



Landscape regulation of microbial use of terrestrial carbon in boreal streams

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Received: 15 June 2023 / Accepted: 25 December 2023
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Abstract

Microbes decomposing leaf litter in aquatic ecosystems are exposed to two major sources of carbon (C), namely, particulate organic C (POC) and dissolved organic C (DOC). The use of DOC relative to POC during litter decomposition likely depends on the availability of DOC, which in turn is regulated by the characteristics of the surrounding landscape, although this extrinsic indirect control of DOC use remains largely unexplored. We have investigated how variations in stream physical and chemical characteristics, distribution of major landscape elements (i.e., forest, mires, and lakes), and riparian vegetation community composition (i.e., relative cover of deciduous vs. coniferous tree species) influence DOC use by leaf-associated microbes (LAM). Specifically, in a boreal stream network of ten first- to third-order streams, we related in-stream characteristics, landscape elements, and riparian vegetation community composition to DOC/POC respiration ratios (i.e., the amount of CO₂ produced by LAM respiration of DOC + POC divided by the amount of leaf C mass lost through decomposition). The results showed that DOC/POC respiration ratios were > 1 in most of the study sites, indicating that LAM use a substantial amount of DOC during leaf litter decomposition. This microbial reliance on DOC varied with in-stream DOC and nutrient concentrations, proportional mire and forest cover, and riparian vegetation community composition. In particular, high mire and coniferous cover increased DOC use by LAM. As such, landscape configuration and how it is modified by land use and climate change must be considered in order to understand microbial turnover of terrestrial C in boreal streams.

Keywords DOC/POC respiration ratio · Microbial respiration · Krycklan Catchment Study · Landscape organization · CO₂ production

Introduction

Landscape characteristics, such as catchment size and type of land cover, together with season and climate, influence the ways in which streams interact with terrestrial surroundings by controlling the availability and quality of the two major sources of terrestrial carbon (C), i.e., particulate organic C (POC), mainly composed of leaf litter, and dissolved organic C (DOC) (Berggren et al. 2007; Kominoski et al. 2011; Bastias et al. 2022). Leaf-associated microbes (LAM; mainly fungi and bacteria) play an important role in decomposing terrestrial C (Webster and Benfield 1986;

Webster et al. 2009); however, although it often is assumed that LAM preferentially acquire leaf C, some recent studies indicate a potential for DOC use (Pastor et al. 2014; Emilson et al. 2017; Bastias et al. 2020). The use of DOC during leaf decomposition could stimulate microbial heterotrophic reliance on exogenous (i.e., from the water column) C yet suppress decomposition of recalcitrant leaf C, modifying nutrients available to higher trophic levels and enhancing organic C storage or export (Halvorson et al. 2019; Bastias et al. 2020). DOC availability may indeed regulate the extent to which LAM use C from DOC, but few studies have attempted to quantify the relative importance of these two C sources to LAM. Further, as in-stream DOC availability often is regulated by the surrounding terrestrial landscape, large-scale catchment-scale drivers may also determine LAM use of DOC; however, this has not yet been fully investigated. Hence, to obtain a better understanding of C cycling in forested streams, landscape controls of microbial

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leaf C and DOC use during leaf decomposition deserve further attention.

Recent studies using radiolabeling techniques (i.e., ^{13}C) suggest that DOC can be an important energy source to LAM (Pastor et al. 2014; Abril et al. 2019; Bastias et al. 2020). Bastias et al. (2022) observed that microbial DOC use increased throughout the decomposition process concurrently with decreasing litter decomposition rates. This shift is likely due to a rapid depletion of simple C sources, such as carbohydrates, polysaccharides, and amino acids, in the litter and subsequent increased concentrations of complex C-polymeric compounds, such as cellulose, hemicellulose, and lignin, as litter decomposition proceeds (Webster and Benfield 1986; Chauvet et al. 1987), making ambient DOC an increasingly attractive and, thereby, important C source (Bastias et al. 2020). In-stream DOC mostly originates from terrestrial surroundings, and its availability and chemical composition are governed by physical, hydrological, and biogeochemical characteristics of the drainage network (Bertilsson and Tranvik 2000; Laudon et al. 2004), with organic-rich riparian soils (Ploum et al. 2020) and mires (Laudon et al. 2011) being the main contributors. The type and spatial configuration of surrounding terrestrial landscapes are therefore likely important drivers of microbial in-stream use of terrestrial C, but this subject remains largely unexplored.

In the boreal region, complex spatial networks of major landscape elements, such as streams, lakes, and mires, surrounded by forests regulate in-stream physical and chemical characteristics, including the availability and chemical composition of DOC (Laudon et al. 2004, 2011; Ploum et al. 2020), with potential effects on the way in which LAM use C from different terrestrial sources. In this region, mire-dominated catchments export more terrestrial DOC than forest-dominated catchments, especially during baseflows (Laudon et al. 2004). Organic-rich forest soils contribute DOC of a lower degree of aromaticity and molecular weight, which is more easily degraded by microbes (i.e., high-quality DOC) than DOC originating from headwater mires, which is more resistant to microbial degradation (i.e., low-quality DOC) (Berggren et al. 2007, 2010; Petrin et al. 2007). However, a high availability of low-quality DOC could still enhance LAM activity (Romani et al. 2006; Bastias et al. 2022) if certain species in the LAM community have the metabolic capability to degrade low-quality DOC. In addition to DOC, nutrient availability in the water column is regulated by catchment-scale processes (Sponseller et al. 2014), and mires play a relevant role in providing reduced forms of dissolved nitrogen (N), such as dissolved organic nitrogen (DON) and ammonia ($\text{NH}_4\text{-N}$) (Sponseller et al. 2018), and phosphorus (P) (Räsänen et al. 2016) to running waters.

