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RESEARCH AND OBSERVATORY CATCHMENTS: THE LEGACY AND THE FUTURE

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Sources and biodegradability of dissolved organic matter in two headwater peatland catchments at the Marcell Experimental Forest, northern Minnesota, USA

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Abstract

Where they are present in catchments, peatlands are a dominant source of dissolved organic matter (DOM) to surrounding waterways due, in part, to high production rates. Despite the preponderance of peatlands in northern latitudes and expected peatland vulnerability to climate change, little is known about peatland DOM degradation relative to a more comprehensive understanding of degradation when DOM is sourced from upland-dominated catchments. We compared DOM biodegradability of various sources of stream water in two catchments having peatlands (22%–33% of the area) surrounded by upland forests (70%–90% of the area, either deciduous or coniferous). We measured total organic carbon (TOC), and biodegradable dissolved organic carbon concentrations; bacterial respiration rates; streamflow; and upland runoff during and after snowmelt (March to June, 2009–2011). We also explored if DOM in upland runoff stimulated biodegradation of peatland-derived DOM (i.e., a priming effect), and if forest cover type affected DOM biodegradability. As expected, the peatlands were the largest sources of both water (72%–80%) and TOC (92%–96%) to the streams although more area in each catchment was in uplands (70%–90%). Several results were unexpected, yet revealing: (1) DOM from peatlands sometimes had the same biodegradability as DOM from uplands, (2) upland sources of DOM had negligible effects on biodegradability in the peatland and downstream, and (3) upland deciduous cover did not yield more degradable DOM than conifer cover. The most pronounced effect of upland runoff was dilution of downstream TOC concentrations when there was upland runoff. Overall, the effects of upland DOM may have been negligible due to the overriding effect of the large amount of biodegradable DOM that originated in bogs. This research highlights that peatland-sourced DOM has important effects on downstream DOM biodegradability even in catchments where upland area is substantially larger than peatland area.

KEYWORDS

bog hydrology, dissolved organic matter, DOM biodegradability, DOM sources, northern peatlands, source areas in upland-peatland catchments, upland forest

1 | INTRODUCTION

Catchment studies have been used to explore how upland and riparian source areas affect the downstream concentration, composition, and degradability of dissolved organic matter (DOM). Although the catchments and studies span the Earth, most studies have been focused on forested, temperate, mountainous catchments with mineral soils (some examples of particular catchments or syntheses: Berggren et al., 2007; Boyer et al., 1997; Buffam et al., 2001; Cory et al., 2015; Creed et al., 2008; Dittman et al., 2009; Hinton et al., 1998; Hood et al., 2003; Kawasaki et al., 2008; Lajtha & Jones, 2018; Laudon et al., 2011; Park et al., 2005; Pellerin et al., 2012; Raymond & Saiers, 2010; Shibata et al., 2001; Urban et al., 1989).

A paucity of information on the effects of various DOM sources on DOM transport and cycling from peatland catchments is glaring relative to the disproportionately large influence that peatlands have in the global storage of carbon (C) and climate regulation (Gorham, 1991; Limpens et al., 2008). In general, catchment characteristics and sources of stream water affect the biodegradability and downstream transport of DOM Ågren et al., 2014; Aiken & Cotsaris, 1995; Battin, 1999; Dillon & Molot, 1997; Fellman et al., 2008; Gergel et al., 1999; Hinton et al., 1997; Hornberger et al., 1994; Laudon et al., 2004; Schiff et al., 1997). Nonetheless, concurrent measurements of sources, transport, and degradability of DOM are rare. It is even more rare for these factors to be studied in landscapes with substantial areas in both peatlands and uplands where DOM properties can be quite different (Ågren et al., 2008; Köhler et al., 2009).

Peatlands comprise 9.7% of the surface area of Northern Hemisphere but store approximately half of the atmospheric carbon pool in peat, between 270 and 455 Pg C (Gorham, 1991, 1995; Solomon et al., 2007; Turunen et al., 2002; Yu, 2012; Yu et al., 2010). Northern peatlands also store 33% or more of global soil carbon (Gorham, 1991; Turunen et al., 2002; Yu, 2012; Yu et al., 2010). Peatlands export nearly one order of magnitude more dissolved organic carbon (DOC) per unit area (5–40 g C m^{-2} $year^{-1}$) than forested uplands (Moore et al., 2002; Thurman, 1986; Urban et al., 1989). Yields of DOC from peatlands may be 22%–38% of annual net C exchange in boreal peatlands (Griffiths et al., 2017). The lowest stream DOC concentrations may occur during stormflow when perennial inputs of peatland runoff to streams are diluted by upland storm runoff (Buffam et al., 2007; Schiff et al., 1997; Urban et al., 2011). Nonetheless, average and maximum stream DOC concentrations in headwater catchments with boreal peatlands are often orders of magnitudes greater than concentrations in headwater catchments with mostly mineral soil uplands (Köhler et al., 2008; Perdue & Ritchie, 2005). In contrast to the known high concentrations, peatland DOM has been considered to have lower biodegradation rates relative to upland sources (Berggren et al., 2007; Berggren & del Giorgio, 2015; Freeman et al., 2001).

Compared with peatlands, streams in upland temperate forests that are most-studied typically have low DOM concentrations, with higher concentrations during stormflow events (Hornberger et al., 1994; Raymond & Saiers, 2010; Zarnetske et al., 2018). In boreal and temperate, mineral-soil dominated catchments, subsurface stormflow (SSF) from near-surface lateral flowpaths is a source of high DOC concentrations in streams (Berggren & del Giorgio, 2015; Inamdar & Mitchell, 2006; Köhler et al., 2008; Schiff et al., 1997; Schiff et al., 1990; Sebestyen et al., 2008). Many researchers have found DOM during stormflow to be compositionally distinct, with more degradable DOM than in groundwater and stream baseflow (Buffam et al., 2001; Dittman et al., 2010; Kaplan & Newbold, 1993; Sebestyen et al., 2008).

Irrespective of contrasts in concentration and degradability between upland and peatland source areas, DOM from uplands may play another pronounced role in peatland C cycling by stimulating biodegradation of peatland DOM through a priming effect (Kuzyakov, 2010). Priming could be considered to occur if DOM of a particular composition or from a particular source stimulated DOM biodegradation downstream. The priming effect has long been recognized in soils (Blagodatskaya & Kuzyakov, 2008) and sometimes, though not always, observed in aquatic ecosystems (Bengtsson et al., 2014; Bianchi et al., 2015; Catalán et al., 2015; Guenet et al., 2010; Hotchkiss et al., 2014). When observed in freshwaters, DOM mineralization has increased by 10%–500% in the presence of biodegradable DOM (de Haan, 1977; Farjalla et al., 2009; Hotchkiss et al., 2014; Shimp & Pfaender, 1985). The occurrence or magnitude of the priming effect may depend on the source of biodegradable DOM, whether that be due to differences in forest cover, soil types, or nutrient availability (Wickland et al., 2012). Nonetheless, it is not known if or how DOM biodegradability and the strength of priming vary among source areas and between contrasting forest cover types.

In this study, we measured DOM biodegradability in two peatland catchments with different upland forest types (coniferous and deciduous). We sampled during and after spring snowmelt events, when most DOM is exported each year from boreal catchments (Kolka et al., 2001; Laudon et al., 2004). Our objective was to measure DOM biodegradability in multiple sources of stream water in catchments where central peatlands are surrounded by upland forests. In addition, we compared DOM biodegradability between upland forest types and we experimentally mixed waters to investigate whether inputs of biodegradable DOM from uplands stimulated microbial degradation of DOM in peatlands. Decomposition rates have been negatively correlated with initial C to N ratios (C:N) of litter types across a wide range of forest ecosystems (Melillo et al., 1982) and C:N of leachates that are sources of DOM tend to be lower from deciduous cover and higher from coniferous cover. Accordingly, we expected runoff from deciduous cover to have greater decomposition rates and produce a more biodegradable DOM in runoff than coniferous litter. We hypothesized that the biodegradability of upland DOM would affect DOM biodegradability in stream waters that drained from the catchments, and that streams would receive more highly biodegradable DOM from deciduous uplands than coniferous uplands.

2 | SITE DESCRIPTION

We studied the S2 and S6 catchments at the Marcell Experimental Forest (MEF). These headwater catchments are part of a 60-year old research program of the Northern Research Station of the USDA Forest Service that is focused on the hydrology and biogeochemistry of catchments with uplands and northern peatlands (Kolka et al., 2011). The MEF is 40 km north of Grand Rapids in north-central Minnesota, USA (Figure 1). In the area, lakes and peatlands are interspersed among upland forests in a low-topographic relief setting. The climate is continental with a wide range of air temperatures from −46 to 38°C and a mean annual temperature of 3.4°C from 1961 to 2019 (Sebestyen et al., 2011). Over that same period, mean annual precipitation was 787 mm, with about one-third of the annual precipitation falling as snow and most precipitation as rainfall during summer. Snow has typically accumulated from November or December until snow melts during a one to three-week period beginning during March or April.

