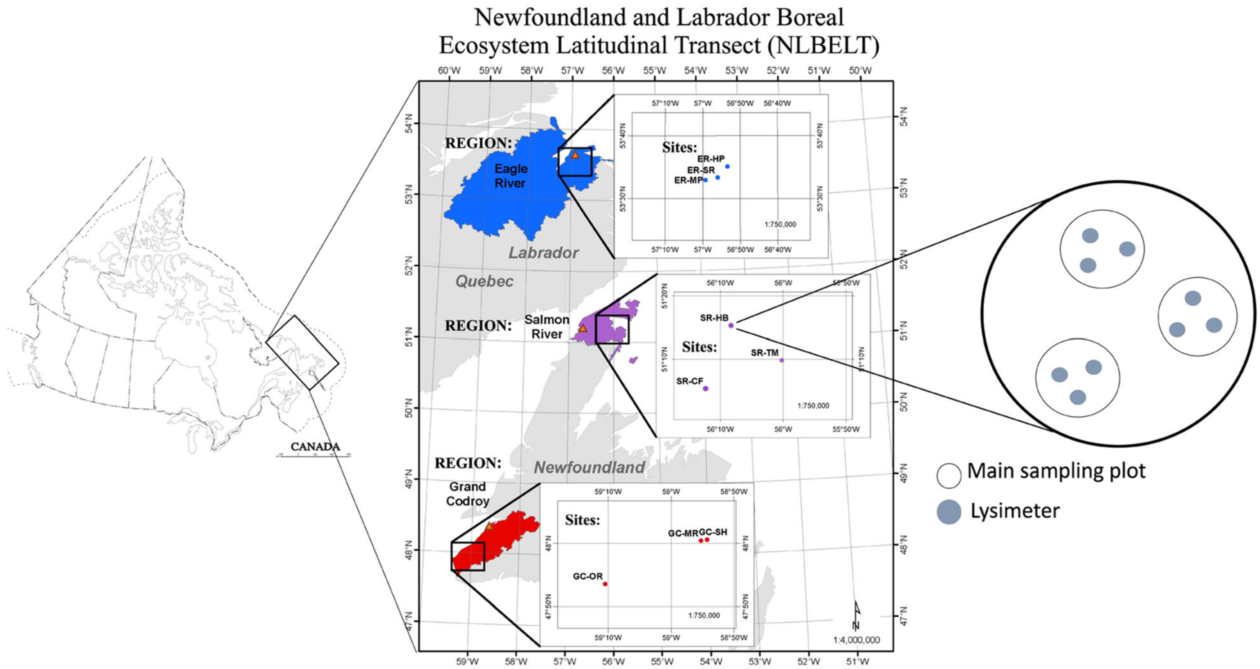

Figure 2. Map of the Newfoundland and Labrador Boreal Ecosystem Latitudinal Transect. Three forest regions that span 5 degrees latitude along the western coast of Newfoundland (Grand Codroy and Salmon River; where south and intermediate sites are located) and southeast coast of Labrador (Eagle River; where north site is located). Three balsam fir forest sites were established per region. Lysimeters were installed in one forest site per region: North (ER-MP), Intermediate (SR-HB), South (GC-OR). Three lysimeters (gray circles) were randomly distributed throughout three sampling plots per site. Climate data were retrieved from Environment and Climate Change Canada climate stations (orange triangles). Map is modified from Ziegler and others (2017).

DOC Fluxes Measured In Situ from Organic Horizons

Passive pan lysimeters were installed at the beginning of the 2011 growing season. Nine lysimeters were installed per forest site, with three distributed throughout three plots (Figure 2; ER-Muddy Pond, SR-Hare Bay, GC- O-Regan's). A 1 m^2 area was measured along the surface of the forest floor. The O horizon was cut and removed as a single, intact unit to permit installation of the lysimeters and was then returned to its original place. To determine the depth of the O horizon overlying each lysimeter, four depth measurements on each side of the removed O horizon were averaged (Table 1C). Slope (%) was determined along the length of each lysimeter (Table 1C). The passive pan lysimeters consist of a 33.5 cm × 18 cm × 15 cm (length × width × depth) high density polyethelene ''pan'', overlain with a hard plastic screen to prevent large soil particles from entering the pan. Tubing connects the pan to an ''overflow'' container (10 L capacity) buried deeper in the mineral soil downslope from the pan lysimeter. Both receptacles have vertical cross-link polyethylene (PEX) tubing from the lowest corner to approximately 30 cm above ground, from which samples were collected using a battery-operated pump. Maximum lysimeter capacity (pan plus overflow) is approximately 14 L. Actual maximum volumes ranged from 12 to 14 L due to topographic heterogeneities that affected the installation of each pan and overflow unit within the landscape.

Lysimeter samples were collected over a four-year period from June 2011–June 2015 at least three times per year to capture relevant seasonal periods of autumn (plant senescence to snowpack formation), winter/snowmelt (persistent snowpack to end of snowmelt), and summer (plant growing season). Three of the nine lysimeters from each site received mercuric chloride through direct addition to the lysimeter pan after each sampling to reduce microbial processing of DOC between sampling dates. The effects of this were tested to determine the degree of sample transformation due to the long periods (up to several months in northern site) between collections, and were found to be insignificant; this practice was therefore stopped after 2 years of collections. Additionally, some lysimeters were damaged by moose and fallen trees

Table 1. Climate, Forest, and Organic Horizon Characteristics of the Study Sites

A: Climate	Station[1]	MAT (°C)	MAP (mm)	PET (mm)	Growing Season (days)	Rainfall (mm)	Snowfall (cm)	S:TP	Peak Snow Depth (cm)
North	Cartwright	0.0	1073	432	101	617	462	0.43	156 (Mar)
Interm	Plum Point	2.4	1211	431	125	805	407	0.34	49 (Mar)
South	Stephenville	5.0	1340	508	158	995	393	0.29	64 (Feb)

