The emerging role of drought as a regulator of dissolved organic carbon in the boreal landscapes

Tejshree Tiwari (✉ tejshree.tiwari@slu.se)

Swedish University of Agricultural Sciences <https://orcid.org/0000-0003-1637-4077>

Ryan Sponseller

Umea

Hjalmar Laudon

SLU <https://orcid.org/0000-0001-6058-1466>

Article

Keywords:

Posted Date: December 9th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-1137926/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at Nature Communications on August 31st, 2022. See the published version at <https://doi.org/10.1038/s41467-022-32839-3>.

Abstract

One likely consequence of global climate change is an increased frequency and intensity of droughts at high latitudes. We use a 17-year record from 13 nested boreal streams to examine the direct and lagged effects of summer drought on the quantity and quality of dissolved organic carbon (DOC) inputs from catchment soils. Protracted periods of drought reduced DOC concentrations in all catchments but also led to large pulses of DOC inputs upon rewetting in autumn. Concurrent changes in DOC optical properties and chemical character suggest that seasonal drying and rewetting triggers soil processes that alter the forms of carbon supplied to streams. Contrary to common belief, the clearest drought effects were observed in larger watersheds, whereas responses were most muted in smaller catchments. Collectively, our results reveal an emerging shift in the seasonal distribution of DOC concentrations and character, with potentially far-reaching consequences for northern aquatic ecosystems.

Introduction

One major effect of ongoing climate change is a greater frequency and severity of hydrological drought ¹. An increased likelihood of such events is notably significant for northern landscapes, which are covered by vast areas of aquatic and wetland ecosystems ², and serve as an important source and conduit for nutrients, metals, and carbon to downstream recipients. Yet, much of our understanding of drought effects on streams and catchments come from research in biomes where such events historically have been common ³. By comparison, the consequences of intensified drying/rewetting cycles at high latitudes for aquatic ecosystems and biogeochemical processes remain poorly investigated [Gomez et al. 2020]. This knowledge gap, together with the large pool of soil organic matter that can be mobilized in northern landscapes ⁴, may lead to dramatic and unexpected impacts on aquatic ecosystems in a future dominated by more extreme weather events.

Northern streams and lakes are often typified by high concentrations of dissolved organic carbon (DOC), which plays a wide range of geochemical ⁵, biogeochemical ⁶, and ecological roles ⁷ and is thus an important indicator of water quality. DOC supply from soils influences the transport and bioavailability of heavy metals and anthropogenic organic compounds ⁸, represents a main energy source for northern aquatic food webs ⁶, and promotes the production of harmful byproducts of chlorine disinfection during drinking water sanitization ⁹. Further, variation in DOC 'quality', as represented by shifts in the relative composition of organic compounds and their degree of biological reactivity, can further shape biogeochemical processes in aquatic systems, including rates of microbial metabolism ¹⁰ and nutrient transformations ¹¹. Given these important roles, environmental changes that result in an alteration in the amount and characteristics of DOC supplied to aquatic systems can result in widespread consequences for northern aquatic ecosystems.

DOC production and mobility in landscapes are driven by the combination of soil biogeochemical processes and the strength and timing of hydrological connections between terrestrial source areas,

deeper groundwater systems, and stream channels¹². It is generally recognized that elevated flow conditions promote DOC supply by strengthening the connections between these terrestrial sources and streams¹³. In this way, the timing of high flows, together with temperature-driven changes in soil processes, can shape the overall seasonality of DOC supply to streams¹⁴. However, much less is known about how the amount, timing, and chemical character of DOC are altered by seasonal drought episodes, which reduce lateral connectivity, but also set the stage for biogeochemical and microbial processes in dry and disconnected soils¹⁵. Such biogeochemical and microbial changes could alter the pool of organic matter that becomes mobilized when flow conditions resume.

Here we ask how the severity of summer drought episodes drives the seasonal patterns of DOC quantity and quality in a boreal stream network. To answer this, we investigated how stream DOC concentrations, the 254/365 nm absorbance ratio, used here as a proxy for low molecular DOC (LMW DOC)¹⁶⁻¹⁸, and the carbon/nitrogen (CN ratio) respond to summer low flow conditions over 17-years in 13 nested catchments that differ in size and land cover. Given the importance of hydrology as a transport vector for DOC, we predicted that droughts would disconnect organic-rich soil layers in upper horizons from lateral flow paths, resulting in lower stream DOC, LMW DOC, and CN ratio, depending on the severity of these events. During the rewetting phase, we tested whether the DOC quantity and quality simply return to pre-drought conditions or whether prolonged dry periods alter the amount and composition of DOC that is mobilized to streams. Finally, we assessed how the variation in drying/rewetting shaped the DOC response across the drainage network depending on catchment properties, specifically variation in land cover and catchment size.