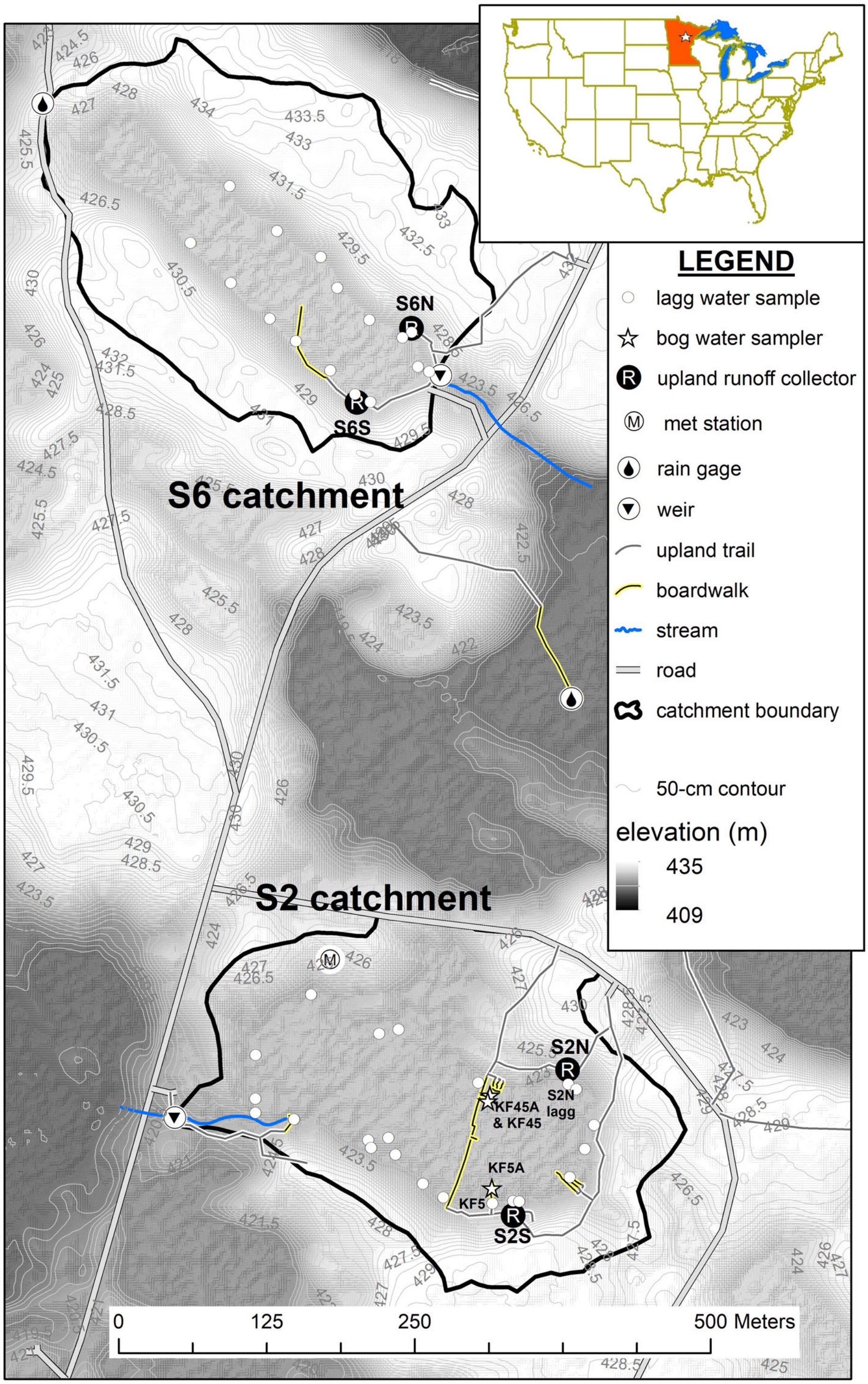


FIGURE 1 Map of the deciduous upland (S2) and coniferous upland (S6) catchments, instrumentation, and sampling sites. Lagg and bog sites in the S2 catchment that were sampled weekly during 2011 are shown (KF5, KF5A, KF45, KF45A, and S2N lagg). For the other sites, indicated only by symbols, 9–10 of the S2 lagg locations and three to 13 of the S6 lagg locations were sampled at a time. Details are provided in an associated data publication (Sebestyen et al., 2020)

Streamflow is intermittent in both catchments, with prolonged periods of no streamflow (Verry et al., 2011).

Physical, geological, lithological, vegetation, and forest management aspects of the two study catchments are listed in Table 1 and described in Sebestyen, Dorrance, et al. (2011). The S2 catchment has a 6.5-ha deciduous upland forest and has been used as a reference basin for paired-catchment studies. The S6 catchment was replanted in conifers during 1983 after a ~60-year old deciduous forest was clearcut during 1981. To identify the catchments, we refer to the S2 catchment as the deciduous catchment and the S6 catchment as the coniferous catchment even though both have coniferous peatland forests (see next paragraph). In the area, soils have developed on top of deep (50 m) outwash sand deposits, with upland subsurface storm runoff occurring through A and B horizons that overlie B2t horizons that are aquitards (Verry et al., 2011). The A and B soil textures varies between the S2 and S6 uplands. The S2 upland A horizon has less sand (69% vs. 84%), more silt (25% vs. 13%), and more clay (6% vs. 3%) than the S6 upland soil (Verry, 1969).

Each catchment has a central, ombrotrophic, raised-dome bog with a black spruce (*Picea mariana*)-*Sphagnum* community growing on hummock and hollow microtopography (Verry, 1984). Most of the total area of the catchments is in uplands: 67% uplands in the deciduous catchment and 78% uplands in the coniferous catchment. The bogs radially drain to laggs (Richardson et al., 2010; Verry et al., 2011; Verry & Janssens, 2011). Laggs, at the transition to uplands (Romanov, 1961), have organic soils and peatland vegetation. The bog was larger in absolute and relative areas in the deciduous S2 (3.2 ha, 94% bog and 6% lagg; Table 1) than in the coniferous S6 (2.0 ha, 65% bog and 45% lagg). An outlet stream in each catchment forms in the lagg.

From 2001 to 2008, sulphate was irrigated on to the S6 peatland during an experiment to study effects of sulphate reducing bacteria on methylmercury production (Coleman Wasik et al., 2015; Jeremiason et al., 2006). By the time of our study (2009–2011), there were no detectable effects of sulphate addition on DOM concentration or composition (Supplement 1).

3 | METHODS

Meteorological and streamflow monitoring is part of the long-term MEF research program (Sebestyen, Dorrance, et al., 2011; Sebestyen et al., in review, this special issue). Total daily rainfall was measured with a Universal Recording Precipitation Gage (Belfort Instruments, Baltimore, MD) until October 2010, and a NOAH IV Digital Precipitation Gage (ETI Instrument Systems, Fort Collins, CO) thereafter (data and metadata provided in Sebestyen et al., 2020). Stream stage was recorded at a 120-degree V-notch weir at the outlet stream of each

TABLE 1 Physical properties and vegetation of the uplands and peatlands of the two studied catchments

	S2 deciduous upland catchment	S6 coniferous upland catchment
Peatland areas	3.2 ha	2.0 ha
Upland areas	6.5 ha	6.9 ha
Elevation range	420–430 m a.s.l.	423–435 m a.s.l.
Upland forest types, dominant species, and management	Deciduous: aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Harvested during 1910s. Since 1960, a reference catchment for paired-watershed studies with no site or forest manipulations (Sebestyen, Dorrance, et al., 2011)	Coniferous: red pine (*Pinus resinosa*) and white spruce (*Picea glauca*) with some aspen and white birch after experimental harvest of an upland aspen/birch forest during 1980. Aspen regrowth was suppressed. Replanted in red pine/white spruce during 1983 (Sebestyen et al., 2011). The canopy closed around 2000
Mineral soil series	Warba sandy clay loam developed in glacial till (fine-loamy, mixed, superactive, frigid Haplic Glossudalfs; Alfisol; Nyberg, 1987)	Menahga loamy outwash sand (mixed, frigid, Typic Udipsamments; Entisol; Nyberg, 1987)
Bogs	3.0 ha. Undrained, natural peatland, with a black spruce (*Picea mariana*)-*Sphagnum* community with some tamarack (*Larix laricinia*) and ericaceous shrubs (primarily *Rhododendron groenlandicum* and *Chamaedaphne calyculata*) and *Sphagnum* sp. Basal area was 23 m^2 ha^{-1} in 1968 when surveyed (Verry, 2018). Trees naturally regenerated since fire during the 1860s	1.2 ha. Undrained, natural peatland, with a black spruce-tamarack-*Sphagnum* community with ericaceous shrubs (primarily *Rhododendron groenlandicum* and *Chamaedaphne calyculata*), and *Sphagnum* sp. About a 1:1 mix of spruce and tamarack trees in the canopy. Basal area was 12 m^2 ha^{-1} in 1968 when surveyed (Verry, 2018). Trees naturally regenerated from an apparent harvest around 1900
Laggs	0.2 ha. 48% of lagg covered with alder (*Alnus incana*; Hill et al., 2016)	0.7 ha. Entire lagg has dense alder cover
Peat series	Loxley peat (Dysic, frigid Typic Haplosaprists); Nyberg, 1987)	Seelyville peat (Euic, frigid Typic Haplosaprists); Nyberg, 1987)
Streamflow	49–288 mm $year^{-1}$ from 1961 to 2014	40–276 mm $year^{-1}$ from 1977 to 2014

catchment (data and metadata provided in Verry et al., 2018). Daily streamflow, as specific discharge in units of cm day^{-1}, was estimated by summing sub-daily, period-weighted streamflow estimates that were calculated from a stage-discharge relationship applied to breakpoint stage data.