B: Forest	Latitude	Longitude	Elevation (m)	Slope (%)	Aspect	Tree age[2] (years)	Basal Area[3] (m^2 ha^{-1})	Litterfall[4] (g m^{-2} y^{-1})
North	53°33′ N	56°59′ W	145	6	N	133 (33)	37.2[a]	182 (77)[a]
Interm	51°15′ N	56°08′ W	31	4	SSW	66 (22)	45.4[ab]	468 (120)[b]
South	47°53′ N	59°10′ W	100	2	S	50 (5)	50.1[b]	465 (73)[b]

C: O horizon	WHC[5] (g H_20 g^{-1} soil)	C stock[5] (kg C m^{-2})	Moss[6] (%)	Slope (%)		Thickness (cm)
				Mean	Range	
North	7.4 (1.8)[a]	2.8 (0.3)[a]	102 (9)[a]	6 (3)	0–16	10.1 (1.1)[a]
Interm	6.1 (1.0)[a]	3.5 (0.6)[b]	57 (6)[b]	9 (5)	0–17	11.1 (1.6)[a]
South	6.2 (0.7)[a]	3.3 (0.5)[b]	42 (15)[b]	3 (1)	1–5	6.8 (1.6)[b]

(A) mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration (PET), growing season length, rainfall, snowfall, proportion of precipitation received as snow (S:TP), and maximum snow depth are calculated from long-term climate normal 1981–2010 provided by Environment and Climate Change stations representative of the three forest regions: North (Eagle River), Intermediate (Salmon River), South (Grand Codroy). The month when maximum snow depth occurred is given in parentheses. (B) The location, elevation, site slope, tree age, basal area, and aboveground litterfall at the forest sites with lysimeters (see Figure 2). (C) The mean water holding capacity (WHC), carbon (C) stock, percent moss coverage, O horizon thickness and percent slope per forest site. Standard deviations of the mean are provided in parentheses. Lower case letters indicate significant site differences (alpha = 0.05). Interm = intermediate.
[1]Environment and Climate Change Canada weather stations and their respective 1981–2010 climate variable averages.
[2]Evaluated by ring count of cores collected at breast height of live trees; Ziegler and others 2017.
[3]Evaluated by measuring the diameter at breast height (dbh) of standing live trees with a diameter > 5 cm; Ziegler and others 2017.
[4]Four years of aboveground litterfall, excluding large woody debris; Ziegler and others 2017.
[5]Three 20 × 20 cm O horizons per 3 plots per site were collected, saturated and dried to determine WHC, and ground and analyzed for C content; Laganiere and others 2015.
[6]Evaluated by assignment of percent moss coverage within 15 1m² quadrats per site, 3D architecture in some sites resulted in values > 100; Kate Buckeridge, 2015, unpublished data.

during the first years of the experiment, so sampling effort was reduced to only 6 of the original 9 lysimeters per site in years three and four. Data analyses from year one and two indicate the 6 lysimeters captured the same spatial variation of soil water and DOC fluxes within each site as the original 9 lysimeter. Each lysimeter sample was filtered (Whatman GF/F) within two days of sampling and filtrate was immediately frozen. Samples were later thawed prior to analysis and DOC content was determined by high temperature combustion analysis (Schimadzu TOC-V). No effect of freeze–thaw on DOC loss via flocculation was observed in additional subsamples tested.

A DOC flux for a given collection period was the product of collected sample volume and measured DOC concentration over the catcher collection area, normalized to the number of collection days. On two occasions in summer 2012 the lysimeters in the south site were emptied and volumes measured but samples were not analyzed for DOC content due to sampling constraints. For these collections, substitute [DOC] values were used from samples of the same lysimeters that were collected during a similar time of year, length of collection period, and collection volume. Estimates of annual DOC flux were determined for each site based on collections between summer 2011 and spring 2015. The 4-year mean annual fluxes were determined by averaging the time-adjusted (365 days) sum of the DOC flux collected over approximately annual periods (range 353–393 days).

Statistical Analysis

Factors representing potential direct and indirect effects of climate on DOC mobilization are summarized in Figure 1 along with hypothesized mechanisms for how each may control soil DOC production or mobilization. All analyses were performed using RStudio Version 1.2.5019. Site differences in forest and O horizon properties were assessed using one-way ANOVAs (Table 1B,C). The relationship between DOC flux variability and four-year interannual temperature and precipitation was assessed using repeated measures: linear