Results And Discussion

Mechanisms underlying drought responses

Over the 17 year record, summer low flow hydrology varied considerably with mean daily minimum discharge ranging several orders of magnitude between the driest and wettest summers (0.0003 to 0.13 mm day⁻¹). The most pronounced summer low flows occurred in 2006 and 2018 with 62 and 41 days where daily discharge was below the 0.1 mm day⁻¹ threshold (Figure 1). This inter-annual variability in hydrology had clear consequences for DOC concentrations, which declined at each site as the severity of summer drought conditions increased. For all catchments, summers with more than 40 days of low flow conditions had the largest percentage decrease in DOC concentrations from the 17-year average (20-55% in small to larger catchments, $p < 0.05$), respectively; Figure 2a). These concentration declines as drought severity increased are consistent with reduced hydrological connectivity to more surficial, organic-rich riparian soils as the groundwater table drops and intersect deeper horizons that store less organic matter^{19,20}. As further support for these mechanisms, DOC concentrations measured in near stream wells also declined as the drought severity increased (Figure 5). Here, DOC concentrations in riparian wells were reduced by 75% compared to pre-drought values ($r^2 = 0.72$, $p < 0.05$), whereas concentrations in nearby mire wells showed only minor changes ($r^2 = 0.11$, $p > 0.1$). By comparison, the wettest years in the

record were associated with elevated DOC concentrations in streams, increasing from 10-20% relative to the long-term mean. Collectively, these inter-annual differences highlight the overwhelming role of hydrological connectivity between streams and near-surface soils (Supplementary Figure S1) that supply DOC to aquatic systems²¹. Importantly, while warmer temperatures have the potential to increase DOC supply from riparian soils²² and peat^{14,23}, our results suggest that potential changes in hydrology, including greater drought frequency, could fundamentally shift the seasonality of DOC in boreal aquatic ecosystems (Figure 3).

Drought episodes also directly influenced DOC's character, yet these effects were more variable and in some cases subtle. For example, the CN ratio declined at all sites as drought severity increased (Figure 4c, Table 1, $r^2 > 0.17$, $p < 0.05$ for 12 out of 13 sites). We attribute the decrease in this ratio to a shift in the contribution to stream DOM from organic-rich, near-surface soils to deeper strata, where soils are more biologically processed and tend to have lower CN ratios^{24,25}. At greater soil depths, there are also higher levels of reduced inorganic nitrogen (ammonium) which can contribute to the lower CN ratio as calculated here^{26,27}. By contrast, the LMW DOC, changed only marginally ($p < 0.05$ for nine out of thirteen sites, Table 1), with bidirectional responses to drought across catchments (Figure 4a), suggesting that the direct effects of drying are less systematic for the character of DOC as represented by this index. Regardless, the decreasing trends for both indexes were mirrored by observations in the riparian and mire wells, with the largest declines observed in years with the longest summer droughts (Figure 5 c, e, respectively, riparian wells $r^2 = 0.82$, mire wells $r^2 = 0.81$, $p < 0.1$). Lower groundwater LMW DOC and CN ratio were synchronous with lower quantities of DOC observed in the streams during drought periods compared to pre-drought conditions. Thus, droughts limit the mobility of organic carbon across landscape types, reduce stream DOC concentrations, and alter key characteristics of DOC across the stream network. Such changes to stream chemistry could have cascading consequences for downstream aquatic ecosystems in the future, should extreme drought events increase in frequency and severity.