Many samples were collected during and after snowmelt from 2009 to 2011 to determine how total organic carbon (TOC) concentrations varied among water types from various source areas and over time. A small subset of those samples was used to measure DOM biodegradability due to the additional labour and need for larger sample volumes than the more frequently analysed TOC. We used short- and long-term measures of DOM biodegradability (Guillemette & del Giorgio, 2011): bacterial respiration (BR) rate as a measure of highly reactive DOM that biodegrades within days, and biodegradable DOC (BDOC) concentration as a measure of all DOM that biodegrades over 1 year. A laboratory experiment was also used to determine if mixtures of various source waters resulted in a priming effect on biodegradation. We provide an overview of sampling and chemistry measurements (Table 2; data and metadata provided in Sebestyen, Funke, et al., 2020).

Event-based water samples for TOC measurement were collected from runoff collectors installed on north-facing (S2S and S6S collectors) and south-facing (S2N and S6N) slopes of the uplands of each catchment (monitoring and data are described by Sebestyen & Kyllander, 2018). Overland flow occurs as runoff through the forest floor overlying mineral soils, typically when soils are frozen (Verry et al., 2011). Subsurface runoff plots were adjacent to overland flow plots. In each plot, lateral SSF from the interface of the A or B (sandy loam) and Bt2 (loamy clay) soil horizons, at about 30-cm depth, infiltrated into a stainless steel well screen in a hillslope trench. Overland flow and SSF were routed into 5-L pails for chemistry sampling, with over flow into 700-L tanks to contain runoff water for volumetric measurement. Volume was read from calibrated stand pipes. At least one water sample was collected every time that a tank was emptied after filling or when flow from the runoff event stopped. Electronic water level recorders and data loggers were used to measure water levels in overland flow and SSF tanks at the south side of the S2 peatland (S2S) every 5 min. Similar systems were installed at the north side of the S2 peatland (S2N runoff collector) during 2010 and at the north side of the S6 peatland (S6N runoff collector) during 2013. The sensor system at S2S was also used to actuate auto-sampling with incremental changes in water heights (0.3 m or about every 30 L of inflow) inside both the overland flow and SSF tanks, resulting in many more samples of overland flow and SSF from the S2S runoff plot than the other three runoff plots.

TABLE 2 Analytes, sampling frequency, and purpose

Lab	Analyte	Frequency	Purpose
Forestry Sciences Laboratory, USDA Forest Service; highest frequency of grab sampling of various waters at the S2 and S6 catchments			
	Total organic carbon (TOC)	Sub-daily to weekly depending, with increasing frequency during snowmelt and stormflow, March-June (2009–2011); n_{bog} = 53, n_{lagg} = 143, $n_{overland}$ = 193, n_{SSF} = 437, n_{stream} = 396	1. Timing patterns, magnitudes, and sources of DOM 2. Calculate TOC yields from peatlands, uplands, and by catchment 3. Show that TOC and DOC are equivalent measures of DOM
	pH	Select samples from those listed above	An ecosystem property that varies among source areas
Aquatic Ecology Laboratory, University of Minnesota; particular waters at the S2 and S6 catchments to assess short- and long-term DOM biodegradability			
	Dissolved organic carbon (DOC)	Select samples: 3/24, 4/19 (2009), 3/16, 3/18, 4/18 (2010), 4/12, 4/18, 4/25, and 28 (2011); n_{bog} = 23, n_{lagg} = 101, $n_{overland}$ = 18, n_{SSF} = 55, n_{stream} = 61	1. Show that TOC and DOC are equivalent measures of DOM 2. Calculation of BDOC and %BDOC
	Bacterial respiration (BR)	Same as previous; n_{bog} = 4, n_{lagg} = 33, $n_{overland}$ = 12, n_{SSF} = 14, n_{stream} = 8	Measure of highly reactive DOM that biodegrades within days
	Biodegradable DOC (BDOC)	Only 2 days (3/24/09 and 4/19/09); $n_{overland}$ = 5, n_{SSF} = 5, n_{stream} = 4	Measure of all DOM that biodegrades over 1 year
	%BDOC	Same as previous	Relative measure of all DOM that biodegrades over 1 year
Aquatic Ecology Laboratory, University of Minnesota; mixing experiment of upland and peatlands waters from the S2 bog			
	DOC	Samples from 4/12, 4/18, 4/25, and 28 (2011); $n_{overland + bog}$ = 4, $n_{loverland + lagg}$ = 4, $n_{SSF + bog}$ = 8, $n_{SSF + lagg}$ = 8	Calculation of BDOC and %BDOC
	BR	Same as previous	Measure of highly reactive DOM that biodegrades within days

Note: Sample numbers (n =) reflect the total numbers that were collected for each laboratory. Some analyses were not possible for every sample due to limited sample volume or analytical issues.

During 2009 and 2010, lagg waters were ladled from pools of standing water at nine or 10 places around the perimeter of the S2 peatland. On several dates during 2010, lagg waters from three to 13 sites in the S6 peatland were sampled. In addition to those synoptic samples, weekly lagg samples were collected from two sites. At the S2N lagg site (adjacent to the S2N upland runoff collector) from 2009 to 2011, lagg water was ladled from a shallow excavation (~20-cm deep) in the peat. Piezometers (5-cm diameter PVC that was screened from 0 to 10-cm depth) were incrementally added during this study to sample near-surface bog or lagg waters when and where there was no standing water. For example, a piezometer was added at the KF5 lagg and the KF45 bog sites during 2010, and at the K5A and KF45A bog sites during 2011 (sites mapped in Figure 1 and names link to published data and metadata in Sebestyen, Funke, et al., 2020).

Concentrations of TOC and pH were measured on unfiltered water samples at the Forestry Sciences Laboratory of the Northern Research Station in Grand Rapids, Minnesota. Methods, instruments, and quality control/quality assurance procedures are detailed in Sebestyen, Funke, et al. (2020). Concentrations of TOC have been measured (instead of DOC) as part of the long-term research program at the MEF. Concentrations of TOC were measured by high-temperature combustion (Standard Method 5310B; APHA 1995) on a Shimadzu (Columbia, MD) TOC-V CPH. Concentrations were measured as total carbon (C) minus inorganic carbon (TC-IC) before June 2010 and as non-purgeable organic carbon afterwards. The two methods are equivalent for the purposes of our study (Sebestyen, Funke, et al., 2020). Every tenth sample was run in duplicate, followed by two reference standards. Method detection limits were 42 μmol C L^{-1} for TOC. For some samples, pH was measured on a Mettler (Columbus, OH) DL53 Auto-titrator using Standard Method 4500-H^+ B (APHA 1995).

3.1 | DOM biodegradability assays

Samples for DOM biodegradation measurements were collected on March 24 and April 19, 2009 from upland runoff collectors, the S2 lagg, and the streams of both catchments. All processing and analyses related to biodegradability measurements were made at the Aquatic Ecology Laboratory at the University of Minnesota, St. Paul, Minnesota. BR rates were measured on additional samples from March and April 2010 (including synoptic samplings in the deciduous S2) and March and April 2011. Though sometimes processed the same day at a field lab (during 2009), unfiltered water samples were usually chilled and stored in polyethylene bottles, shipped overnight, and processed the next day.

Rates of BR were calculated as the total oxygen (O_2) concentration loss over the first 48 hours during dark incubations of unfiltered water in sets of nine 6-ml septum vials without headspace at 4°C. Mercuric chloride ($HgCl_2$, 1% by volume) was added to three vials after 0, 1, and 2 days to stop bacterial activity and preserve samples until analysis. During 2009, the time 0 stopping of BR (with $HgCl_2$) was done at the Marcell Research Center within hours of collection. Dissolved O_2 concentrations were measured on a membrane-inlet mass spectrometer (Bay Instruments, Easton, Maryland) using ultra-pure water (<18.2 MΩ cm^{-1}) in gaseous equilibrium with an air-saturated headspace at 4°C as a reference standard (Kana et al., 1994).

Samples for DOC concentration measurement were filtered through muffled Whatman GF/F filters (0.7 μm nominal pore size) using low vacuum pressure. Samples for DOC analyses were acidified to a pH of 2 and stored in muffled vials at 4°C in the dark prior to measurement.

BDOC was determined by filling 1-L muffled, amber glass bottles with 750 ml of filtered water (muffled 0.7-μm glass fibre filters). Bottles were incubated in the dark at room temperature (22°C) for 1 year with 20-ml subsamples removed at time points of 0, 3, 7, 21, 58, 154, and 370 days to measure changes in DOC concentration over time. At each time point, a bottle was inverted gently to re-aerate the water and prevent oxygen limitation of DOM biodegradation.

Decreasing DOC concentrations over time were plotted to visually determine if DOM degradation had reached a horizontal asymptote within the 370 day incubation period (Supplement 2). Since DOC concentrations for all BDOC measurements were asymptotic, we calculated BDOC concentration as the initial concentration of DOC (highest concentration during the first 3 days of the incubation since there was some minor variability) minus the final concentration of DOC. We also report BDOC as a % of the initial DOC concentration (DOC_i).

Concentrations of DOC, whether initial or later during BDOC incubations, were measured as non-purgeable organic carbon on a Shimadzu TOC-V analyser (Standard Method 5310B; APHA 1995). Concentrations of DOC and TOC were occasionally measured on the same samples. In a comparison of results from the University of Minnesota and the Northern Research Station, DOC_i and TOC concentrations were highly correlated (p << 0.0001) and plotted on a 1:1 relationship (see supplements to Sebestyen, Funke, et al., 2020). Hereafter, while we do specify the specific measure in figures and a data publication (Sebestyen, Funke, et al., 2020), we treat DOC_i and TOC concentrations as equivalent. Method detection limits were 50 μmol C L^{-1} for DOC, and 20 μmol O_2 L^{-1}.