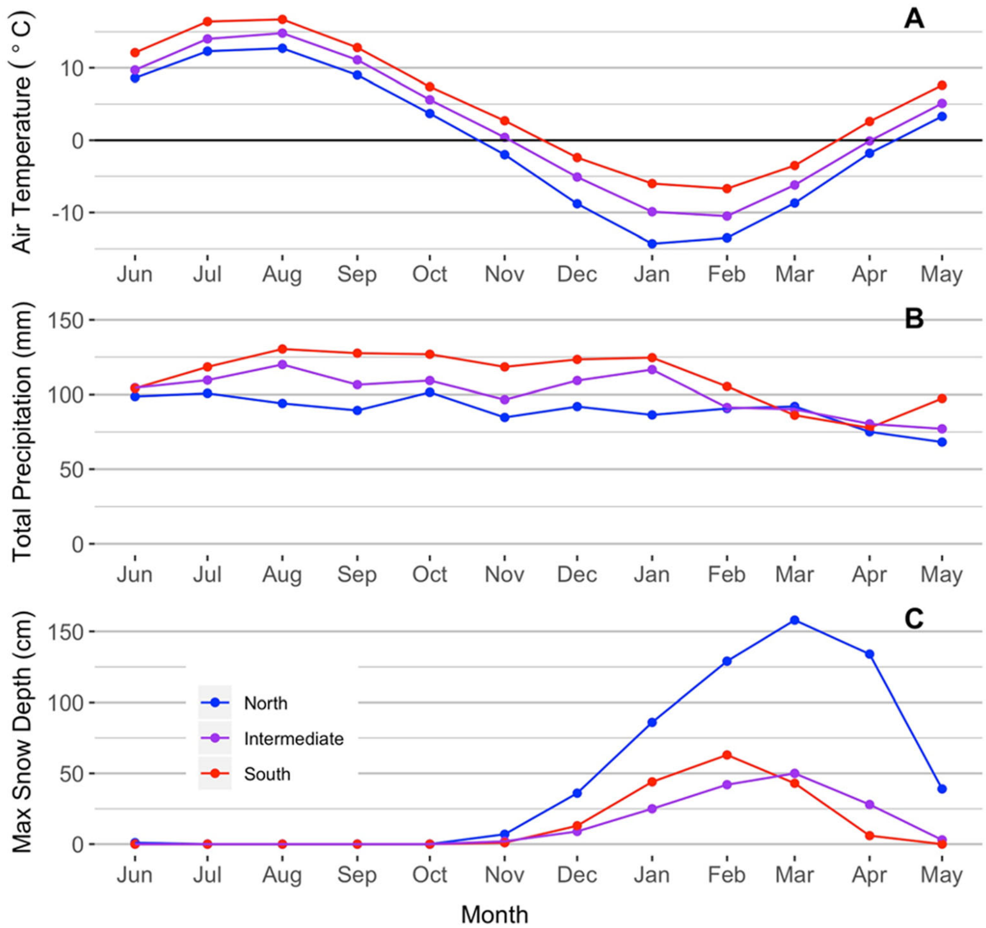

Figure 3. Regional comparison of 30-year mean monthly temperature, maximum snow depth, and total precipitation. Data are derived from 1981 to 2010 climate normals retrieved from Environment and Climate Change Canada Stations within each of the three regions: north (Eagle River), intermediate (Salmon River) and south (Grand Codroy).

mixed effects (rm-lme) models using the 'car' (Fox and others 2020) and 'nlme' (Pinheiro and others 2020) packages with forest site set as the random effect. Additional hydrometeorological indices likely to be affected by climate change were developed from the available data to reflect annual variations in precipitation form, snowpack formation and snowmelt dynamics and DOC production. The ''snowmelt days'' index was calculated as the number of days rising above 0 °C when snow was on the ground over the course of the year (total snowmelt days) and during winter (winter snowmelt days) (Figures 4, 5).

A set of rm-lme models was designed from these indices with site included as the random effect in all. We note only one fixed effect parameter per model was included because of the small sample size (n = 4 years per site) and because many of the indices were correlated (Figure 6). All models were ranked by Akaike Information Criterion corrected for small sample size (AICc) using the 'AICcmodavg' package (Mazerolle, 2019). Top ranked models were models with ΔAICc = 0, which was calculated as the difference in AICc between the model and the focal model (model with the lowest AICc). Models with ΔAICc < 2 are considered equally supported or not differentiable from the top ranked model. The null hypothesis was included as the ''site-only'' model which states that DOC flux variations are described by differences in forest site properties and that there is no effect of interannual (that is, short-term) variations in climate on DOC flux. These forest site properties developed under different historical climate conditions across the transect and are therefore, in part, a representation of the indirect, long-term effects of climate on DOC mobilization. Forest properties related to water movement and DOC production include organic horizon thickness, moss coverage, C stock, litterfall, tree density, and slope, all of which differed across

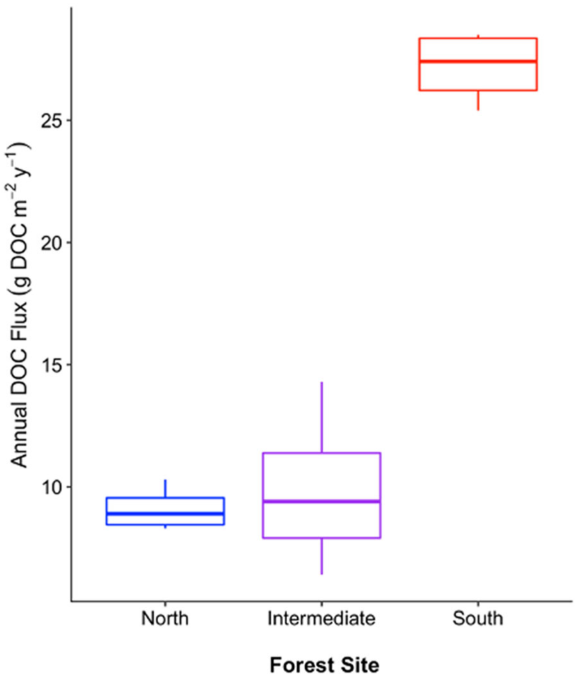

Figure 4. Mean annual dissolved organic carbon (DOC) fluxes across NLBELT. Sites are listed from North to South, increasing mean annual precipitation (MAP) and increasing mean annual temperature (MAT). Box plots showing median and confidence intervals of four years of lysimeter captured annual DOC fluxes (g C m^{-2} y^{-1}) per site.

the latitudinal transect (Table 1). The southern site is characterized by less moss coverage, gentler slopes, a thinner O horizon, and a greater O horizon C stock compared to the northernmost site. The intermediate site resembles the northern site in some respects, while resembling the southernmost site in others. For instance, moss coverage and litterfall were similar in the intermediate and southern sites, whereas organic horizon depth is similar in intermediate and northern sites (Table 2).

Results

Environmental Variability over 4-Year Study Period in Comparison to 30-Year Means

All sites exhibited above average annual temperature and received approximately average annual precipitation during the 4-year study period (Table 3), when compared to the 1981–2010 (30-year) means (Table 1A). The 4-year (short-term) latitudinal trend in mean annual precipitation and temperature was similar to the 30-year (long-term) means. There was an approximate 5.6 °C difference in annual temperature and an approximate 200 mm difference in annual precipitation between the northernmost and southernmost sites.