Post-drought recovery of stream biogeochemistry to summer droughts

Periods of low flow conditions, which cause longitudinal fragmentation and lateral flow disconnections can also lead to increased production of DOC in upper soil horizons that may be mobilized when dry periods are terminated²⁸. Consistent with this, the rewetting periods following summer drought were associated with high DOC concentrations in streams across the Krycklan network, with the largest increases observed during years where rewetting followed the most severe dry periods. Indeed, the driest summers resulted in 100-150% increases in DOC concentration after rewetting across all catchments (Figure 2b, $p < 0.05$, Table 1). As above, these episodes of DOC flushing in streams were also mirrored in observations from riparian (50% increase, $r^2 = 0.31$, $p < 0.05$) and mire wells (150% increase $r^2 = 0.79$, $p < 0.05$) (Supplementary Figure S1 b). In addition to the effects on concentration, DOC properties were also influenced by the severity of the preceding drought during rewetting periods. Specifically, the LMW DOC increased linearly in 12 of the 13 catchments ($p < 0.05$), while the CN ratio increased in 11 out of 13 sites, from pre-drought conditions in the study streams (Figure 5b, d, Table 1). Patterns in groundwater

LMW DOC and CN ratio during these rewetting periods were also similar to stream observations where both showed increasing trends in riparian and mire wells ($p < 0.1$) (Figure 5 d, f). Thus, the changes in both DOC quantity and quality parameters suggest that seasonal low flow periods mobilize accumulated solutes during the following rewetting period to an extent that is proportional to the severity of the drought across all landscapes.

Elevated DOC concentrations following the drought periods are in line with the reconnection of near-surface organic-rich soil horizons. Yet, the increases in the DOC concentration, as well as changes in DOM properties, as summer droughts became more severe suggests that biogeochemical processes strongly influenced the soil DOC pools during dry periods. Several mechanisms have been linked to small-scale increases in soil organic matter mineralization and DOC production in response to drying/rewetting cycles. For instance, droughts have been found to decrease phenolic microbial inhibitor compounds in wetlands resulting in increased organic matter decomposition and an increase in carbon loss in peats²⁹. Additionally, droughts increase the temperature and degree of aeration of soils that are normally inundated, upregulating organic matter decomposition^{30,31}. Finally, rewetting these exposed soils also trigger the physical and microbial processes that promote organic matter mineralization [Borken and Matzner, 2008]. While we cannot resolve amongst these mechanisms, the observed patterns suggest that processes in seasonally-exposed organic soils support a large pulse of DOM upon rewetting, including a greater fraction of LWM forms that are more bioavailable for aquatic organisms³². In fact, based on prior studies in the Krycklan catchment³², the changes in LMW DOC we observe in response to rewetting (ca. 0.2- 0.5 units) in both surface and groundwaters could correspond to as much as a 50% increase in microbial growth efficiency in streams. In addition to these implications for energy mobilization by aquatic microbes, increased autumn pulses of DOC may also have implications for the fate and transport of a variety of hazardous pollutants such as mercury⁸, and, when combined with longer-term browning trends, contribute to poorer water quality and higher water treatment cost³³.

Network Scale responses

Responses to drought at different time intervals were notably variable across the river network, reflecting differences in the sensitivity to low flow disturbance. Yet, the importance of the catchment size as a mediator of these responses differed depending on the time frame considered. For example, larger catchments showed both the greatest decline in DOC concentration in response to drought (Figure 6a) and the largest increases in DOC upon rewetting during the post-drought period (Figure 6b). Strong drought responses in the larger catchment likely relate to their greater distance to near-surface organic DOC sources that feed headwaters (Figure 6, Table 1). Isolation from these sources is exacerbated by the increasing influence of deeper and DOC-poor groundwater as catchment size increases¹². As a result, even small losses in connectivity to more DOC-rich headwaters during drought may cause the chemistry of larger rivers to shift abruptly towards the character of deeper groundwater sources. Upon rewetting, these larger streams and rivers have such low DOC concentrations that the sudden reconnection to upstream headwaters creates a strong chemical response (Figure 6b, $p < 0.05$ for 10 of the 13 catchments,

Table 1). By comparison, headwaters are seldom supported by these deeper groundwater sources ³⁴, and hence their responses to drying and rewetting events are more attenuated. In this sense, larger river systems may be less prone to complete water loss during drought than headwaters, but nonetheless, show stronger biogeochemical responses to such events. Thus, while larger rivers may sustain aquatic communities during low flow periods, dramatic increases in DOC after rewetting may lead to a host of ecological and societal challenges ³³ including greater stress for organisms in cases of rapid pH declines ⁶ and ultimately higher cost for the production of potable water ³⁵.