As microbial activity in boreal streams can be strongly N limited (Burrows et al. 2015), supplies of C and nutrients from terrestrial surroundings—in particular from mires—may impact stream functioning by indirectly acting as the ultimate regulators of how LAM use different types of terrestrial C.

In addition to the spatial distribution of forest, lakes and mires within the catchment, riparian vegetation community composition can influence the chemical composition of in-stream DOC (Kaiser et al. 2001; Yamashita et al. 2011) and therefore possibly the way in which LAM use this C resource. In sites dominated by coniferous tree species such as pine (*Pinus* spp.), terrestrial DOC inputs to streams tend to be of low-quality fractions, while higher concentrations of high-quality DOC occur in streams running through forests dominated by deciduous species (Hongve 1999; Kaiser et al. 2001). Hence, it is a challenge to disentangle the main driver of terrestrial C use by LAM across heterogeneous landscapes with several potential drivers of DOC quality.

In the present study, we asked how heterogeneous in-stream physical and chemical characteristics, landscape elements, and riparian vegetation community composition (hereafter, ‘riparian composition’) across a boreal drainage network influence the relative use of leaf C and DOC during leaf litter decomposition. Specifically, we used previously reported data on leaf litter decomposition rates (k) and microbial respiration in ten streams within the network (Bastias et al. 2022) and estimated the DOC/POC respiration ratio associated to LAM (as the amount of CO_2 produced by LAM respiration of DOC + POC divided by the amount of C contained in the litter mass lost through decomposition) to explore the reliance of LAM on DOC relative to leaf C. We then explored among-site variation in k , microbial respiration, and DOC/POC respiration ratios against a set of variables: (1) in-stream variables, such as DOC concentrations and quality (based on both the ratio of absorption at 254 nm and 365 nm, respectively [a_{254}/a_{365}] and specific UV absorbance at 254 nm [SUVA_{254}]); (2) relative land cover of major landscape elements, such as forest, lakes, and mires; and (3) riparian vegetation community composition (i.e., relative cover of deciduous and coniferous species), to understand how LAM reliance on DOC relative to POC changes across spatial gradients observed in boreal ecosystems. We hypothesized that DOC is a more important C source to LAM than leaf C (i.e., DOC/POC respiration ratio > 1) due to its high availability, especially in sub-catchments dominated by mires, but that the generally lower quality of DOC originating from mires could counteract this expectation. We further hypothesized that sub-catchments dominated by deciduous forests contain more fractions of high-quality DOC, making DOC a more important C source to LAM than leaf C.

Methods

Study sites

The study described here was conducted in streams (i.e., study sites) located in the Krycklan Catchment Study (KCS; 67.9 km², 64°14'N, 19°46'E), which is representative of the boreal forest landscape of northern Sweden (Laudon et al. 2013, 2021). The region has a subarctic climate, with a mean annual temperature of 1.8 °C and mean annual precipitation of 614 mm (30-year average for KCS; Laudon et al. 2021). Measurements of leaf litter decomposition rates and LAM respiration were carried out from 6 October 2016 to 3 July 2017 in ten first- to fourth-order streams (denoted C1, C2, C4, C5, C6, C7, C9, C10, C13, and C15), which have been continuously monitored in terms of hydrology and biogeochemistry during the last 30 years by the KCS and are well-preserved from human pressure (Ågren et al. 2008; Berggren et al. 2010; Laudon et al. 2013; see following sections for additional details on the environmental characteristics of the sub-catchments). Land areas directly adjacent to the sites consisted of well-developed riparian forest composed primarily of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), or younger forests dominated by birch (*Betula pendula* Roth and *Betula pubescens* Ehrh). Alders (*Alnus* spp.) are also present, mostly located in the riparian areas of the highest-order streams (sites C13, C15 and C16).

Characteristics of the streams

During the study period, 18 stream water samples were collected at each site following the KCS monitoring program (Laudon et al. 2013), which occurred biweekly during the snow-free period, monthly during winter, and up to 3 times per week during the snowmelt. Water samples were analyzed for DOC concentrations. Specifically, water samples were filtered in the laboratory through a 0.45-µm mesh and then stored and refrigerated (at approx. 4 °C) prior to analysis. DOC was analyzed within a few days after sampling using the combustion catalytic oxidation method on a Shimadzu TOCVCPH analyzer (Shimadzu Europa GmbH, Duisburg, Germany). For each site, we used the ratio between absorbance of DOC at 254 nm and 365 nm (a_{254}/a_{365}) as a proxy for DOC chemical composition. This ratio is negatively related to the molecular weight of dissolved humic substances (Strome and Miller 1978; De Haan 1993; Dahlen et al. 1996), and low-molecular-weight fractions of DOC are considered to be the more bioavailable C source for bacteria (i.e., high-quality DOC) than high-molecular-weight compounds (i.e., low-quality

DOC; e.g., Berggren et al. 2007; Berggren 2009). In addition, we divided the specific absorbance at 254 nm by the DOC concentrations (mg L⁻¹) to estimate SUVA₂₅₄ (in units of L mg⁻¹ C m⁻¹) (McKnight et al. 2001). This coefficient is positively related to DOC aromaticity (e.g., Weishaar et al. 2003) and has previously been used in our streams to characterize the DOC chemical composition (e.g., Ågren et al. 2008).