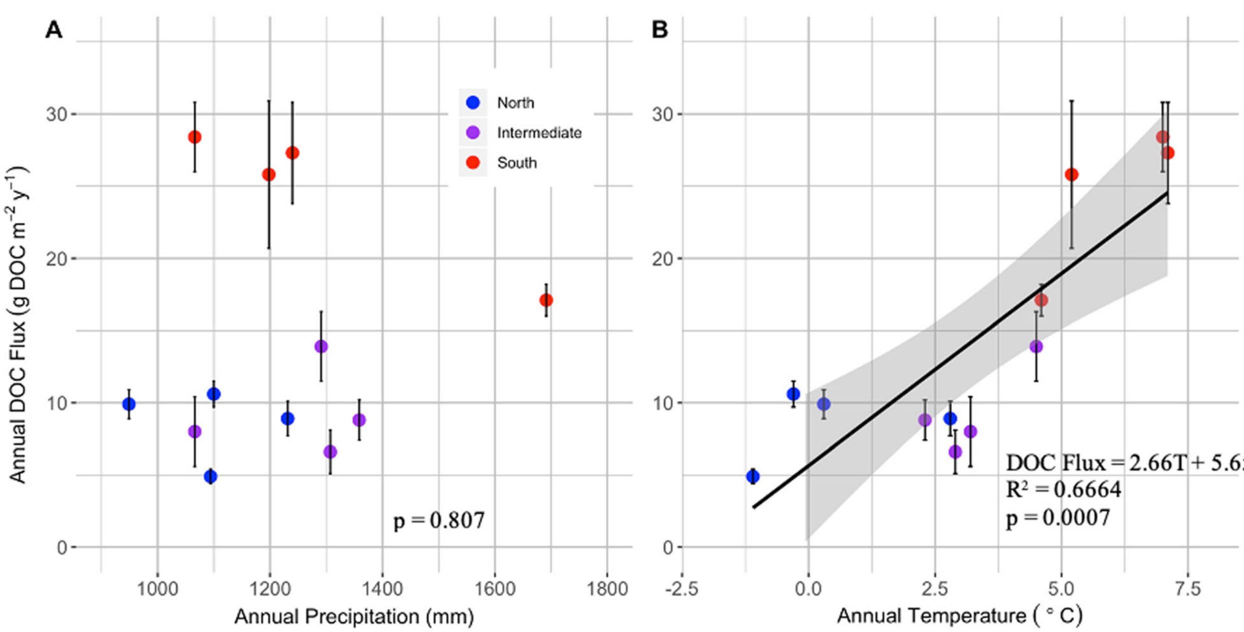

Figure 5. Relationships between DOC flux and (**A**) precipitation and (**B**) air temperature. The lysimeter captured dissolved organic carbon (DOC) fluxes measured over four years in south (Grand Codroy; red), intermediate (Salmon River; purple), and north (Eagle River; blue) forest sites. Error bars show standard deviation of the mean of all lysimeter collections per site per year. Trend line and 0.95 confidence interval (gray shading) demonstrates the significant linear relationship between DOC flux and air temperature.

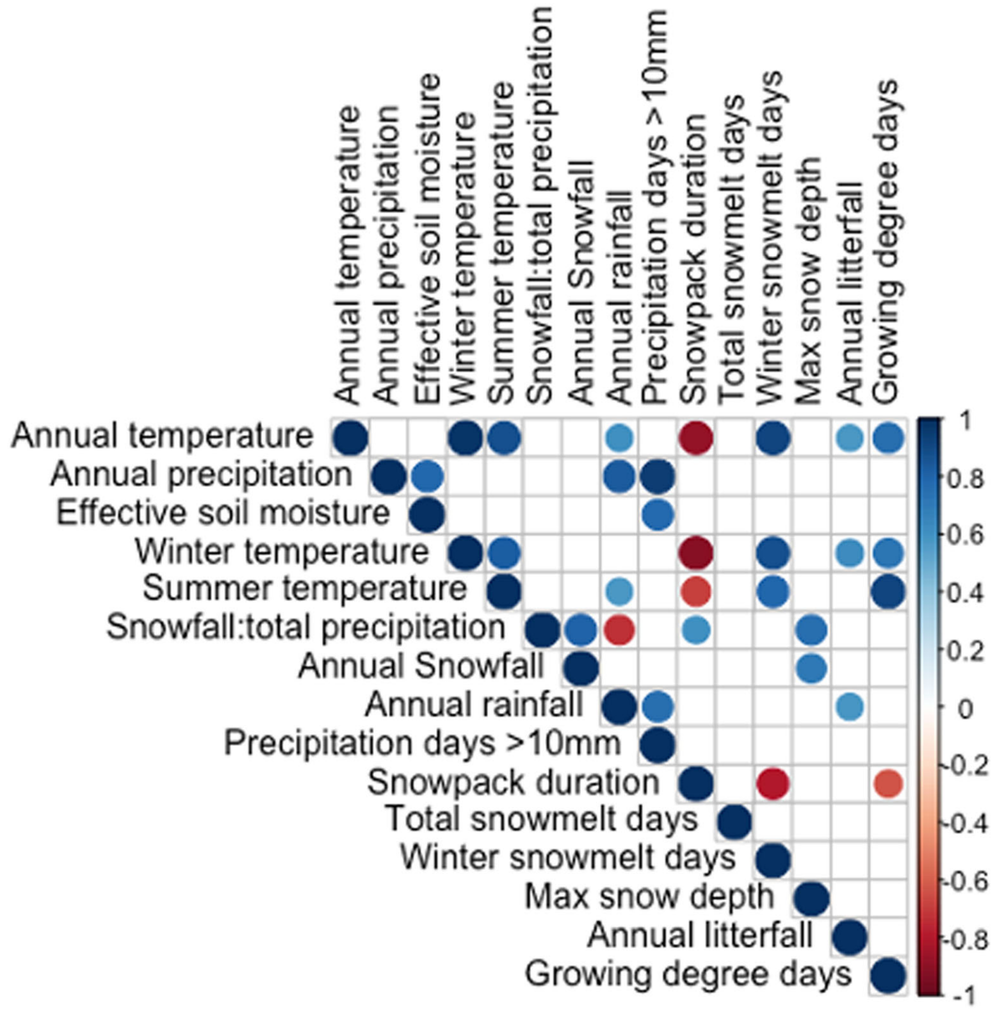

Figure 6. Correlation matrix of hydrometeorological factors included in multiple hypothesis testing. An explanation of each factor is provided in Table 4. Correlation information for each pair of factors is provided within the horizontal and vertical cross section. A blank cross section indicates no correlation. For correlated factors, the strength of the correlation is demonstrated by both the size of the circle and the color gradient. The color gradient is provided on the right-hand side of the figure (ranging from −1 to 1).