While catchment size clearly plays an overarching role in regulating stream chemistry following prolonged dry periods, it is not possible to exclude the influence of land cover effects. For instance, several small catchments are dominated by peat-forming mires and display the lowest response to droughts (Figure 6b). Contrastingly, the stronger response by larger, forest-dominated catchments could also be an indication of the degree to which they dry during more severe droughts, as reduced mire cover is linked to lower water storage capacity, and greater evaporative losses, and thus potentially weakened ecohydrological resilience to drought ³⁶. Conversely, catchments with greater peat coverage, showed the weakest post-drought response, suggesting these landscape elements confer resilience to such events, likely by acting as important water storage zones ³⁷ with the potential to dampen effects of long-term environmental change ³⁸.

Conceptualizing drought impacts on stream chemistry

Integrating long-term monitoring data of biogeochemistry and hydrology with modeling techniques provide a more comprehensive understanding of how climate extremes feedback on the mobilization and biogeochemical cycling of soil organic carbon across temporal and spatial scales in boreal catchments. Observed seasonal variation in amplitude of DOC, LMW DOC, and CN ratio demonstrate differential responses in catchment biogeochemical processes to droughts, such that stream water quality is not only affected by reduced soil water supply, but also by declines in the leaching and availability of organic resources important for aquatic microbial processes. Further, the combined responses of the three variables suggest that, while drought effects on stream water chemistry are direct and immediately result in lower than average DOC responses (Figure 7a), the indirect, lagged effects are magnified and extend beyond the duration of the disturbance itself (Figure 7b). Overall, increases in the intensity of seasonal drying/rewetting cycles have the potential to shift the seasonality of DOC in boreal streams by reducing summer peaks in concentration while causing anomalously high concentrations during periods of hydrological reconnection later in the autumn (Figure 7b). Therefore, how recipient aquatic ecosystems cope with such changes during and following droughts, remains a key question.

Almost two decades of monitoring data show that inter-annual variation in summer low flows shape the seasonality in DOC quantity and quality in boreal streams more than is currently appreciated. While much emphasis is currently placed on the direct effects of climate warming at high latitudes³⁹, our study indicates that potential hydrological changes will likely be another important driver of carbon mobilization and water chemistry change. In light of the current climate projections of an increase in

drought frequency in Scandinavia⁴⁰, our results suggest the immediate declines in the quality and quantity of organic carbon in streams during summer followed by lagged increases during rewetting. Despite the variations in landscape properties, all catchments showed similar responses to droughts, however, the magnitude of these responses was more pronounced in the largest catchments. Changes to both the quantity and quality of carbon across the stream network can potentially have vital implications for the aquatic ecosystems that rely on the seasonal balance of DOC production and mobilization from catchment soils⁴¹. Overall, these results highlight the importance of integrating responses at multiple temporal and spatial scales and present a step forward in establishing a unifying theory of drought impacts in boreal biogeochemistry.

Methods

The Krycklan Catchment Study (KCS) (64.23° N, 19.77° E) is located in Northern Sweden and consists of 13 long-term monitoring streams. The sub-catchments vary in size from small headwaters (0.12 km²) to the large outlet (67 km²; ⁴²). Land cover is dominated by forest till soils (47% to 100% among monitoring sites), lakes (0 to 6%), and peatlands (referred to as mires) (0% to 51% areal coverage). Fluvial sediments dominate the lower parts of the catchment below the highest postglacial coastline (Supplementary Table S1.). The bedrock consists of 94% metasediments/metagraywacke, 4% acid and intermediate metavolcanic rocks, and 3% basic metavolcanic rocks. Soil mineralogy is dominated by quartz (31–43%), plagioclase (20–25%), K-feldspar (16–33%), amphiboles (7–21%), muscovite (2–16%), and chlorite (1–4%)⁴³. Forests are predominantly Norway spruce (*Picea abies*, 25%) and Scots pine (*Pinus sylvestris*, 66%), with 9% deciduous forest. Mean annual precipitation recorded between 1991–2010 was 610 mm from which 35% was classified as snow during winter (December–April)⁴⁴. In January, the average air temperature is $-9.5 \pm 4.1^\circ\text{C}$ while July temperatures are $14.5 \pm 1.7^\circ\text{C}$ ⁴⁴. During the spring, (mid-April), snowmelt accounts for approximately 40% of the annual runoff. There are low impacts from land use with 2% agricultural lands, less than 100 inhabitants and 0.63% of the catchment was subject to final felling, annually (1999-2010). The hydrological regime, landscapes, and land uses of Krycklan Catchment are considered representative of much of the boreal landscape [Laudon et al., 2013].