3.2 | DOM-mixing experiment to assess priming

We experimentally mixed waters from different sources to determine if we could detect a priming effect on biodegradation (deciduous S2 catchment, only). We took a different approach than the typical mixing of a water sample with a sugar compound or leachate of organic matter (e.g., leaves or needles). Instead, we variously mixed upland waters (overland flow or SSF) with peatland waters (bog or lagg) as a model of two types of DOM that would naturally mix during transport through peatlands. Upland runoff conceptually corresponds to DOM that is freshly solubilized from deciduous leaves, roots, and other organic matter when the forest floor is wetted during snowmelt or rainfall. Overland flow chemistry differs from that of SSF because overland flow has less contact with mineral soil surfaces that absorb DOM than SSF (Kaiser & Guggenberger, 2000; Kaiser et al., 2002). Both overland flow and SSF are circumneutral (pH = 5.2–6.4; Figure S1). Peatlands, with permanent, near-surface saturation and a lower pH (pH = 3.8–4.4), have a DOM pool comprised of *Sphagnum* leachates, evergreen vegetation exudates, and a large amount of humic DOM that is solubilized from recently formed to centuries-old peat. These mixtures are representative of natural processes. During and following stormflow events that transport upland runoff to laggs, bog and upland waters mix in laggs at the interface between upland oxic conditions and peatland acidic, anoxic and saturated conditions (Verry et al., 2011; Verry & Janssens, 2011).

Water samples were collected from overland flow and SSF in the upland runoff collectors and from standing water in the lagg and bog of the deciduous S2 catchment on April 12, 18, 25, and 28 during 2011. All samples were collected when possible, but overland flow and SSF did not occur on all dates. Mixing experiment samples were shipped overnight and processed the next day at the Aquatic Ecology Laboratory. Water samples were filtered through 0.2 μm nominal pore-size filters (Millipore) to remove >95% of bacterial cells (Biddanda et al., 2001). Additional lagg and bog water aliquots were filtered through Whatman GF/B filters, which allowed substantial microbial passage (1.6 μm nominal pore size). The bog water microbial inoculum was added to samples with bog water and the lagg water inoculum was added to samples with lagg water to reflect the dominant microbial community and acidic waters of the peatland into which upland runoff mixed. In the laboratory, we examined BR rates in upland (overland flow or SSF) and peatland (lagg or bog) runoff mixed 1:1 (in triplicate) and on upland and peatland runoff alone (in triplicate) for a total of 24 mixed and 50 field samples: overland flow + lagg (n = 4), overland flow + bog (n = 4), SSF + lagg (n = 8), SSF + bog (n = 8), overland flow, SSF, lagg, and bog. Mixtures and individual waters were amended with ~40 μmol monopotassium phosphate (KH_2PO_4) L^{-1} and ~630 μmol ammonium chloride (NH_4Cl) L^{-1} based on an estimated average DOC concentration of ~4200 μmol C L^{-1} for most samples, for an approximate final C:nitrogen:phosporus of 106:16:1 (Redfield, 1958) to minimize nutrient limitation of BR (Cotner et al., 2000). Rates of BR were measured and calculated as previously described.

3.3 | Apportionment of streamflow into bog and upland runoff and solute yield calculations

We applied a hydrograph separation approach that was previously developed for the S2 catchment (Timmons et al., 1977) to estimate runoff from peatland and upland areas of both catchments. Briefly, we isolated streamflow values from all days on which streamflow was less than that on the preceding day. Then, using sensor-derived daily upland runoff values (Sebestyen & Kyllander, 2018), we identified days on which streamflow recession and overland flow or SSF occurred. We used a correlation-type recession analysis (Eckhardt, 2008; Langbein, 1938) to determine the recession equations for periods when there was streamflow from peatland and upland runoff, and periods when there was streamflow from only peatland runoff. Using the relationships (specific to each catchment), we calculated daily amounts of streamflow that originated from peatland runoff. Then, we subtracted the daily peatland runoff estimates from daily streamflow to estimate daily upland runoff. For the S2 catchment, where overland flow and SSF were logged on both north- and south-facing hillslopes during 2010 and 2011, we further apportioned upland runoff into overland flow and SSF components by multiplying the fraction of daily flow that occurred as overland flow or SSF times the upland runoff amount. Since there were no logged data from the north-facing hillslope in S6, we only report runoff, not the apportioned amounts of overland flow and SSF. Details and data are provided in two data publications (Sebestyen & Kyllander, 2017; Sebestyen & Kyllander, 2018).

We calculated TOC exports and yields (area-weighted exports) from peatlands, uplands, and both catchments, as described in Supplement 3. For the deciduous S2 catchment, we further apportioned upland TOC exports and yields into both overland flow and SSF. For the deciduous S6 runoff catchment, we calculated TOC export and yield for upland runoff. Further apportionment into overland flow and SSF for the S6 catchment was not possible because there only was logged data from one of the two runoff collectors.

3.4 | Data analysis

To show the variation of TOC and nutrient concentrations over time and compare source areas and catchments, we focus our narrative on snowmelt and spring of 2011 when weekly samples of lagg and bog waters (in S2) were collected in addition to upland runoff waters (measured 2009–2011 in both catchments). We include data for 2009, 2010, and 2011 in tables, figures, and supplements (Sebestyen, Funke, et al., 2020; Sebestyen & Kyllander, 2017).

Correlations were tested to determine if relationships existed between chemical and biodegradability parameters. Probabilities (*p* values) less than $\alpha = 0.05$ were considered statistically significant. A Pearson's correlation coefficient (*r*) is provided for each regression.

We visually compared the concentrations, BR rates, and BDOC (concentrations and as a % of DOC_i) by water type (overland flow, SSF, lagg, stream), catchment (deciduous, conifer), and date (3/24 or 4/19, 2009). We did not test for differences because there were only one or two samples (no upland runoff samples during times of no upland runoff) within each category for biodegradation measurements.

With many more samples for BR rate measurement among the various water types and over many dates, those samples spanned baseflow to stormflow (0–0.7 cm day^{-1}), but not the full range of streamflow (0–1.1 cm day^{-1}). Though collected for exploratory purposes rather than statistical testing, we used these data to demonstrate how BR rates varied with catchment wetness. With mixed sample numbers by water type and catchment, in addition to pseudoreplication over time, these data were not amenable to statistical testing.

Effects of mixing upland and peatland waters were assessed based on a weighted average of the measured BR rates for the different source waters and the 1:1 proportion in which they were mixed. We compared the measured BR rates of the mixture assuming conservative mixing (i.e., no stimulation of BR rate due to mixing), normalized to DOC_i concentration. A relative effect of ~0% indicated that the BR rate of DOM from a particular water type did not affect the rate for DOM in the mixture, meaning that no priming effect was observed. Stimulation of BR rates was considered to have occurred when the observed BR rate on a mixed sample was statistically ($p < 0.05$ in a two-tailed T-test) greater than BR calculated for conservative mixing of various DOM sources.

4 | RESULTS

During 2011, there was one major snowmelt peak on April 11 in response to a rain-on-snow event, followed by several smaller peaks during mixed rain and snow events (Figure 2). The apportionment of runoff from peatlands and uplands through recession analysis (Figure 2(b)) and monitoring of upland runoff plots (Figure 2(c-d); Table S1) showed that upland runoff was a source of water to the stream on some, but not all days of stormflow events. Runoff of SSF (3956 m^3 over 63 days) was 33× larger in magnitude and 4× longer in duration than overland flow (119 m^3 over 15 days).

The ranges and magnitudes of DOC concentrations were highest when streamflow was low, and decreased during higher streamflow and when there were inputs of upland runoff (Figures 3 and 4). On the days (67%) that daily stream TOC concentration was greater, daily stream TOC concentration was 1.2× higher in the deciduous catchment than in the coniferous catchment. Stream TOC concentrations (4766 ± 1170 μmol L^{-1}, n = 386) were similar to concentrations in bog (4424 ± 1384 μmol L^{-1}, n = 49) and lagg waters (4883 ± 1860 μmol L^{-1}, n = 141) in both catchments. In general, ranges of TOC concentrations were narrower, and concentrations were lowest in SSF (1724 ± ;771 μmol L^{-1}1, n = 437; Figures 3(e) and S2).

TOC exports (Figure 5; Table S2) and yields (Figure S3) were larger in stream, peatland, and upland waters draining the deciduous catchment than the coniferous catchment. Most streamflow originated from peatland runoff, rather than upland runoff, in the deciduous (72% of stream water) and coniferous (73%) catchments (Figure 5; Table S2) even though the catchments are mostly upland by area (67% at S2 and 78% at S6).

Bog waters were more acidic (pH from 3.8 to 4.3) than upland waters (pH from 5.2 to 6.4 aside from one low value of 4.1; Figure S1). Lagg and stream waters (pH from 3.8 to 5.7) in the deciduous S2 catchment spanned most of the pH ranges of bog and upland runoff waters.