Mean winter and summer temperature increased with decreasing latitude, however, winter temperature was more variable (CV: 18–31%) than summer temperature (CV: 6–9%) at all sites. Congruent with the 30-year means, there was a larger latitudinal range in 4-year mean winter temperature compared to summer temperature (8.2 °C and 3.5 °C temperature range in winter and summer, respectively). Rainfall decreased with increasing latitude and was slightly above average in the northern and intermediate sites, but slightly below average in the southern site. Snowfall was approximately average in the northern and southern sites and was below average in the intermediate site. Snowfall in the southern site was above average and was comparable to mean snowfall received in the northern site, however, large interannual variations in snowfall occurred in the southern site (CV = 48%). Similarly, maximum snowpack depth in the southern site was much greater than the 30-year average and was comparable to the snowpack depth in the northern site. There was large interannual variability of maximum snowpack depth at all sites, which increased with decreasing latitude (CV: north = 38%, intermediate = 47%, south = 54%). Snowpack duration (number of days from the beginning of a consistent snowpack to end of the melt) increased with latitude (from 109 to 169 days). The number of within-winter snow melt days decreased with latitude as did the amount of winter rainfall, but the total number of snowmelt days (total melt days

Table 2. Hydrometeorological Indices and DOC Mobilization Hypotheses

Index (Fixed effect)	DOC mobilization mechanism
1. Annual Air Temperature (°C)	Regional comparison of field studies show no temperature effect on annual DOC fluxes (Michalzik and others 2001)
	Positive relationships between DOC concentration and temperature, and negative relationship between water fluxes and temperature suggests an interactive temperature effect at the seasonal scale (Bowering and others 2020)
	Soil incubation studies demonstrate greater DOC production at higher temperatures (Moore, 2008)
2. Total Annual Precipitation (mm)	Precipitation mobilizes DOC but uncertainty exists in regional comparison study on whether this is a direct control (Michalzik and others 2001)
	A meta-analysis showed that DOC fluxes in runoff was determined by amount of annual precipitation (Pumpanen and others 2014)
3. TP–PET (mm)	Available water or ''effective soil moisture'' correlated to predicted DOC release and storage in mineral soils (Kramer and Chadwick, 2018)
	Temperature and precipitation interaction term
4. Rainfall (mm)	Rain is a direct delivery of water to forest flow thereby increasing soil infiltration
5. Snowfall (cm)	Snow can be intercepted by the canopy and losses of water are possible via sublimation from the canopy or snowpack
	Snow can reduce soil infiltration by increasing overland flow or runoff
6. Snow: total precipitation	Partitioning of precipitation controls water flow paths through the landscape, similar to, but more specific than, total snow
7. Snowpack duration (days)	Losses of water from snowpack is possible through sublimation and overland flow, attributed to total days on the ground
	Insulated soil protects soil from freezing which results in less physical fracturing of soil and less DOC produced (Haei and others 2010), or warmer soils and greater DOC losses (Moore, 2008)
8. Maximum Snow Depth (cm)	Deep snowpacks result in greater soil insulation and a larger spring snowmelt event
9. Snowmelt Days	Snowmelt water compared to rainfall results in different hydrological pathways through the ecosystem, greater losses of are water possible through overland flow and sublimation of intercepted snow
10. Precipitation > 10 mm	Increased frequency of large precipitation events predicted in these regions (Finnis and others 2018)
11. Aboveground Litterfall	Field manipulation studies demonstrate leaching of fresh litterfall as a key source of soil DOC (Kalbitz and others 2008)
12. Growing Degree Days	Drives soil decomposition and tree activity (that is, root exudation and litterfall) that contributes DOC
13. Winter Rain	Winter rain increases the frequency of midwinter melting events, creating a more dynamic snowpack, and mobilizing DOC before respiratory losses over winter
14. Winter Snowmelt Days	Midwinter snowmelt reduces snowpack depth and meltwater mobilizes DOC
15. Winter Temperature (°C)	Winter temperatures are predicted to be most sensitive to climate change (Finnis and others 2018)
	Winter temperatures drive precipitation form and snowpack dynamics
16. Summer temperature (°C)	High summer temperatures correlate with highest concentrations of DOC on an annual basis (Bowering and others 2020)

Annual temperature, total precipitation, total precipitation minus potential evapotranspiration (TP-PET), snowfall, rainfall, snowfall as a proportion of total precipitation (snow:precipitation), number of days with snow on the ground (snowpack days), maximum snowpack depth, snowmelt days (number of days above 0 °C when snow is on the ground), precipitation > 10 mm (number of days receiving more than 10 mm of precipitation. aboveground litterfall, and GDD (cumulative growing degree days > 5 °C), mean winter temperature, and total winter rainfall.

per year) was similar at the three sites. Growing degree days were above average at all sites and decreased with latitude. No clear short-term latitudinal trend in the number of days receiving more than 10 mm of precipitation, the snowfall to total precipitation ratio, or effective soil moisture (total precipitation − potential evapotranspiration) was observed over the study period.