Discharge data

Discharge measurements used to classify summer low flow conditions were based on a small, centrally located headwater sub-catchment (C7, 0.45 km²) for which we have the longest, most detailed record in the Krycklan Catchment. The C7 sub-catchment drain a mix of forest (81%) and mire (19%) land cover, has a mean specific runoff that falls near the average for all streams in the Krycklan Catchment, and hence provides a reasonable proxy for discharge including drought condition in the area⁴⁵. Using this standardized runoff also made it possible to compare the responses between catchments to the same drought period. Stage height was determined from a 90° V-notch weir in a heated house with a pressure transducer connected to a Campbell Scientific data logger⁴⁶. Daily discharge was calculated from

measurements of stage height and an established rating curve based on more than 1000 manual salt dilution and bucket-method measurements ⁴⁷.

Surface and groundwater sampling

During summer, surface water samples were collected every other week from each site in acid-washed, high-density polyethylene bottles, which were kept in cold storage until analysis. Samples were collected monthly in winter. Sampling was synchronous across all sub-catchments occurring mostly on the same day, which provided 190 monthly DOC averages during the investigated period (2003-2019) for each of the 13 catchments (Unity Svartberget Data, <https://franklin.vfp.slu.se/>). In addition, groundwater was sampled from a nest of suction lysimeters that collect riparian soil water from 0.10 to 0.65 m at ~0.10 m intervals. Finally, mire groundwater samples were collected from wells installed from 2 to 2.5 m. Both sampling of forest riparian soil solution and mire groundwater occurred seasonally; here we used samples collected at the onset of summer (end of May-June) and mid-summer/early autumn (Jul-Sep). The averages of all depths were used for the analysis for both the riparian and mire wells. Annual sampling in the riparian zone began in 2003. Similar sampling in the mire started later (2009) with sufficient seasonal samples for our purposes, collected on average every second year.

In the laboratory, surface water (total 7060 samples from all sites) and groundwater samples (827 samples from both riparian and mire wells) were analyzed for DOC and total nitrogen (TN) concentrations using a Shimadzu TOC-VCPH analyzer after acidification to remove inorganic compounds ³⁸. The CN ratio was calculated by dividing DOC by TN. We did not subtract the dissolved inorganic carbon (NH_4 , NO_2 , NO_3) from TN estimates due to the limited data in the larger sites, however, since the proportion of inorganic N is relatively small (9% of the TN during the summer period) compared to total organic nitrogen, we do not expect that this would affect our results. Filtered water samples were also analyzed for absorbance (243 surface samples and 72 groundwater) using wavelength ranging from 200 to 600 nm, at 1 nm intervals at a scan speed of 240 nm min⁻¹ and a slit width of 2 nm using a Lambda 40 UV-visible spectrophotometer (Perkin Elmer, Waltham, MA, USA). A 1 cm quartz cuvette with Milli-Q water as the blank was used for measuring the samples. We used the absorbance wavelengths A_{254} and A_{365} nm for the ratio (Abs ratio A_{254}/A_{365}) in this analysis to trace the effects of droughts on the low molecular weight DOC compounds (LMW DOC). The 254/365 absorption ratio is positively correlated to bacterial production in natural waters ¹⁶ and negatively to the molecular weight of DOC ^{17,18} thus can be used as a qualitative measure of low molecular weight DOC.

Hydrological droughts

We represented inter-annual variation in the extent of summer drought over the 17 years study period using the occurrence of low flow conditions as a proxy. Within this study period, a threshold of 0.1 mm day⁻¹ was used to represent low flow conditions, which corresponds to daily discharge less than the 10th percentile value based on summer observations over the last 30 years. For this estimate, the summer season was defined based on air temperatures (July-Sept) ⁴⁸. The ggrridges density distribution function

from the ggplot 2 package in R was then used to display the proportion of discharge below the thresholds in each year and to visualize changes in the distribution over space and time. Ridge line plots calculate density estimates from actual data (jitter point, Figure 1 b) and plot those using ridgeline visualization. From the density distribution of all the years, we can observe that the majority of days during the driest summers (2006, 2018) had discharge levels below the 10th percentile (0.1 mm day⁻¹) (Figure 1). Years with no low flow days below the threshold were 2012, 2016, and 2017 which showed an almost even distribution of discharge over the summer season (Figure 1). The years with the average number of low flow days were 2005 and 2015 (15 and 16 days respectively, Figure 1).