4.1 | DOM biodegradability

For the subset of samples that were collected on March 24 and Apr 19, 2009 from both catchments to determine DOM biodegradability,

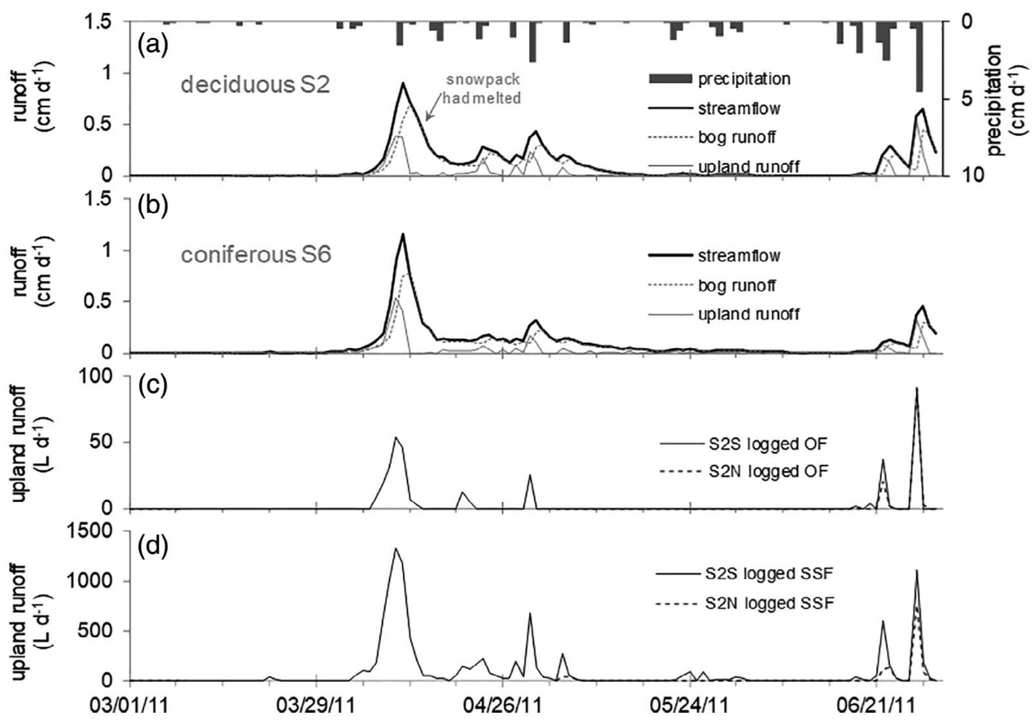


FIGURE 2 (a) Precipitation and streamflow, apportioned peatland runoff, and apportioned upland runoff in the (a) S2 and (b) S6 catchments, and (c) upland overland flow (OF) and (d) SSF volumes from the S2 runoff collectors. Upland runoff was not logged in the S6 catchment during 2011

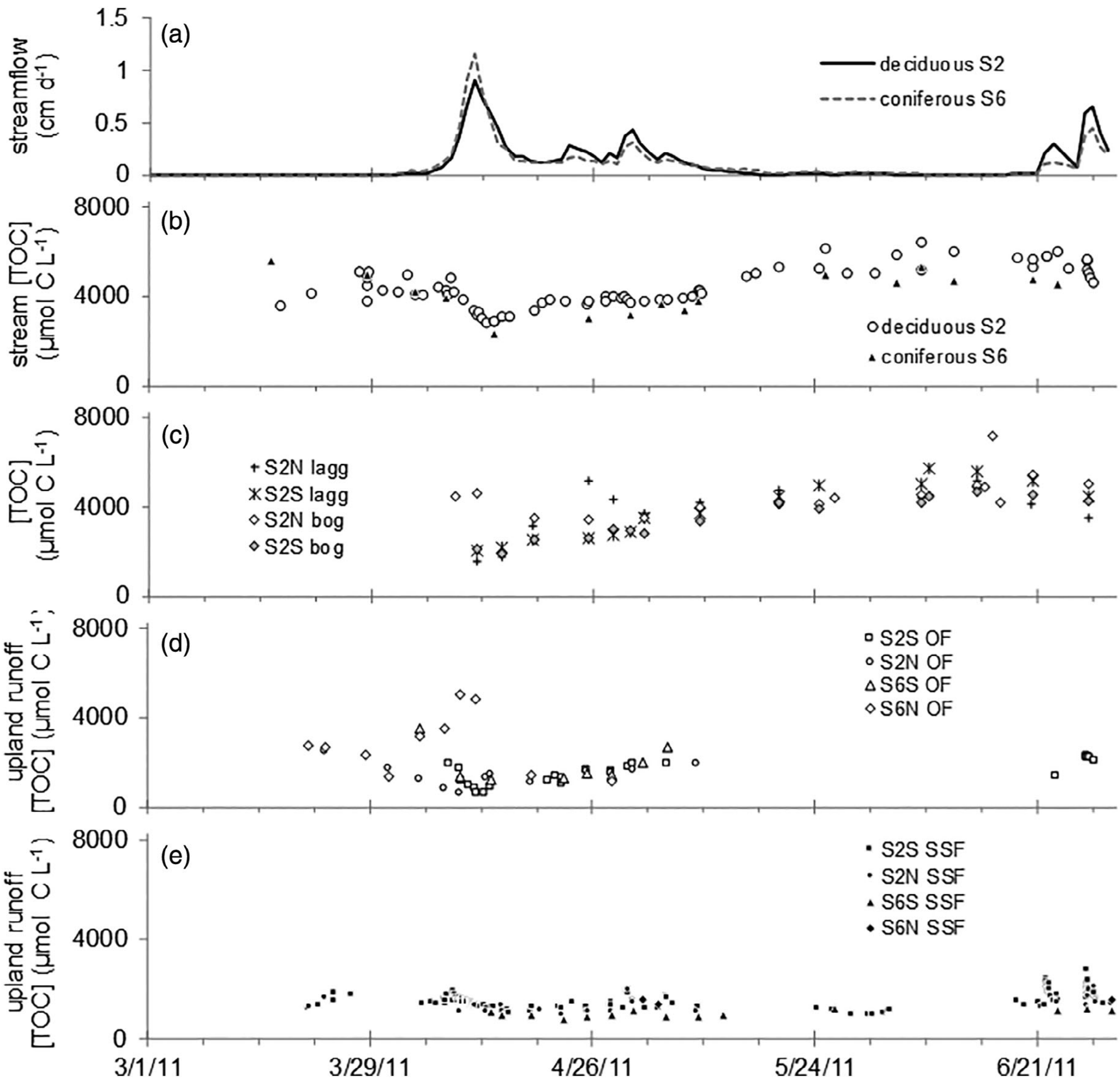
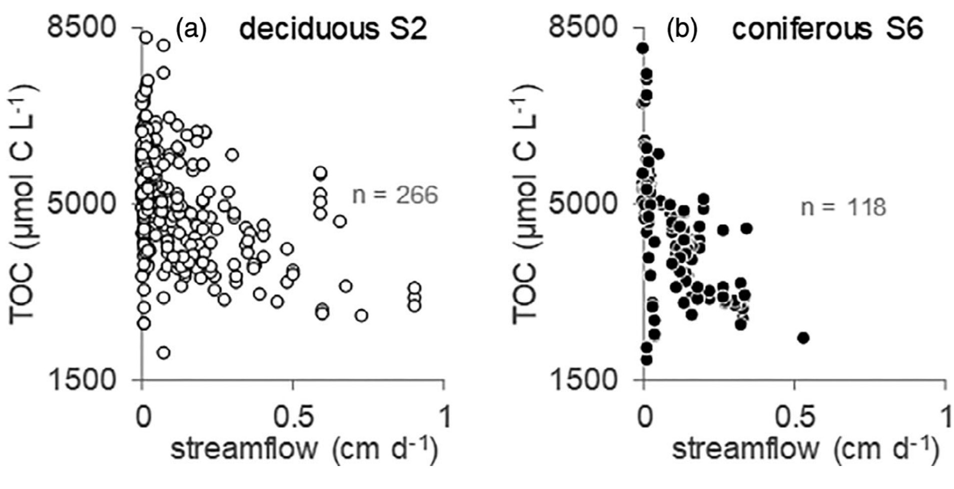


FIGURE 3 (a) Streamflow, and (b–e) TOC concentrations in (b) stream, (c) lagg and bog, (d) upland overland flow (OF), and (d) upland SSF waters for the S2 (deciduous upland cover) and S6 (coniferous upland cover) catchments during and after snowmelt 2011

FIGURE 4 Bivariate plots of TOC concentrations in stream waters versus streamflow in (a) the deciduous, and (b) coniferous catchments. Samples are from both catchments from 2009 to 2011