Table 3. Four-year Means and Variability of Hydrometeorological Indices in Three NLBELT Regions

Variable		North	Interm	South
Annual temperature (°C)	Mean	0.4	3.1	6.0
	sd	1.7	1.1	1.3
	cv	26%	34%	21%
Annual precipitation (mm)	Mean	1094	1256	1301
	sd	115	130	269
	cv	11%	10%	21%
TP–PET	mean	775	770	750
	sd	169	82	315
	cv	22%	11%	42%
Rainfall (mm)	Mean	662	898	930
	sd	135	125	189
	cv	20%	14%	20%
Snowfall (cm)	mean	437	357	424
	sd	70	44	202
	cv	16%	12%	48%
Snow:Total Precipitation	Mean	0.40	0.29	0.32
	sd	0.08	0.04	0.13
	cv	20%	14%	40%
Snowpack duration	Mean	169	130	109
	sd	17	28	26
	cv	10%	22%	24%
Maximum snow depth (cm)	Mean	202	75	167
	sd	77	35	90
	cv	38%	47%	54%
Total number of snowmelt days	Mean	29	23	28
	sd	9	3	5
	cv	31%	13%	18%
Number of days w precipitation >10 mm	Mean	33	41	38
	sd	5	5	11
	cv	15%	13%	29%
Litterfall (g C m^{-2})	Mean	182	469	465
	sd	77	120	73
	cv	42%	26%	16%
GDD	Mean	944	1171	1595
	sd	165	125	376
	cv	17%	11%	24%
Winter (DJF) rainfall	Mean	22	70	112
	sd	21	17	17
	cv	99%	24%	15%
Winter (DJF) snowmelt days	Mean	1.3	4.3	10.3
	sd	1.5	2.2	3.5
	cv	120%	52%	34%
Winter (DJF) temperature (°C)	Mean	−12.7	−7.8	−4.5
	sd	2.3	1.8	1.4
	cv	18%	23%	31%
Summer (JJA) temperature (°C)	Mean	12.6	14.0	16.2
	sd	1.1	0.9	0.9
	cv	9%	6%	6%

North (Eagle River), Intermediate (Salmon River), and South (Grand Codroy). sd: standard deviation, cv: coefficient of variation.

Temperature and Precipitation Effects on Soil DOC Mobilization Differ with Timescale

Regional comparison of the four-year trend along the latitudinal transect revealed greater mean annual mobilization of soil DOC in the south site that is characterized by both highest MAT and MAP ($p < 0.0001$; Figure 4). Less DOC was mobilized in the north and intermediate sites. The amount of DOC mobilized in the intermediate and north sites was not significantly different despite a 2.6 °C difference in MAT and 130 mm difference in MAP. There was no relationship between annual precipitation and DOC flux ($p = 0.8070$; Figure 5A). There was, however, a positive relationship with annual temperature, with each one degree increase in annual temperature associated with an increase in DOC flux of 8.31 g m^{-2} y^{-1} ($p = 0.0007$; Figure 5B).

Model Selection Indicates Strong Effect of Interannual Air Temperature and Snowpack Duration

Annual temperature, snowpack duration, effective soil moisture (TP-PET), snowfall, and winter temperature were within 2 ΔAICc of one another and ranked above the null model (intercept + site effect; Table 4, Figure 7A). Indices related to total precipitation, rainfall, summer air temperature and productivity did not perform better than the null model. Annual air temperature explained 79% of the variance in DOC fluxes with wAICc = 0.23. This model describes greater annual DOC mobilization at higher air temperatures. Winter temperature explained 74% of the DOC flux variance with wAICc = 0.09. Congruent with the annual air temperature relationship, more DOC is mobilized during warmer winters. The model including snowpack duration explained 69% of the DOC flux variance with wAICc = 0.20, describing greater annual DOC mobilization during years with a shorter snowpack season. Air temperature and snowpack duration were highly negatively correlated (Figure 7B), suggesting that air temperature indirectly controls DOC mobilization through a direct effect on snowpack duration (that is, warmer years result in a shorter snowpack season and more DOC mobilized). In contrast, total snowfall and effective soil moisture were not correlated to air temperature, and both parameters explained less of the DOC flux variance (48% and 53%, respectively).

Discussion

We found that, on average, more soil dissolved organic carbon (soil DOC) is mobilized in the warmest, wettest region and less DOC is mobilized in the cooler, drier region of the Newfoundland and Labrador Boreal Ecosystem Latitudinal Transect (NLBELT). These results suggest that climate change-driven increases in precipitation and temperature projected to occur in mesic boreal forests by the end of this century will drive increased mobilization of soil DOC. Evidence from many forest studies show a positive relationship between DOC fluxes and precipitation and no relationship

Table 4. Results of Model Selection of Hydrometerological Indices

Model	Fixed Effect	K	Log L	AICc	ΔAICc	AICc	Pseudo R^2	Marginal R^2
1	Annual Temperature 2.2 (0.82, 3.57)	4	−33.04	79.80	0	0.23	0.49	0.79
2	Snowpack Days −0.12 (−0.19, −0.05)	4	−33.18	80.07	0.27	0.20	0.48	0.69
3	TP-PET −0.01 (−0.02, −0.01)	4	−33.52	80.75	0.95	0.14	0.46	0.48
4	Snowfall −0.02 (−0.04, −0.01)	4	−33.54	80.78	0.98	0.14	0.46	0.53
5	Winter Temperature 1.10 (0.18, 2.20)	4	−33.97	81.65	1.85	0.09	0.41	0.74
NULL	Site only	3	−37.11	83.21	3.41	0.04	0	–

The interannual effect of air temperature, total precipitation, precipitation type (snowfall, rainfall, snowfall:precipitation) snowpack dynamics (snowpack duration, number of snowmelt days, maximum depth), precipitation event size (number of days exceeding 10 mm total precipitation), productivity (growing degree days, litterfall), and winter dynamics (winter temperature, winter rainfall, winter snowmelt days). We included 16 linear mixed effects models in the model set, only those that ranked above the null are shown here. All models included site as the random effect. The null model includes the model intercept and random effects. Models are ranked with Akaike information criterion, corrected for small sample size. The fixed effects estimates and 0.95 confidence intervals (in parentheses) are included for the top ranked models.