Drought impacts on DOC, LMW DOC, and CN

The impacts of low flow conditions on DOC concentrations were investigated at two temporal scales to explore the direct drought effects as well as the subsequent responses during the rewetting stage. The direct response captures changes in DOC, LMW DOC, and CN that occur during summer low flow periods. The post-drought effects investigated the change in these same response variables after the first rewetting. We similarly investigated drought effects on groundwater DOC, LMW DOC, and CN ratio in forested riparian and mire soils during summer low flows and post-drought after the first rewetting.

The effects of prolonged summer low flow on both surface water and groundwater DOC were determined by first averaging the DOC concentrations during the summer period (Jul and Sept) in each catchment for each year. We then calculated the difference between individual summer averages and the long-term summer average of the 17 years and expressed as percentage change, following:

$$DOC_d = \left(\frac{DOC_a - DOC_b}{DOC_b} \right) \times 100 \quad \text{equation. 1}$$

where the drought effect (DOC_d) was determined as the percentage difference in DOC each summer (DOC_a) compared to the long-term summer average (DOC_b). We used linear regression with the number of low flow days in the summer period to test the prediction that average DOC concentrations would decline with drying severity (Figure 2). Finally, we used a similar regression approach to test whether DOC in forest and mire groundwater were also affected by drought severity by comparing values measured in the summer to pre-drought values (end of May-June average).

The effect of prolonged summer low flows on the initial flush of DOC (DOC_d) upon rewetting was estimated as the difference between DOC measured after the longest low flow period (when there was a rain event that caused an increase in runoff) (DOC_a) and DOC measured before the onset of low flows each summer (DOC_b) (equation. 1). Here, we expected that DOC produced in soils during the dry periods would be flushed out in the first rewetting event, reflecting processes hindering DOC consumption or favoring DOC production during drought. We used linear regression with the number of low flows in each summer to test whether changes in DOC were related to the duration of the low flow periods. For

groundwater analysis, similar calculations were used to show the differences between the post-summer (September values) and pre-summer (-June) values and to ask whether there were any post-drought effects on groundwater in either the forest soils or mires (Fig. S2). All differences were expressed as percentage changes from the pre-drought concentrations. As above, we used the linear regression with the number of flow days below the 0.1 mm day⁻¹ threshold to test whether the magnitude of these (lagged) effects was related to the severity of summer drying.

Drought and Post-drought effects on LMW DOC and CN ratio

The drought and post-drought effects analysis for LMW DOC and CN ratio followed the same procedure as used in the DOC modeling for stream water and groundwater data. With these two independent variables of carbon character, we expected that changes that occur as a result of the prolonged dry summer periods would be reflected in the quality of the carbon (LMW DOC and CN ratio) when soils are flushed during rewetting. In these analyses, we expected that if the drought and post-drought effects on DOC are purely hydrological, there would be no change in the LMW DOC and CN ratio indicating that the quality is unaffected by prolonged dry periods. Here, an increasing trend in the absorption ratio (254/365 nm) signifies a shift to carbon with low molecular weight and higher bacterial productivity^{16,49} while increasing CN ratio may indicate increasing biodegradability of DOC⁵⁰. Conversely, decreasing absorption ratios indicates a shift to more aromatic compounds with higher molecular weight, while a lower CN ratio indicates DOC supply from more strongly processed soils at lower depths⁵¹.

Slope relationships with land cover and catchment area

To better understand the drivers of drought response, we tested how the slope of the regression relating DOC change to drought duration at each site varied with catchment features. The slope of this relationship represents the rate of change in DOC concentration as drought magnitude increases at each stream, thus providing an integrative assessment of drought sensitivity. We used stepwise multiple linear regression (in Minitab 18.1) to test whether this response varied among streams as a function of subcatchment size, as well as the percentage of peat soils, forest, lake, and sedimentary soil cover in each subcatchment.