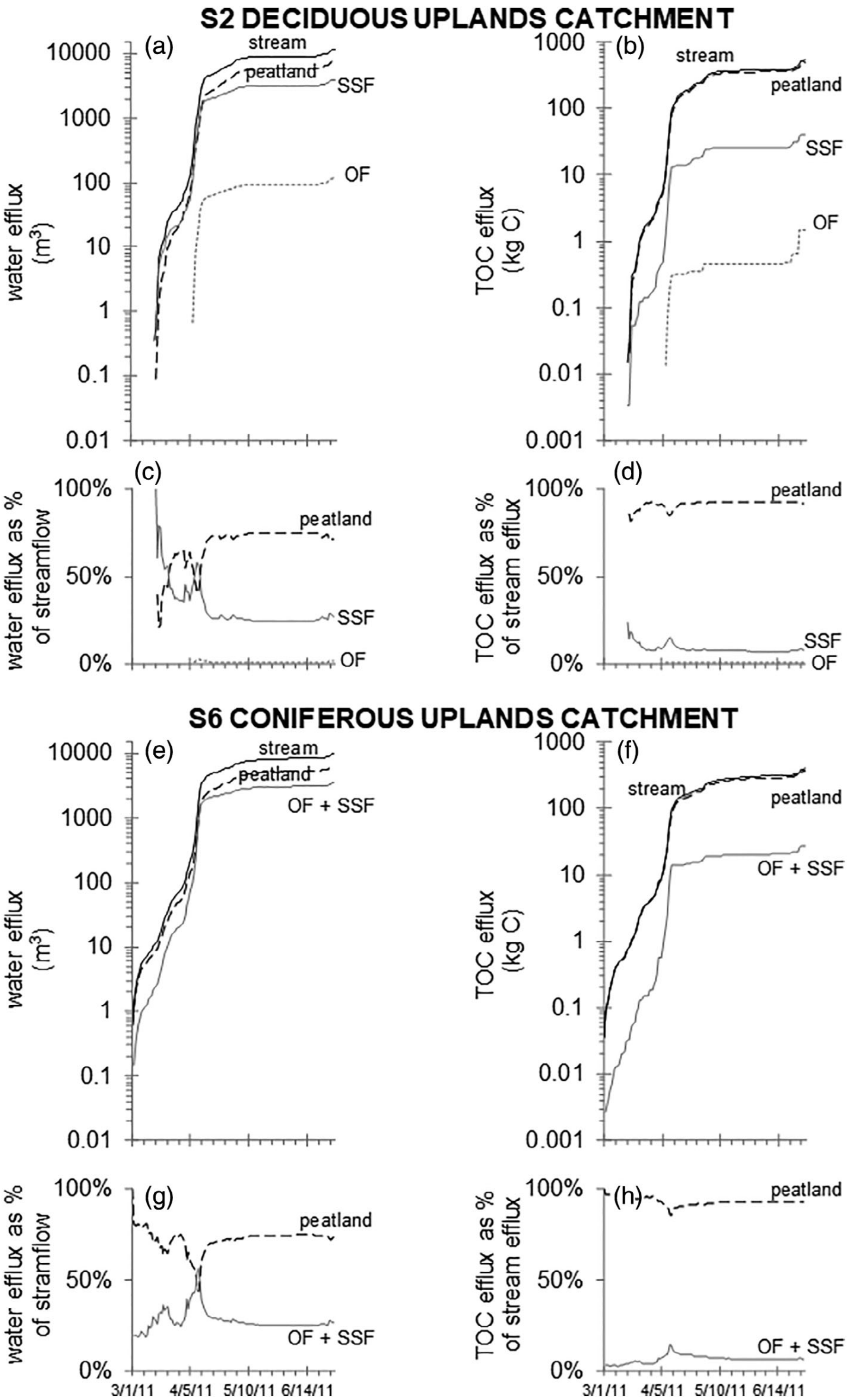


FIGURE 5 Catchment exports of (a, e) water and (b, f) TOC in stream, peatland runoff, and upland runoff waters of the (a–b) S2 deciduous and (e–f) S6 coniferous catchments from March 1 to June 30, 2011. In some panels, the stream and peatland lines have overlapping portions. Panels (c–d, g–h) show the percentages of exports from peatland and upland source areas. The exports from S2 uplands are apportioned into overland flow (OF) and SSF, while exports from S6 uplands are shown as upland runoff (OF + SSF)

initial DOC concentrations were lowest in SSF (730–1800 μmol C L^{-1}), higher in overland flow (970–2900 μmol C L^{-1}), somewhat higher in lagg water (1600–2500 μmol C L^{-1}), and highest in stream water (2500–4100 μmol C L^{-1}; Figure 6).

BR rates were lowest in SSF (0.6–1.5 μmol O_2 L^{-1} day^{-1}), higher in lagg water (2.4–7.2 μmol O_2 L^{-1} day^{-1}), stream water (0.6–5.4 μmol O_2 L^{-1} day^{-1}), and overland flow (3.9–17.4 μmol O_2 L^{-1} day^{-1}; Figure 6(b)). Rates of BR were at least 2× higher in stream water of the coniferous catchment than the deciduous catchment on each date. In addition, BR rates were greater in overland flow of the coniferous catchment than in overland flow of the deciduous catchment on both sampling dates, March 24 and April 19.

Concentrations of BDOC were lowest in SSF (69–125 μmol C L^{-1}) compared with lagg (234–378 μmol C L^{-1}), overland flow (219–566 μmol C L^{-1}), and stream (263–594 μmol C L^{-1}) waters (Figure 6). In March, BDOC in the stream of the coniferous catchment (594 μmol

C L^{-1}, 23% of DOC_i) was greater than BDOC in the deciduous catchment (372 μmol C L^{-1}, 9% of DOC_i), with opposite, though marginal differences during April.

The different measures of biodegradation, BR rate for short-term degradability and BDOC for long-term degradability, were positively correlated (Figure 7). Despite considerable variation around the regression line and one sample with a considerably higher BR rate than the rest, the correlation between BDOC concentration and BR rate was significant whether the highest BR value was included in the correlation (r = 0.61, p = 0.009) or not (r = 0.75, p = 0.0009). The correlation between %BDOC and BR rate was only significant when the highest BR value was included in the correlation (r = 0.73, p = 0.001).

Rates of BR were not correlated with TOC or TN concentrations (Figure S4). Concentrations of BDOC and TOC were positively correlated (slope = 0.1, p = 0.002; Figure 8). Considering all waters from many different dates, BR rates were highest and most variable when streamflow was lowest (Figure 9). Rates of BR were lower and less variable at higher streamflow.

4.2 | Mixing experiment

There was no detectable stimulation of BR in peatland waters (bog or lagg) when mixed with upland waters (overland flow or SSF;

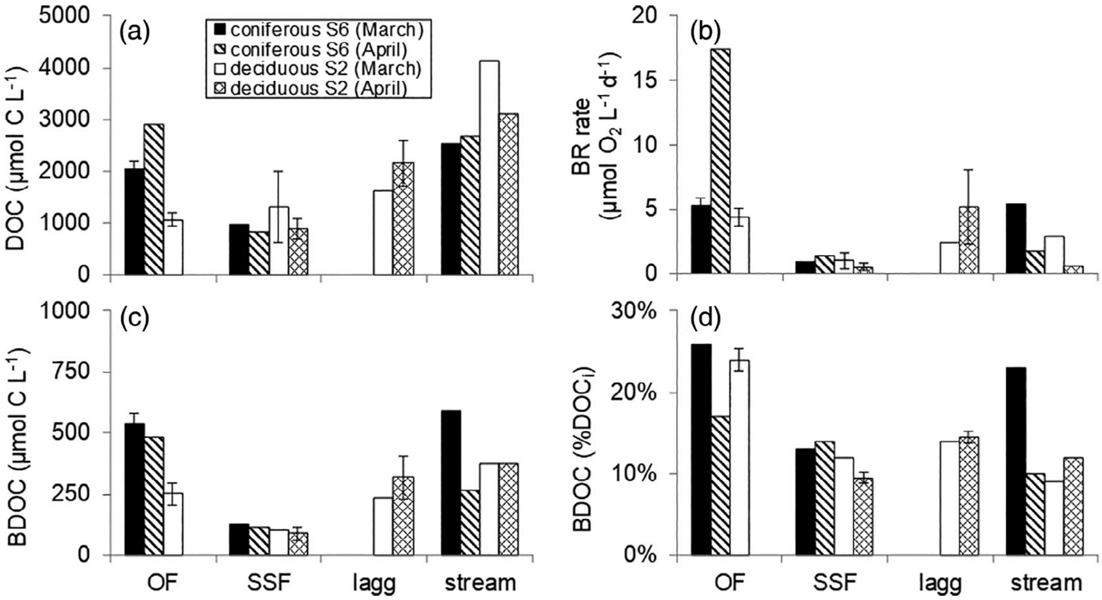


FIGURE 6 (a) Dissolved organic carbon concentration, (b) BR rate, (c) BDOC concentration, and (d) BDOC as % initial DOC concentration (% DOC_i), by location (overland flow, SSF, lagg, and outlet) and by catchment upland forest cover type. Error bars, when present, show ±1 standard deviation of the mean of two values when it was possible to sample from north and south locations (upland overland flow and SSF; not streams)