Water temperature and pH were measured when the water samples for DOC concentrations were taken, and additional water samples were frozen (− 25 °C) for later (within 6 h) determination of concentrations of ammonium (NH₄⁺; Method G-171–96 Rev. 12), nitrate (NO₃⁻; Method G-384–08 Rev. 2), and soluble reactive phosphorus (SRP; Method G-297–03 Rev. 1). These nutrients were analyzed using the SEAL Analytical AutoAnalyzer 3 system (SEAL Analytical Inc., Mequon, WI, USA). All analyses were conducted at the Swedish University of Agricultural Sciences in Umeå, Sweden.

During the study period, physical and chemical variables varied among sites (Table 1), which mirrored patterns previously observed in KCS (e.g., Laudon et al. 2013, 2021), including discharge (0.58–135 L s⁻¹), concentrations of DOC (12.2–33.3 L s⁻¹), pH (4.36–6.36), concentrations of NH₄⁺ (4.5–25.8 µg L⁻¹), NO₃⁻ (7.5–59.4 µg L⁻¹), and SRP (1.2–5.3 µg L⁻¹), and DOC chemical composition (i.e., a_{254}/a_{365} [3.78–4.42] and SUVA₂₅₄ [3.69–4.24] (see Table 1).

Landscape elements and riparian composition of the sub-catchments

Physical and chemical variables were complemented with characterization of the landscape surrounding each study site, including sub-catchment area and forest age, percentage of sub-catchment area covered by forest, mires, and lakes, as well as percentage of forest area covered by trees of birch, spruce, and pine, which are the most common tree species in the riparian zones (as defined by Laudon et al. 2021) of the study sites (Table 1). These data have been obtained through Light Detection and Ranging (LiDAR) measurements conducted across the entire Krycklan catchment with a resolution of 10–15 measurements per square meter (Laudon et al. 2011), and they provide the spatial distribution of water bodies as well as detailed forest characteristics within the entire catchment area (Neumann et al. 2012). Briefly, study sites encompassed gradients in sub-catchment area (12–1913 km²) (Table 1; adopted from Laudon et al. 2013), with relative land cover of forest (54–99.9%), mire (0–44.1%), and lake (0–6.5%) (Table 1; Laudon et al. 2013). Study sites also encompassed gradients in riparian vegetation community composition, showing differences in the relative cover of birch (0–12%; Table 1; adopted from Laudon et al. 2013),

Table 1 Data on in-stream physical and chemical characteristics for each study site during the leaf litter incubation period; major landscape elements for each study site; riparian vegetation community composition; and dissolved organic carbon/particulate organic carbon respiration ratios across study sites

Sites	In-stream physical and chemical variables									
	Discharge (L s ⁻¹)	pH	Temperature (°C)	DOC (mg L ⁻¹)	pH	NH ₄ ⁺ (µg L ⁻¹)	NO ₃ ⁻ (µg L ⁻¹)	SRP (µg L ⁻¹)	a ₂₅₄ /a ₃₆₅	SUVA ₂₅₄ (L mg ⁻¹ C m ⁻¹)
C1	2.3 (2.9)b	2.1 (2.6)a	21.4 (6.2)bc	5.64 (0.4)bc	22.9 (12.3)ab	47.3 (38.8)ab	2.2 (1.4)bc	4.42 (0.1)a	3.61 (0.8)a	
C2	0.53 (0.8)b	2.4 (2.6)a	19.3 (6.2)bc	5.24 (0.4)cde	4.5 (3.6)c	7.5 (14.7)c	2.8 (1.5)abc	4.39 (0.1)a	3.71 (0.3)a	
C4	1.1 (1.5)b	2.8 (3.1)a	33.3 (8)a	4.36 (0.3)d	25.8 (23)a	8.7 (3.1)c	4.8 (2.7)ab	3.81 (0.9)b	3.73 (0.6)a	
C5	2.1 (0.5)b	4.1 (5.2)a	22.4 (4.2)bc	4.88 (0.3)e	14.3 (9.1)abc	26 (13.4)bc	2 (0.7)bc	3.91 (0.1)ab	4.24 (0.8)a	
C6	4.6 (2.9)b	4.6 (2.9)a	17.9 (3.9)c	5.61 (0.5)bc	10.7 (5.2)c	25.5 (14)bc	2.3 (1.3)bc	3.94 (0.1)ab	4.28 (0.5)a	
C7	2.4 (3.3)b	2.9 (3.4)a	24.3 (5.2)b	5.06 (0.5)e	7.9 (4.6)de	23.6 (8.7)bc	5.3 (3.4)a	4.03 (0.2)ab	3.92 (0.84)a	
C9	82 (170.2)b	2.1 (2.5)a	17 (4.9)cd	5.95 (0.5)ab	12.3 (7)bc	26.2 (10.3)bc	2.9 (2.1)abc	3.99 (0.3)ab	3.91 (0.39)a	
C10	15.5 (19.2)b	2.2 (2.7)a	20 (6.5)bc	5.49 (0.6)bcd	10 (6.4)c	21.5 (13.5)c	3 (2.2)abc	3.78 (0.7)b	3.85 (0.9)a	
C13	62.6 (76.3)b	3 (3.8)a	20.7 (3.8)bc	5.67 (0.3)bc	6.8 (3.8)c	12.2 (5.4)d	1.7 (1)bc	4.09 (0.16)ab	3.99 (0.36)a	
C15	135 (122)a	3.1 (3.9)a	12.2 (4.2)d	6.36 (0.3)a	8.2 (10.2)c	59.4 (53.5)a	1.2 (0.7)c	4.12 (0.13)ab	3.69 (0.42)a	
Sites	Landscape element variables ^a					Riparian vegetation community composition variables ^b				
	Sub-catchment area (ha)	Forest (%)	Mire (%)	Lake (%)	Stand age (years)	Birch (%)	Spruce (%)	Pine (%)	DOC/POC respiration ratios ^c	
C1	48	98	2	0	90	2	63	35	1.46	
C2	12	99.9	0	0	106	0	36	64	1.90	
C4	18	55.9	44.1	0	60	0	45	55	2.16	
C5	65	54	39.5	6.4	53	12	26	62	0.66	
C6	110	71.4	24.8	3.8	72	4	26	70	1.76	
C7	47	82	18	0	89	1	35	64	1.59	
C9	288	84.4	14.1	1.5	81	6	29	65	1.24	
C10	336	73.8	26.1	0	63	12	21	68	1.21	
C13	700	88.2	10.3	0.7	81	8	25	68	1.13	
C15	1913	81.6	14.5	2.4	57	10	26	64	1.32	