Declarations

Acknowledgments

We thank the funders of the Krycklan Catchment Study, including the Swedish Science Foundation (VR), Swedish Infrastructure for Ecosystem Science (SITES), the VR extreme event project, Future Forest, Kempe Foundation, the Swedish Research Council for Sustainable Development (FORMAS), HiFreq (Horizon 2020) and the Swedish Nuclear Waste Company (SKB). It should be noted that there are no data sharing issues and information necessary to reproduce this research can be obtained from the catchment website (<http://slu.se/Krycklan>).

Author Contributions: Tejshree Tiwari created the models and prepared the manuscript, Ryan Sponseller was part of designing the study, interpreting the results, and writing the manuscript, Hjalmar Laudon initiated and conceptualized the study, provided the data, assisted in the interpreting and writing the manuscript, and acquired the funding.

References

1. Buntgen, U. *et al.* Recent European drought extremes beyond Common Era background variability. *Nat Geosci*, doi:10.1038/s41561-021-00698-0 (2021).
2. Vonk, J. E. *et al.* Reviews and syntheses: Effects of permafrost thaw on Arctic aquatic ecosystems. *Biogeosciences* **12**, 7129–7167, doi:10.5194/bg-12-7129-2015 (2015).
3. Granados, V. *et al.* The interruption of longitudinal hydrological connectivity causes delayed responses in dissolved organic matter. *Sci Total Environ* **713**, doi:10.1016/j.scitotenv.2020.136619 (2020).
4. Bradshaw, C. J. A. & Warkentin, I. G. Global estimates of boreal forest carbon stocks and flux. *Global Planet Change* **128**, 24–30, doi:10.1016/j.gloplacha.2015.02.004 (2015).
5. Aiken, G. R., Hsu-Kim, H. & Ryan, J. N. Influence of Dissolved Organic Matter on the Environmental Fate of Metals, Nanoparticles, and Colloids. *Environ Sci Technol* **45**, 3196–3201, doi:10.1021/es103992s (2011).
6. Creed, I. F. *et al.* Global change-driven effects on dissolved organic matter composition: Implications for food webs of northern lakes. *Global Change Biol* **24**, 3692–3714, doi:10.1111/gcb.14129 (2018).
7. Karlsson, J. *et al.* Light limitation of nutrient-poor lake ecosystems. *Nature* **460**, 506–U580, doi:10.1038/nature08179 (2009).
8. Dittman, J. A. *et al.* Mercury dynamics in relation to dissolved organic carbon concentration and quality during high flow events in three northeastern US streams. *Water Resour Res* **46**, doi:10.1029/2009wr008351 (2010).
9. Ritson, J. P. *et al.* The effect of drought on dissolved organic carbon (DOC) release from peatland soil and vegetation sources. *Biogeosciences* **14**, 2891–2902, doi:10.5194/bg-14-2891-2017 (2017).
10. Brailsford, F. L. *et al.* Microbial uptake kinetics of dissolved organic carbon (DOC) compound groups from river water and sediments. *Sci Rep-Uk* **9**, doi:10.1038/s41598-019-47749-6 (2019).
11. Rodriguez-Cardona, B., Wymore, A. S. & McDowell, W. H. DOC:NO₃⁻ ratios and NO₃⁻ uptake in forested headwater streams. *J Geophys Res-Bioge* **121**, 205–217, doi:10.1002/2015jg003146 (2016).
12. Tiwari, T., Laudon, H., Beven, K. & Agren, A. M. Downstream changes in DOC: Inferring contributions in the face of model uncertainties. *Water Resour Res* **50**, 514–525, doi:10.1002/2013wr014275 (2014).
13. Zarnetske, J. P., Bouda, M., Abbott, B. W., Saiers, J. & Raymond, P. A. Generality of Hydrologic Transport Limitation of Watershed Organic Carbon Flux Across Ecoregions of the United States.

Geophys Res Lett **45**, 11702–11711, doi:10.1029/2018gl080005 (2018).