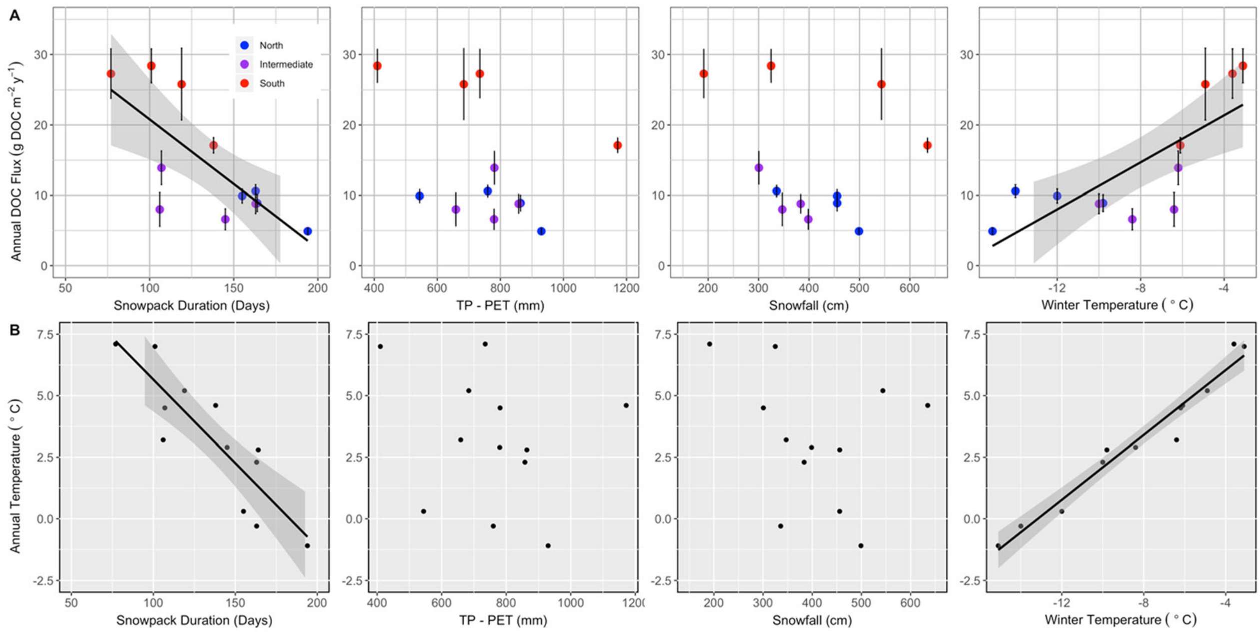

Figure 7. Plots of top models explaining interannual dissolved organic carbon (DOC) flux variation by site and relationship to air temperature. (**A**) Top models selected by AICc included air temperature, effective soil moisture (total precipitation minus potential evapotranspiration), snowfall, and winter air temperature. Points represent annual values in south (Grand Codroy;red), intermediate (Salmon River;purple), and north (Eagle River;blue) forest sites (**B**) Top model factors plotted against annual air temperature. See Table 4 for parameter estimates (0.95 confidence intervals) and model selection results.

with temperature at large temporal and spatial scales (Michalzik and others 2001; Schmidt and others 2010) however, others show no such relationship at smaller, regional scales (Froberg and others 2006; Lindroos and others 2008; Borken and others 2011). We found no relationship between DOC mobilization and interannual bulk precipitation measured at our mesic boreal forest sites over four years (Figure 5A), but rather, a positive relationship with interannual temperature (Figure 5B). By exploring additional hydrometerological factors over four years, we found that a significant part (69%) of the variation in DOC mobilization could be explained by snowpack duration, which in turn was strongly correlated to temperature (winter and annual; Figure 7B and Table 4). Furthermore, the remaining variability captured by other site attributes (that is, the significant site factor in our models) suggests an additional influence of forest properties that are driven by differences in historical climate across the transect. For example, differences in organic horizon thickness and moss abundance developed under long-term differences in climate conditions across the sites (Table 1C) and are important components of both soil hydrology and C accumulation in boreal forest soils (Hobbie and others 2000; Kane and Vogel 2009). These site conditions interact with the short-term environmental conditions to result in site-specific mobilization of water and DOC. Together, these results support a combined influence of direct, short-term hydrometeorological variation and indirect, longer-term climate and on DOC mobilization (Figure 1).

Temperature and Snowpack Dynamics Explain Short-Term DOC Mobilization Dynamics

Although many laboratory studies show that more DOC is extracted from soils incubated at higher temperatures (Christ and David 1996; Moore and others 2008; Lee and others 2018), this effect has proven difficult to measure in field studies likely due to the overriding influence of hydrology (Kalbitz and others 2000). Weekly to biweekly DOC flux patterns usually resemble soil water fluxes, and not DOC concentration (Buckingham and others 2008; Wu and others 2014; Bowering and others 2020), supporting the hypothesis that hydrology, and not DOC production mechanisms, ultimately determine the quantity of DOC mobilized. However, observations of seasonal soil DOC mobilization dynamics show seasonally dependent shifts in the relative importance of temperature compared to hydrology (Bowering and others 2020). This is congruent with seasonal patterns of soil DOC export to streams observed at the catchment scale (Wen and others 2020). In this 4-year study, annual and winter air temperature, together with snowpack duration and snowfall, ranked above production related indices such as growing degree days and litterfall, highlighting the potential importance of winter conditions and temperature-hydrological linkages on annual DOC fluxes, particularly in mesic boreal forests.

Air temperature and snowpack duration were highly correlated across all sites and years of this study (Figure 7B). The timing and accumulation of the snowpack is driven by air temperature (Brooks and others 2011; Campbell and Laudon 2018) and, although correlations prevented testing of this interaction in our models, evidence from other studies suggests that the effect of these two factors on DOC mobilization could be linked. In permafrost boreal regions, thaw is resulting in the release of DOC (Wickland and others 2018). In cold, continental boreal regions that receive less snowfall, increased soil exposure and subsequent freeze–thaw episodes during winter is expected to be a consequence of climate change, with resultant increases in DOC export from soils to streams (Haei and others 2010). However, in this non-permafrost, maritime boreal forest study, all sites developed deep snowpacks early in the winter season that protected soils from extreme freezing (Figure S1; 0 °C soil temperatures were measured at the northern and intermediate sites). This suggests that the effect of increasing air temperature and decreasing snowpack duration on DOC is not explained by increased soil freezing in these sites.