Values are presented as the mean + 1 standard error (in parentheses). Different lowercase letters following values indicate a statistically significant ($P < 0.05$) difference among sites based on Tukey's HSD pairwise comparisons

a₂₅₄/a₃₆₅ Ratio between absorbance of DOC at 254 nm and 365 nm, C carbon, DOC dissolved organic carbon, NH₄⁺ ammonia, NO₃⁻ nitrate, POC particulate organic carbon, SRP soluble reactive phosphorous, SUVA₂₅₄ specific UV absorbance at 254 nm

^aMajor landscape elements for each study site included sub-catchment area; percentage coverage by mires, forest and lakes; and stand age of the forest

^bCalculated as the % of each sub-catchment's forest area covered by birch, spruce, or pine

^cCalculated as a mass balance of C based on the amount of carbon dioxide (CO₂) produced by LAM per amount of leaf C decomposed (g C-CO₂ g⁻¹ leaf C decomposed)

spruce (21–63%), and pine (35–70%) (Table 1). Forest stand age also varied among sites, ranging from 53 to 106 years (Table 1; adopted from Laudon et al. 2013).

Microbial respiration

Data on LAM respiration and leaf litter k , including three replicates per study site and sampling date, were obtained for this study from Bastias et al. (2022). These data are based on leaf litter from birch (*B. pendula*), the most dominant riparian tree species in the study region (Laudon et al. 2013,

2021; Lidman et al. 2017). Briefly, microbial respiration associated with leaf litter (mg O₂ g⁻¹ dry matter [DM] h⁻¹) at each site and sampling date were based on O₂ consumption during 3-h laboratory incubations at room temperature in the dark, with correction for background O₂ consumed by suspended microbes (following Burrows et al. 2015). We assumed that respiration rates were mostly related to LAM, which was examined by calculating the percentage of total respiration attributed to water controls (average among samples = 1.91 ± 0.00007%; $n = 153$). Prior to incubation, stream water was stored in the laboratory refrigerator

(4 °C) for 6 h and was filtered through a 250- μm mesh to remove larger particles. Because microbial incubations were run at 17.4 ± 0.05 °C, whereas field conditions were run at approximately 4 °C, we standardized the respiration rates to 4 °C to more closely resemble field conditions, based on the assumption that O_2 consumption rates double with a temperature increase of 10 °C (i.e., $Q_{10} = 2$; Davidson and Janssens 2006) (see Bastias et al. 2022, for further details). Further, the total amount of microbial respiration at each sampling date was calculated as accumulated microbial respiration (MR_{accum} ; $\text{g O}_2 \text{ g}^{-1} \text{ DM}$). Briefly, MR_{accum} was estimated by linearly interpolating the mean of instantaneous microbial respiration rates between sampling dates and summing the resulting values for the study period (Simon et al. 2009).

In the present study, these previously collected microbial measures (Bastias et al. 2022) were examined against in-stream physical and chemical characteristics, landscape elements, and riparian composition estimated for each sub-catchment.

Leaf litter k

As a determinant of leaf C availability to microbes, we used the values of birch leaf litter k from our study sites as reported in Bastias et al. (2022). Briefly, senescent leaf litter of birch was collected in September 2016 from trees at three sites (C2, C6, and C7) that were within a distance of approximately 1.5 km from each other; the collected litter was mixed and then placed in 250- μm mesh-size bags following the methods reported by Webster and Benfield (1986). Fifteen of these litter bags were deployed at each of the study sites, anchored to the streambed with metal bars, and incubated from autumn (6 October 2016, i.e., peak senescence) to the beginning of summer (3 July 2017). From each site, three litter bags were collected 11, 41, 94, 169, and 270 days after deployment, followed by oven-drying and weighing to determine leaf mass loss and to calculate k .

DOC/POC respiration ratios

To understand the microbial reliance on leaf C versus DOC, we developed a mass balance of C based on the amount of carbon dioxide (CO_2) produced by LAM per amount of leaf C decomposed (i.e., DOC/POC respiration ratio; $\text{g C-CO}_2 \text{ g}^{-1}$ leaf C decomposed). More specifically, for each site, we considered the observed equations predicting progression of mass-specific microbial respiration rates and leaf mass loss over the study period (Bastias et al. 2022). Then, for each site, we estimated accumulated oxygen (O_2) consumption rates ($\text{mg O}_2 \text{ g}^{-1} \text{ DM day}^{-1}$), which were converted into C- CO_2 production (g C-CO_2) by assuming a respiratory quotient of 1. We calculated the DOC/POC respiration ratio in terms of C balance, by dividing accumulated microbial