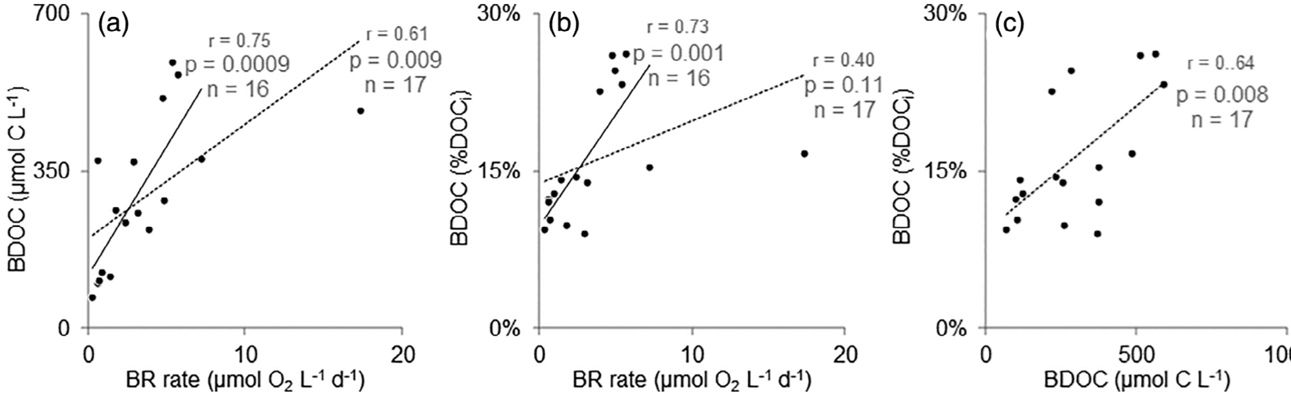


FIGURE 7 Bivariate plots of (a) BDOC concentration versus BR rate, (b) BDOC as a percent of initial DOC (%DOC_i) versus BR rate, and (c) % BDOC versus BDOC concentration. Lines show correlations: The hashed trendline includes the highest BR rate value (17.4 μmol O_2 L^{-1} day^{-1}) while the solid trendline excludes that highest value. Data from both catchments, all water types, and two dates (March 24 and April 19, 2009) are shown

Figure 10). Mixing bog waters with overland flow (–0.07% ±0.15%) and SSF (–0.06% ±0.07%) waters resulted in a non-significant inhibition of BR rate normalized to DOC_i concentration averaged over the four sampling dates (April 12, 18, 25, 28). Mixing lagg water with overland flow and SSF waters resulted in a non-significant stimulation of BR rates that were normalized to DOC_i concentrations (+0.01% ±0.05% and +0.06% ±0.02%, respectively) averaged over the four dates.

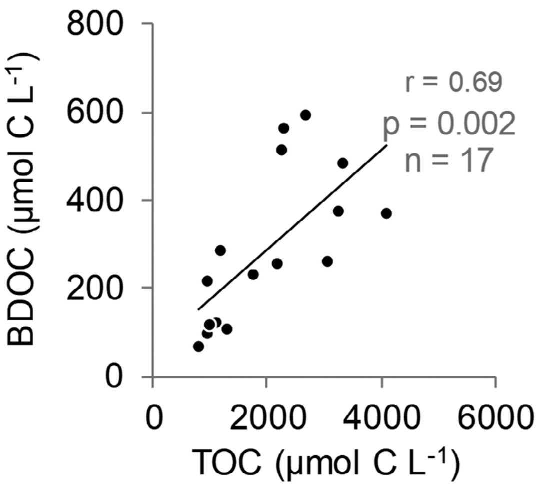


FIGURE 8 Correlation of BDOC with TOC concentration. Data from both catchments, all water types, and two dates (March 24 and April 19) are shown

5 | DISCUSSION

Understanding export, yields, and interactions of DOM from different sources is critical to quantifying the role of peatlands in local landscapes as well as the global carbon cycle. Here, we compared DOM concentrations and biodegradability among various waters for two catchments with peatlands (forested bogs) and different upland forest cover types and soils. Importantly, the landscape has been forested since revegetated after the last glaciation (Verry & Janssens, 2011), the peatlands have not been hydrologically or biogeochemically affected by anthropogenic drainage (Holden et al., 2004), and similar headwater peatlands are abundant throughout the region and the boreal peatland zone. Other studies of DOM biodegradability or composition in peatland landscapes have included: other peatland types

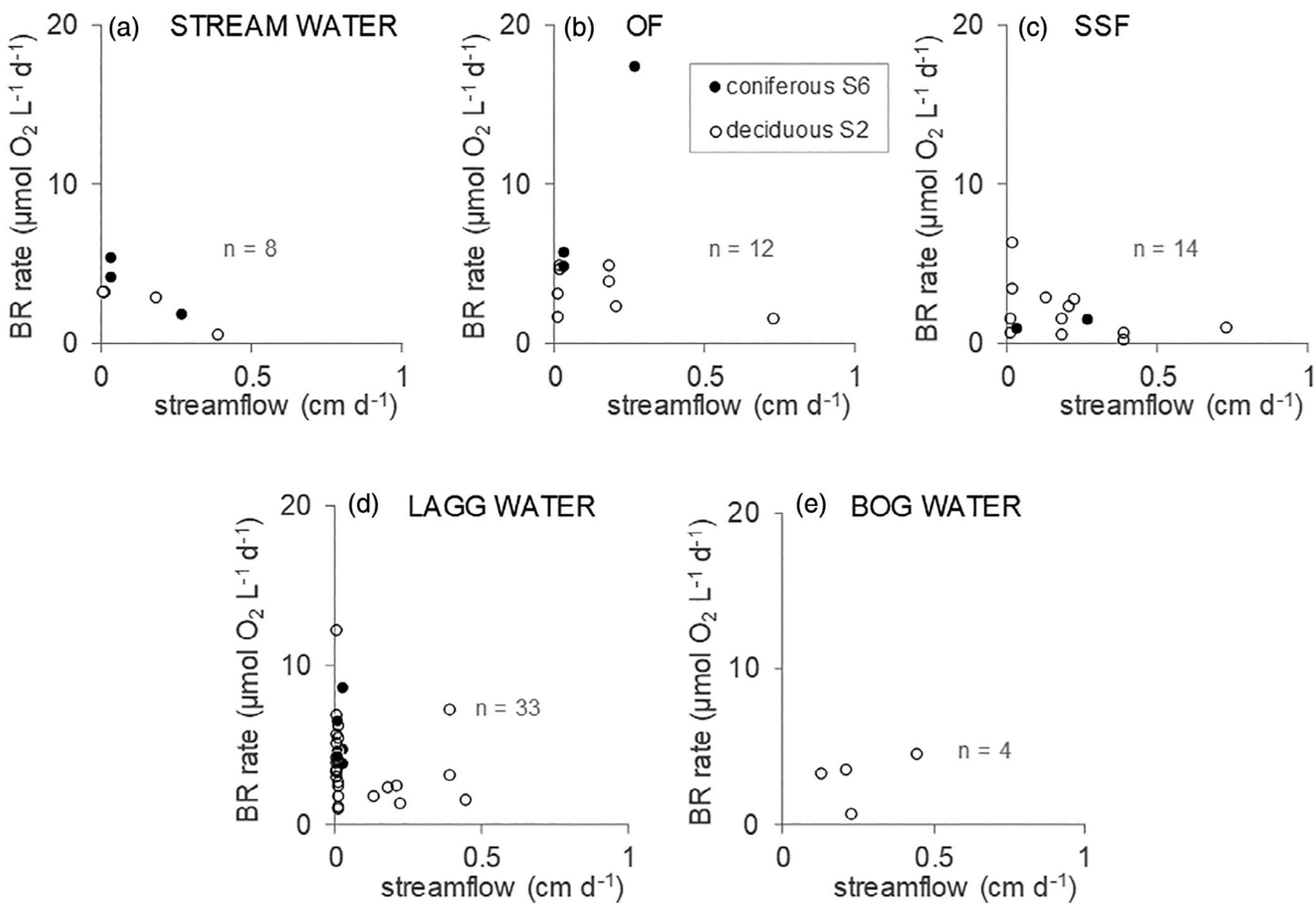


FIGURE 9 Bivariate plots of BR rate versus streamflow for (a) stream, (b) overland flow, (c) SSF, (d) lagg, and (e) bog water. BR rates were highest and most variable during low streamflow, indicative of the effect of increased upland contributions of water with increasing catchment wetness. Samples were collected in both catchments on various dates from 2009 to 2011

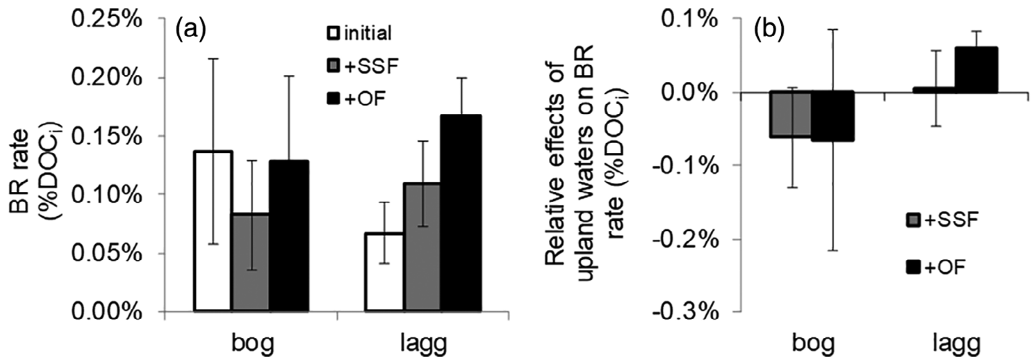


FIGURE 10 (a) Bacterial respiration rate normalized to initial DOC (DOC_i) concentration for bog and lagg waters and those waters mixed with SSF (bog or lagg water with SSF) and overland flow (bog or lagg water with overland flow). (b) Effects of mixing upland and peatland waters presented as the relative difference between the predicted BR rate and measured BR rate of the mixed DOM. A relative effect of ~0% indicates that the BR rate of the individual DOM components was the same as the mixed DOM components and therefore no priming effect was observed. Mixing effects were not statistically significant (i.e., no difference from zero or between mixtures due to high variability among samples)

(i.e., minerotrophic vs. our ombrotrophic) with and without forests, higher stream orders (≥1), anthropogenic drainage, relatively recent land-use changes, effects of impounded water, or permafrost (Ågren et al., 2008; Berggren et al., 2010; Berggren et al., 2009; Clark et al., 2007; Hribljan et al., 2014; Shirokova et al., 2019; Vonk et al., 2015; Wallin et al., 2015; Wickland et al., 2012). Our study of catchments at the MEF with undrained, forested bogs and no permafrost is distinct from those studies. Accordingly, our research fills a gap for widespread and similar, yet understudied landscapes along the southern boundary of boreal peatland zone. This zone of peatlands is also expected to be particularly vulnerable to effects of climate change (Bridgham et al., 2008; Gorham, 1995; Hanson et al., 2020; Hopple et al., 2020; Tarnocai & Stolbovoy, 2006).