Two alternative explanations exist for our results describing a role for decreasing snowpack duration controls on soil DOC: 1) reduced winter heterotrophic soil C and 2) increased soil water infiltration associated with reduced snowpack duration and winter melting. First, variations in the duration of the soil insulation period likely control DOC mobilization through length of the decomposition period. Soil respiration occurring underneath the snowpack can account for up to 50% of soil respiration in seasonally snow-covered systems (Brooks and others 2011) and, as decomposition of organic matter proceeds in the absence of fresh litter inputs, the soluble fraction can decrease (Berg 2000; Hilli and others 2008). Consequently, the water-soluble organic C fraction of soil is reduced during years with a longer snowpack season. In support of this, the chemical composition of dissolved organic matter (DOM) during snowmelt is measurably distinct from autumn, suggesting that deep snowpacks do have a significant effect on DOC decomposition (Bowering and others *unpublished manuscript*). However, soil temperature records from our study sites indicate the warmer soil temperatures in the southern sites persist throughout winter as compared with the more northern sites (Figure S1).

Secondly, and a more likely explanation for these forest sites, soil infiltration is impacted by canopy interception and water flow paths during snowmelt. For instance, rain has greater leaching potential than snow because greater proportions of precipitation received as snow can be intercepted by the canopy and lost via sublimation resulting in decreased throughfall (Starr and Ukonmaanaho 2003). The negative relationship between DOC mobilization and snowfall at all sites suggests a role of this process (Figure 7A), but with a strong site influence explained by decreasing stand density (Table 1B) and decreasing annual snowfall variability with increasing latitude (Table 3). Additionally, water movement within the snowpack can reduce the proportion of precipitation that infiltrates the soil and increase direct snowpack runoff. During large snowmelt events, within-snowpack water flow results in greater connection of the snowpack to the streams (Wever and others 2014), and could in part explain why less soil DOC is mobilized during longer snowpack years.

Forest Site Properties are Congruent with an Influence of Long-Term Climate on DOC Mobilization

Differences in forest site properties across the transect suggest that long-term climate conditions explain the remaining DOC mobilization variability, indicating an indirect role of climate on DOC mobilization. The northern forests of this transect and the intermediate-latitude forests have thicker O horizons compared to the southern forests (Table 1C), which influences the interception potential of the forest floor. This could partly explain why the DOC fluxes in the south are consistently larger, even in years when total precipitation is equal across all sites (Figure 4A). Consistent with this, both water and DOC fluxes were larger through the thinner organic horizons of harvested plots compared to adjacent mature forest plots (Bowering and others 2020). Accumulation of C in organic horizons is ultimately determined by climate conditions controlling the balance between decomposition and inputs. On a global basis, low temperatures explain the accumulation of soil organic C in boreal forests compared to tropical forests. Within boreal forests, however, the driving mechanisms are not as clear (Ziegler and others 2017), and are influenced by drainage class (Callesen and others 2003; Olsson and others 2009; Wickland and others 2010), N deposition (Kleja and others 2008) and soil temperature (Kane and others 2005; Kane and Vogel, 2009; Vogel and others 2008). Moss abundance can also describe C accumulation trends in O horizons because of the relatively recalcitrant nature of moss litter compared to leaf litter (Hobbie and others 2000; Philben and others 2018). At large spatial scales, moss abundance increases with latitude (Berdugo and others 2018), but within boreal forests, moss abundance is influenced by many factors including water availability and light (Bisbee and others 2001), slope and aspect (Kane and Vogel 2009), and deciduous litterfall (Jean and others 2020). Similar to organic horizon interception, mosses can also influence large interception losses (Price and others 1997). The northern forest site in this study has significantly more moss coverage than the intermediate and southern sites, is north-facing, and receives significantly less litterfall than the intermediate and southern sites (Table 4B,C) all of which could contribute to less mobilization of soil DOC. Although the driving mechanisms behind these site factors require further investigation, differences in the structure of the organic horizon and associated moss layer are likely driven by long-term climate differences across the transect, with impacts on DOC mobilization predominantly through differences in soil hydrology.

Conclusions and Future Directions

This study demontrates that climate change-driven increases in air temperature will have direct consequences on the duration of snow cover and, consequently, DOC mobilization patterns in boreal forests. While, on average, more DOC was mobilized in the wettest, warmest forest site, there was no relationship between DOC fluxes and annual precipitation when analyzed interannually. Instead, annual temperature appears to be positively linked to DOC fluxes and multiple hypothesis testing of a suite of hydrometeorological factors showed that air temperature and snowpack duration explained a large amount of interannual DOC mobilization variability. The known interplay between temperature and snow cover conditions suggests an interactive effect of these two factors on soil DOC mobilization patterns and that, in these systems, increased losses of soil DOC will occur under a warming climate due to a shorter snowpack season. Additionally, soil properties, such as O horizon thickness and moss coverage, that developed over long-term differences in climate conditions across this boreal forest transect may decouple water and DOC fluxes from annual precipitation, contributing to a strong site effect and resulting in no relationship with annual precipitation. These observations from individual forest sites suggest more work is needed to understand (1) the mechanisms behind air temperature and snow controls on soil DOC losses across snow-covered ecosystems and (2) the combined indirect and direct effects of climate on DOC mobilization and the importance of each under rapidly changing environmental conditions. This will improve our ability to predict soil DOC mobilization across the boreal zone and provide a better understanding of the contribution of soil DOC losses to the overall forest C balance and aquatic C pools.

ACKNOWLEDGEMENTS

Thanks to Memorial University Grenfell Campus students Danny Pink, Amanda Baker, Sara Thompson and Canadian Forest Service, Atlantic Forestry Centre employees, Darrell Harris, and Gordon Butt for field assistance and contributions to field site establishment and maintenance.

FUNDING

Funding was provided by NSERC-Strategic Partnership Grant, 479224-15, Newfoundland and Labrador Agrifoods and Forestry Agency, Natural Resources Canada, Canada Research Chairs Programme, Natural Sciences and Engineering Research Council of Canada, RGPIN-2018-05383.

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