respiration per gram of leaf C decomposed, which was estimated based on leaf litter k (day^{-1}) at each study site. Thus, we assumed that the kinetics of C mineralization at each site was well-captured by leaf litter k (Webster and Benfield 1986; Webster et al. 2009). If LAM preferred leaf C as a C source, values of DOC/POC respiration ratio would be < 1 , whereas DOC/POC respiration ratio values > 1 indicate that LAM acquired substantial amounts of C from DOC in the water column during leaf litter decomposition, suggesting an additional functioning of LAM. DOC/POC respiration ratios could be partially overestimated due to mechanical fragmentation of leaf litter by macroinvertebrates and physical abrasion, or the leaching process, but we did not observe macroinvertebrates or many litter fragments in our fine-mesh litter bags (except in site C5 for last pickup), and a subset of leaf litter samples immersed in stream water containers (i.e., 3 g of leaf litter in 1 L of stream water) during 24 h in the laboratory revealed that leachates represent only a small fraction of the leaf mass loss (i.e., 4–8% of initial litter mass).

Statistical analysis

We explored potential among-site relationships between in-stream physical and chemical characteristics, landscape elements, and riparian composition, using principal component analysis (PCA). This analysis was standardized to avoid some variables becoming dominant due to their large measurement units.

DOC/POC respiration ratios were based on cumulative estimates (i.e., MR_{accum} and leaf litter mass lost), and thus these ratios do not have error estimates. To incorporate uncertainty in the DOC/POC respiration ratios, we regressed MR_{accum} with the amount of leaf C decomposed at each sampling date and site and used the standard error (SE) of these regressions (i.e., SE of the slopes) as a source of error associated with DOC/POC respiration ratios. We further explored among-site variability in these slopes. To do that, we used one-way analysis of covariance, with MR_{accum} as dependent variable, leaf C decomposed as covariate (i.e., continuous variable), and site as fixed factor. We used the interaction between leaf C and site (leaf C \times site) to test the null hypothesis that regressions between MR_{accum} and the amount of leaf C decomposed did not differ among sites and Tukey's HSD pairwise comparison to test specific among-site differences in these regressions.

Partial least square (PLS) regression analyses were used to explore which set of in-stream physical and chemical stream characteristics, landscape elements, and riparian composition was associated with leaf litter k , MR_{accum} , and DOC/POC respiration ratios. In these models, we used the full range of study variables as independent variables, whereas k , MR_{accum} , and DOC/POC respiration ratios

were used as dependent variables. The evaluation of the PLS regression models was based on the level of variance explained (r^2), loadings of the independent variables, and the variable influence on projection (VIP). The limit for a variable to be included in the final model was a VIP value of 0.7 (Eriksson et al. 2006). PLS regression does not assume normally distributed data, so no variable transformations were performed. Finally, we used multiple linear regression analyses to explore how k , MR_{accum} , and DOC/POC respiration ratios were related to the most important variables from PLS. The statistical analyses were performed in R version 3.5.2 (R Core Team 2022).

Results

Relationships among in-stream, landscape and riparian composition variables

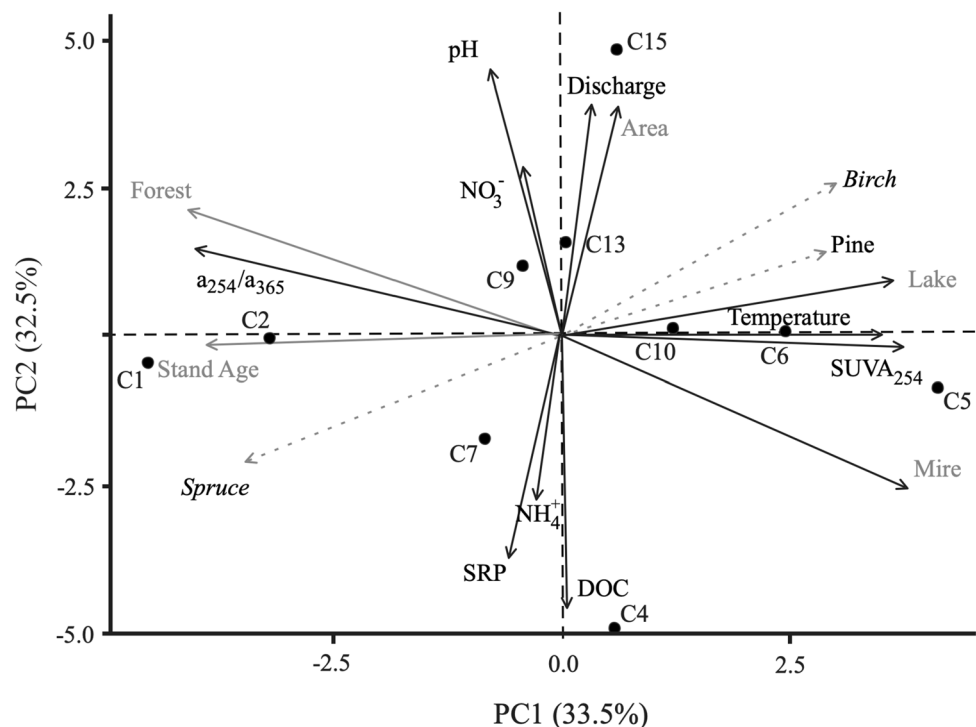
Over the study period, there were strong relationships among in-stream physical and chemical characteristics, landscape elements, and riparian composition (Fig. 1). Specifically, the PCA showed that birch cover was positively correlated with pine cover and negatively correlated with spruce cover (principal component 1 [PC1] on Fig. 1). Forest cover was positively correlated with a_{254}/a_{365} (i.e., positively correlated with DOC quality) and negatively correlated with mire cover (PC1, Fig. 1). Lake cover was positively correlated with water temperature and $SUVA_{254}$ (i.e., negatively correlated

with DOC quality), and negatively correlated with stand age (PC1, Fig. 1). The PCA also showed that concentrations of NH_4^+ , SRP, and DOC were positively correlated with each other and negatively correlated with stream discharge, sub-catchment area, pH, and NO_3^- concentration (PC2, Fig. 1).