In our study, most TOC originated from peatland runoff in both the deciduous (92% of stream TOC) and coniferous (93%) catchments. Concentrations and DOM biodegradation rates were highest during low flow when water and DOM wholly or mostly originated from the bogs (Figures 4 and 9). Both peatlands were also mostly bog by area. Therefore, bogs were the predominant DOM sources and had larger effects on stream DOM concentrations and biodegradability than laggs or uplands.

Stream TOC concentration was associated with variation in streamflow, especially when peatland TOC concentration was diluted with inputs of less concentrated upland runoff. Of the upland inputs, overland flow was a particularly small source of stream water (<2%) and TOC (<0.4%; Table S2). Upland runoff occurred on fewer days than peatland runoff (Figures 2 and 5; Table S2). For example, upland runoff was 4075 m^3 over 61 of 122 days versus peatland runoff of 7894 m^3 over 113 days in the deciduous S2 catchment. Furthermore, upland runoff was mostly in the form of SSF. Larger relative and absolute amounts of runoff from the peatlands than the uplands reflect the effect of downslope drainage and a large potential storage volume that needs to be refilled before upland runoff occurs. By contrast, bogs have permanent, near-surface saturation and rapid runoff generation through surficial peat to the stream (Verry et al., 2011). The routing of bog water along surficial flowpaths corresponds to most decomposition, production, and leaching in shallow peat (i.e., the acrotelm; Beer et al., 2008; Moore & Basiliko, 2006; Sebestyen, Dorrance, et al., 2011; Tfaily et al., 2014; Wilson et al., 2016). Finally, there was no evidence of upland DOM priming biodegradation of bog or lagg DOM.

Beyond differences in exports of water and DOM that led to peatlands being larger sources of biodegradable DOM than uplands, there were differences in biodegradability among runoff types (Figure 6). In general, DOM biodegradation rates vary by orders of magnitude over time and space (Fellman, Hood, D'Amore, et al., 2009; Fellman, Hood, Edwards, et al., 2009; Guenet et al., 2010; Vonk et al., 2015; Wickland et al., 2012). We observed greater BR rates, BDOC concentrations, and %BDOC in overland flow than in SSF, lagg, or stream waters. Assuming a respiratory quotient of CO_2 to O_2 of 0.8 from Biddanda et al. (2001), our estimates of CO_2 production rates due to BR (0.2–13.9 μmol C L^{-1} day^{-1}) were of similar magnitude to previously published means of BR rates in streams of boreal forested catchments (5.5–15.9 μmol C L^{-1} day^{-1}; Berggren et al., 2007, 2009). The range of %BDOC for all of our samples (9% to 26% of DOC_i, Figure 5(d)) was similar to %BDOC reported for many lakes and rivers (Coble et al., 2019; del Giorgio & Davis, 2003; Søndergaard & Middelboe, 1995; Stets & Cotner, 2008; Vonk et al., 2015) and for peat and forest floor extracts (4%–9%; Kalbitz et al., 2003). Biodegradability of DOM from these peatlands at the southern margin of the boreal peatland zone is strikingly different from peatlands in the permafrost region where DOM was not bio- or photo-degraded during a 1-month incubation (Shirokova et al., 2019).

Despite considerable variances, short-term and long-term biodegradation were positively correlated (Figure 7). For BR rate, there were many more measurements over time and across a range (0–0.7 cm day^{-1}) of streamflow values. Those data show that BR rates were highest when streamflow was low, and the variance and magnitude of BR rates decreased as streamflow increased. The highest TOC concentrations and BR rates at low flow, when upland runoff was low or not occurring, reinforce the importance of the bog as a biodegradable DOM source and reiterates that the upland DOM sources had limited volumetric or kinetic effects on the biodegradation of bog, lagg, or stream DOM.

We did not observe any stimulation of BR rates when lagg or bog waters were mixed with overland flow or SSF waters (Figure 10). Others have considered upland DOM to have important effects on biodegradation of peatland DOM (Berggren et al., 2007; Berggren & del Giorgio, 2015; Freeman et al., 2001; Mitchell et al., 2008), which is why we experimented in the lab to determine if mixing of peatland and upland waters resulted in a priming effect on biodegradation. Our findings are similar to studies finding no priming effect in freshwaters (Bengtsson et al., 2014; Catalán et al., 2015). Our findings also contrast with Hotchkiss et al. (2014), whom found that additions of soil leachates, glucose, and algal leachates sometimes, but not always caused a priming effect on DOM biodegradation in river waters of the western and midwestern United States. While we do not know why priming only occurs sometimes, it may relate to intrinsic properties such as nutrient availability in the background matrix (Wagner et al., 2014; Wickland et al., 2012) and differences in DOM produced as plant tissues decompose (Enríquez et al., 1993; Farjalla et al., 2009; Webster & Benfield, 1986). While the residence time of water in SSF is unknown, DOM does contact mineral surfaces and microbial communities in the subsurface of upland soils. Therefore, some of the upland DOM may have degraded or sorbed to mineral surfaces before the mixing experiments since there likely was significant processing of leaf leachate and root exudates (Wang et al., 2019) in typically unsaturated mineral soils before event-scale wetting and lateral transport through the soils. In addition, lagg DOM may already have been mixed with and stimulated by upland DOM by the time we sampled so that any further addition of upland DOM in the lab would not have resulted in a priming effect. Despite no priming effect, it is important to note that BR occurred, indicating that there was still biodegradable DOM in the samples despite a 1-day lag from sampling to the start of the experiment due to transport to the lab.

Contrary to our hypotheses, we did not observe DOM that was more biodegradable in a stream draining a catchment with deciduous uplands than from one with coniferous uplands. The catchment with deciduous upland cover yielded more DOM (Figure S3) and DOM that was either as, or less biodegradable than that from the coniferous upland (depending on date and degradability measure; Figure 6). Similar to our comparison of runoff waters from deciduous and coniferous forests, Don and Kalbitz (2005) observed higher rates of DOM mineralization in leachates from spruce and pine litter than from maple and ash litter. Overall, these findings do not fit typical conceptions of how deciduous versus coniferous forest covers affect downstream DOM. For example, we expected but did not observe higher TOC concentration downstream of the coniferous forest (Cronan & Aiken, 1985). We cannot rule out confounding factors such as differences in peatland geometry (long and narrow vs. ovoid in shape, Figure 1), dominant upland vegetation type, or soils. For example, soils in the coniferous forest were sandier, with less loam than the deciduous forest. The differences in soil texture may have caused more mineral surface contact for SSF in the deciduous catchment, with enhanced capacity for DOM absorption and degradation during water transit through upland soils relative to the coniferous forest. Forest floor DOM is typically less degraded than DOM from the subsoil (Qualls & Haines, 1992) because DOM degrades or sorbs to mineral surfaces during transport to lower soil horizons (Thurman, 1986).

6 | CONCLUSIONS

Northern and boreal catchments may include lowland peatlands and mineral soil uplands, with both land areas having distinct compositions, concentrations, and downstream yields of DOM. Accordingly, knowledge of aquatic DOM concentrations, yields, biodegradation, and priming effects from each area is important to a basic understanding of DOM processing in those catchments. The peatlands were only a small factional area of the two studied catchments (10%–30%), yet had overriding effects on C transport and processing relative to uplands. We found BR of DOM and BDOC in peatland runoff to be similar to subsurface runoff from upland mineral soils. However, DOM biodegradation was highest when TOC concentrations were highest, TOC concentrations were highest when streamflow was lowest, and the uplands were not sources of stream TOC when streamflow was lowest. The results demonstrate that peatland runoff, which accounted for most water (70%–80%) and DOM (92%–96%) in the stream, had more important effects on stream DOM biodegradability and whole-catchment DOM yields than inputs of upland runoff or differences in upland forest cover and soils. Ultimately, bogs as sources of DOM and how their carbon cycling processes change with climate will affect whether C is stored in the atmosphere as carbon dioxide or downstream in lake sediments as particulate carbon. Consequently, changing climate has implications for DOM downstream of peatland catchments. Until recently, peatland C transport and cycling processes were not explicitly represented in global climate models (Anderson et al., 2019; Limpens et al., 2008; Ricciuto et al., in press; Schmidt et al., 2011; Shi et al., 2015). Beyond an improved understanding of how connectivity of uplands and peatlands affects carbon cycling and transport, even a null result, such as our finding of no priming effect of upland DOM on peatland or downstream DOM biodegradation, is important when considering what and how to represent peatland catchments and carbon cycling processes in these models.

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DATA AVAILABILITY STATEMENT

Data collected for or used in this research have been released via freely accessible stable repositories, as cited in the article and supplements. Each data publication is accessible via a DOI as listed in the references.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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