Microbial reliance on leaf C versus DOC

DOC/POC respiration ratios were $>$ than 1 in all sites, with the exception of site C5, where the DOC/POC respiration ratio was 0.66 (Table 1). The highest microbial respiration (MR_{accum}) relative to leaf C decomposition, obtained from the slope of the regression between these two variables (Electronic Supplementary Material [ESM] Fig. S1), was observed in sites C4 and C7, and the lowest microbial respiration relative to leaf C decomposition was observed in site C5 (ESM Fig. S1). Significant among-site differences in the slopes of these regressions indicate that our exploration of DOC/POC respiration ratios across sites was reliable. Among-site variability in DOC/POC respiration ratios was best explained by a combination of in-stream, landscape, and riparian composition variables (PLS; Fig. 2a). Specifically, the DOC/POC respiration ratio was positively associated with stream discharge, water temperature, and concentrations of DOC and SRP, and negatively associated with pH, NO_3^- concentration, and $SUVA_{254}$ (i.e., positively associated with DOC quality) (Fig. 2a). For landscape and riparian composition variables, DOC/POC respiration ratios were positively

Fig. 1 Results from principal component analysis showing associations among study variables. Black arrows refer to in-stream physical and chemical characteristics. Gray arrows refer to landscape elements. Gray dotted arrows refer to riparian vegetation community composition. See [Methods](#) section for further details on groups of variables. Variance explained by PC1 and PC2 was 33.5% and 32.5%, respectively. a_{254}/a_{365} Ratio between absorbance of DOC at 254 nm and 365 nm, C carbon, C1, C2, C4–C7, C9, C10, C13, C15 study streams, DOC dissolved organic carbon, NH_4^+ ammonia, NO_3^- nitrate, PC principal component, SRP soluble reactive phosphorous, $SUVA_{254}$ specific UV absorbance at 254 nm



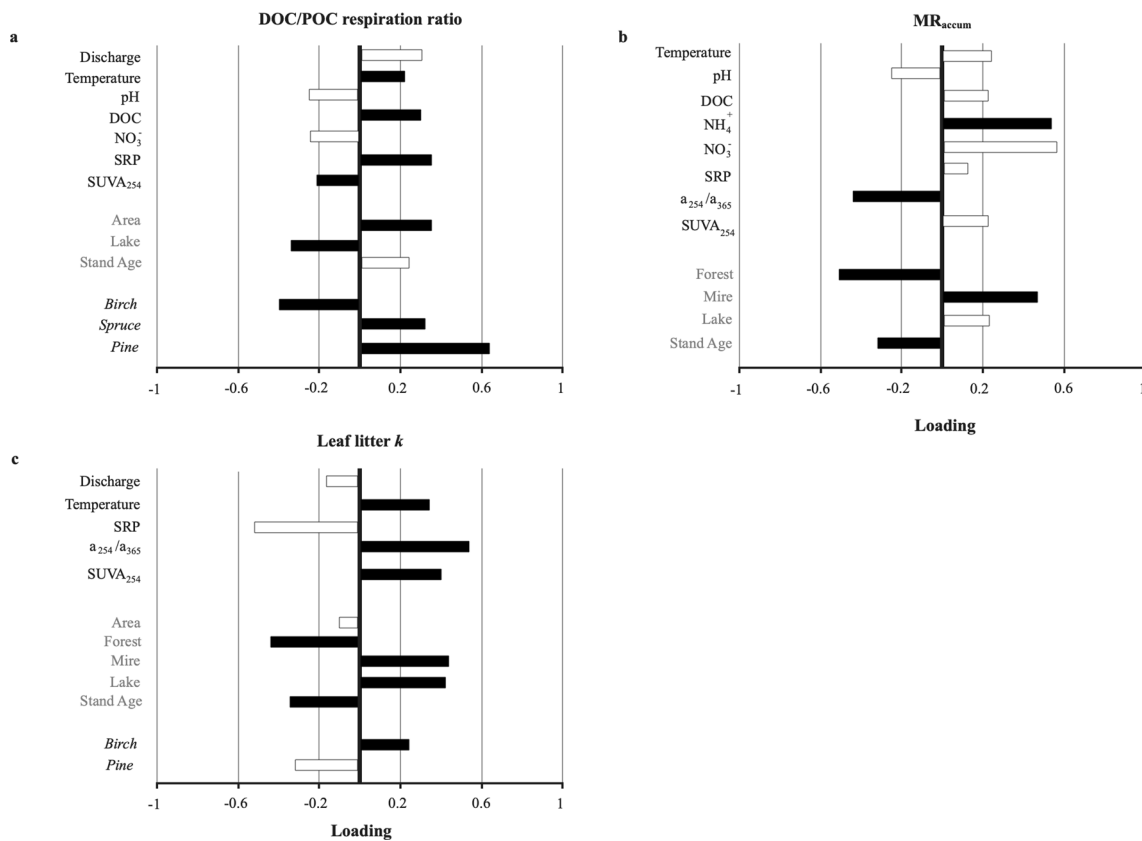


Fig. 2 Results from partial least square regression analyses on DOC/POC respiration ratios (a), MR_{accum} (b), and leaf litter decomposition rates (k) (c). Variance explained was 78%, 90%, and 82% (two components) for DOC/POC respiration ratios, MR_{accum} and leaf litter k , respectively. Predictor variables with a variable influence on projection (VIP) > 0.7 are presented, and black bars indicate a VIP > 1.0. Variables in regular black font are in-stream physical and chemical characteristics, landscape elements are presented in gray font, and

riparian vegetation community composition variables are presented in italics. See **Methods** section for further details on groups of variables. *DOC/POC* Amount of CO_2 produced by leaf-associated microbe respiration of dissolved organic carbon + particulate organic carbon divided by the amount of carbon contained in the litter mass lost through decomposition, k leaf litter decomposition rate, MR_{accum} total amount of microbial respiration at each sampling date, calculated as accumulated microbial respiration

associated with sub-catchment area, stand age, and spruce and pine cover, and negatively associated with lake cover and birch cover (Fig. 2a). In addition, birch cover best explained among-site variation in DOC/POC respiration ratios (multiple linear regression; $F_{1,8} = 19.8$, $r^2 = 0.68$, $P < 0.01$), i.e., a lower ratio (lower reliance on DOC relative to POC) with greater cover of a higher-quality riparian vegetation.

Among-site variability in MR_{accum} and leaf litter k was also explained by a combination of in-stream, landscape, and riparian composition variables (PLS; Fig. 2b, c). MR_{accum} was positively associated with stream water temperature, concentrations of DOC and nutrients (i.e., NH_4^+ , NO_3^- , and SRP), $SUVA_{254}$ (i.e., negatively associated with DOC quality), and mire and lake cover, and was negatively associated with a_{254}/a_{365} (i.e., negatively associated with DOC quality), pH, stand age, and forest cover. In addition, among-site variation in MR_{accum} was best explained by concentrations of NH_4^+ (positively) and a_{254}/a_{365} (negatively, i.e., a negative

influence of DOC quality) (multiple linear regression analyses; $F_{2,7} = 19.7$, $r^2 = 0.81$, $P < 0.01$).

k was positively associated with water temperature, $SUVA_{254}$, a_{254}/a_{365} , mire, lake, and birch cover, and was negatively associated with stream discharge, SRP concentrations, catchment area, stand age, and forest and pine cover. In addition, among-site variation in k within the catchment was best explained by birch cover (positively), a_{254}/a_{365} (positively, i.e., a positive influence of DOC quality), and forest cover (negatively) (multiple linear regression analyses; $F_{3,7} = 12.8$, $r^2 = 0.78$, $P < 0.01$).

Discussion

Our results show that landscape configuration determines microbial C mineralization in boreal streams by influencing the relative use of DOC and POC during leaf litter decomposition (Miller 1987; Christina et al. 2020). Specifically, as

we hypothesized, DOC/POC respiration ratios were mostly > 1 , indicating that LAM use a substantial amount of DOC during leaf litter decomposition. This higher DOC use was associated with spatial gradients of DOC concentrations, for which mire and forest cover within the catchment are important determinants (Berggren et al. 2010; Burrows et al. 2017). Moreover, DOC/POC respiration ratios were higher in catchments dominated by coniferous forest (i.e., pine and spruce) and lower in catchments dominated by deciduous forest (i.e., birch), indicating that riparian vegetation community composition also exerts a strong influence on microbial C cycling in boreal streams. As such, our results suggest that LAM to a great extent use DOC from the water column, not mainly leaf C, and that this pattern is largely determined by large-scale (i.e., mire and forest cover) and local (i.e., riparian composition) landscape characteristics. Hence, modified terrestrial landscapes as a consequence of land use (Esseen et al. 1997; Hylander et al. 2002) and climate change (IPCC 2019) need to be considered to enable accurate predictions of C turnover in boreal streams.

Landscape regulation of microbial terrestrial C use in boreal streams

One goal of this study was to test how landscape configuration, through its influence on stream physical and chemical conditions, influence the relative use of leaf C and DOC by LAM. Our results confirm our hypothesis and show a disproportionately high use of DOC relative to POC (i.e., DOC/POC respiration ratios > 1) in nine out of the ten study sites. The likely explanation for this result is the high supply of DOC coming from adjacent soils and mires, reducing microbial reliance on litter C (Miller 1987; Pastor et al. 2014; Bastias et al. 2022), which reflects an important influence of landscape configuration on LAM activity. This influence of landscape configuration on LAM DOC use is supported by regression analyses between MR_{accum} and decomposed leaf C, showing the highest slopes in DOC-rich mire-dominated streams (Fig. 1; ESM Fig. S1), and by the influence of mire cover on stream nutrient concentrations (i.e., SRP and NH_4^+) as well as the positive association between these variables and MR_{accum} . This result is consistent with nutrient limitation that was widely observed in other studies on leaf litter decomposition in streams (e.g., Bastias et al. 2020; Woodward et al. 2012) and on heterotrophic biofilms in our streams (Burrows et al. 2015, 2017), reflecting a strong influence of landscape configuration on microbial C mineralization in boreal ecosystems. Additionally, one important note related to these results is that the k found in the present study (i.e., $< 0.005 \text{ day}^{-1}$; Bastias et al. 2022) falls within the lower range of k values reported for birch litter (Webster and Benfield 1986), further supporting terrestrial leaf litter

not being a major C source to LAM and that alternative C sources (e.g., DOC) may be more important.

One question that emerges from our results is how landscape configuration mechanistically, by influencing DOC quality, may control LAM activity. Absorbance ratios (i.e., $SUVA_{254}$ and a_{254}/a_{365}) show that DOC originating from mires is the most aromatic and has highest molecular weight within the study catchment (Kalbitz et al. 2003; Berggren et al. 2007; Ågren et al. 2008), and previous studies in our streams have found a negative influence of mire cover on microbial activity in water samples (Berggren et al. 2007) and heterotrophic artificial substrates (Burrows et al. 2017). Our results, however, are in contrast with these previous observations and show positive relationships between DOC aromaticity and molecular weight and MR_{accum} . This unexpected result could be explained by LAM producing a wide range of enzymes for degrading recalcitrant C (Romani et al. 2006; Ylla et al. 2012; Fitch et al. 2018), enabling them to efficiently capitalize on low-quality DOC resources. The positive relationships between DOC aromaticity and molecular weight and MR_{accum} could also be explained by the negative among-stream correlation between DOC concentrations and quality, and that LAM favor DOC quantity over quality to satisfy C demands, which could also explain why they favor DOC over litter C. Either way, our results indicate that LAM are not limited by low-quality DOC resources, but rather that they are sensitive to changes in both DOC concentrations and chemical composition, which reinforces the strong influence of landscape configuration on LAM function in boreal streams (Berggren et al. 2007; Ågren et al. 2008; Kothawala et al. 2015).

In addition to physical and chemical characteristics of the streams, DOC/POC respiration ratios may respond to riparian vegetation community composition. Specifically, in contrast to our expectations, we found a higher use of DOC relative to POC in sites dominated by coniferous species (i.e., pine and spruce) and less use of DOC relative to POC in sites dominated by birch. This result could be explained by recalcitrant DOC resources, which are typically associated with coniferous-dominated forest (Hongve 1999; Kaiser et al. 2001), being a preferred DOC source by LAM (Ylla et al. 2012; Bastias et al. 2020) or—perhaps more likely—by the fact that birch leaf litter is preferred by LAM over coniferous needles as a C source, reflecting microbial adaptation to high-quality litter inputs (Lidman et al. 2017). Our results partially support these two explanations because we found a positive relationship between MR_{accum} and DOC molecular weight, in addition to a positive relationship between leaf litter k and birch cover. Hence, our results indicate that the relative use of DOC and POC is not only regulated by land cover, but also by more local terrestrial characteristics, such as the riparian vegetation community composition. In northern Europe, wetlands can cover approximately 25% of

the land area (Laudon et al. 2004), and the dominant forest management method (i.e., clear-cutting) favors coniferous over deciduous species (Esseen et al. 1997; Laudon et al. 2011). Climate change impacts, such as wetland physical and chemical alterations, and the transformation of forest community composition need to be simultaneously considered for a comprehensive understanding of C turnover in boreal streams.

The role of LAM for in-stream respiration: estimates and regional up-scaling

To further explore the repercussions of our results, we estimated CO₂ production per unit of stream area and year (expressed as g C-CO₂ m⁻² y⁻¹). To do this, we used previously reported estimates of birch leaf input to streams in the KCS and adjacent catchments (Lidman et al. 2017) and combined these data with data on microbial respiration in the study sites over the hydrologic year (i.e., from leaf fall to spring floods; Bastias et al. 2022). Across our sites, rates of CO₂ production per stream area ranged from 15.6 to 23.8 g C-CO₂ m⁻² y⁻¹. This LAM respiration contributes to a low fraction of the total CO₂ production from our catchment, which ranges from 1455 to 6411 g C-CO₂ m⁻² y⁻¹ (Wallin et al. 2013). More specifically, our estimates may represent from a low of approximately 1 ± 0.71% of the total CO₂ production from our streams up to 8% when comparing our rates with previous estimates from streams in the boreal region (Hope et al. 2001). More broadly, comparing our results with a summary of CO₂ data from published studies of streams and rivers in temperate and boreal regions, our estimates average approximately 2 ± 0.65% of the total CO₂ production (data summarized in Wallin et al. 2013). The relatively low contribution of LAM to the total CO₂ production that we find could be explained by low levels of leaf input (51.63–98.05 g DM m⁻², *n* = 20; Lidman et al. 2017), which falls in the lower range of leaf input reported from temperate and tropical streams (0–963 g DM m⁻², *n* = 212; Datry et al. 2018). However, the relatively low contribution of LAM to the total CO₂ could be also explained by LAM translocating a substantial fraction of C into microbial biomass, which is in accordance with microbial C limitation observed in our streams (Burrows et al. 2017).

Conclusions

Our results provide evidence that landscape configuration regulates microbial use of different terrestrial C sources during leaf litter decomposition, and that these microbial functions require assessment of DOC acquisition to be fully understood. We propose that the estimation of DOC/POC respiration ratios, which integrates this process, could be

replicated across catchments with different landscape configurations. If values of DOC/POC respiration ratios are > 1, as for our streams, DOC is more efficiently used than leaf C by LAM. Such information is important to be able to predict how C turnover and ecosystem function in boreal stream will respond to intensified land use and climate change.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-023-01041-y>.

Acknowledgements This research was supported by a Carl Tryggers Stiftelse grant to MJ (CTS 17: 234). The authors additionally thank Hjalmar Laudon and personnel from the Krycklan Catchment Study (www.slu.se/krycklan) for supplying water chemistry and discharge data, and Irene Moragas and Javier Montoro for field assistance.

Author contributions EB and MJ designed the study, carried the field work, and performed the laboratory analysis. EB and MJ took part in statistical analyses and manuscript writing, which was led by EB.

Funding Open access funding provided by Umea University.

Declarations

Data availability statement The data that support the findings of this study are not openly available and are available from the corresponding author upon reasonable request.

Conflict of interest The authors declare no conflict of interest.

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