14. Christ, M. J. & David, M. B. Temperature and moisture effects on the production of dissolved organic carbon in a Spodosol. *Soil Biol Biochem* **28**, 1191–1199, doi:10.1016/0038-0717(96)00120-4 (1996).
15. Roth, V. N. *et al.* Persistence of dissolved organic matter explained by molecular changes during its passage through soil. *Nat Geosci* **12**, 755–, doi:10.1038/s41561-019-0417-4 (2019).
16. Berggren, M., Laudon, H. & Jansson, M. Landscape regulation of bacterial growth efficiency in boreal freshwaters. *Global Biogeochem Cy* **21**, doi:10.1029/2006gb002844 (2007).
17. Dehaan, H. Solar Uv-Light Penetration and Photodegradation of Humic Substances in Peaty Lake Water. *Limnol Oceanogr* **38**, 1072–1076, doi:10.4319/lo.1993.38.5.1072 (1993).
18. Dahlen, J., Bertilsson, S. & Pettersson, C. Effects of UV-A irradiation on dissolved organic matter in humic surface waters. *Environ Int* **22**, 501–506, doi:10.1016/0160-4120(96)00038-4 (1996).
19. Ledesma, J. L. J. *et al.* Towards an Improved Conceptualization of Riparian Zones in Boreal Forest Headwaters. *Ecosystems* **21**, 297–315, doi:10.1007/s10021-017-0149-5 (2018).
20. Gomez-Gener, L., Lupon, A., Laudon, H. & Sponseller, R. A. Drought alters the biogeochemistry of boreal stream networks. *Nat Commun* **11**, 1795, doi:10.1038/s41467-020-15496-2 (2020).
21. Laudon, H. *et al.* Patterns and Dynamics of Dissolved Organic Carbon (DOC) in Boreal Streams: The Role of Processes, Connectivity, and Scaling. *Ecosystems* **14**, 880–893, doi:10.1007/s10021-011-9452-8 (2011).
22. Winterdahl, M. *et al.* Riparian soil temperature modification of the relationship between flow and dissolved organic carbon concentration in a boreal stream. *Water Resour Res* **47**, doi:10.1029/2010wr010235 (2011).
23. Pastor, J. *et al.* Global warming and the export of dissolved organic carbon from boreal peatlands. *Oikos* **100**, 380–386, doi:10.1034/j.1600-0706.2003.11774.x (2003).
24. Gundersen, P. *et al.* Do indicators of nitrogen retention and leaching differ between coniferous and broadleaved forests in Denmark? *Forest Ecol Manag* **258**, 1137–1146, doi:10.1016/j.foreco.2009.06.007 (2009).
25. Rumpel, C. & Kogel-Knabner, I. Deep soil organic matter-a key but poorly understood component of terrestrial C cycle. *Plant Soil* **338**, 143–158, doi:10.1007/s11104-010-0391-5 (2011).
26. Callesen, I., Raulund-Rasmussen, K., Westman, C. J. & Tau-Strand, L. Nitrogen pools and C: N ratios in well-drained Nordic forest soils related to climate and soil texture. *Boreal Environ Res* **12**, 681–692 (2007).
27. Marty, C., Houle, D., Gagnon, C. & Courchesne, F. The relationships of soil total nitrogen concentrations, pools and C:N ratios with climate, vegetation types and nitrate deposition in temperate and boreal forests of eastern Canada. *Catena* **152**, 163–172, doi:10.1016/j.catena.2017.01.014 (2017).
28. Werner, B. J. *et al.* High-frequency measurements explain quantity and quality of dissolved organic carbon mobilization in a headwater catchment. *Biogeosciences* **16**, 4497–4516, doi:10.5194/bg-16-

- 4497-2019 (2019).
29. Fenner, N. & Freeman, C. Drought-induced carbon loss in peatlands. *Nat Geosci* **4**, 895–900, doi:10.1038/Ngeo1323 (2011).
 30. Bragazza, L. *et al.* Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global Change Biol* **22**, 4114–4123, doi:10.1111/gcb.13319 (2016).
 31. Stirling, E., Fitzpatrick, R. W. & Mosley, L. M. Drought effects on wet soils in inland wetlands and peatlands. *Earth-Sci Rev* **210**, doi:10.1016/j.earscirev.2020.103387 (2020).
 32. Berggren, M., Laudon, H. & Jansson, M. Bacterial utilization of imported organic material in three small nested humic lakes. *Int Ver Theor Angew* **30**, 1393+ (2010).
 33. Kritzberg, E. S. *et al.* Browning of freshwaters: Consequences to ecosystem services, underlying drivers, and potential mitigation measures. *Ambio* **49**, 375–390, doi:10.1007/s13280-019-01227-5 (2020).
 34. Peralta-Tapia, A. *et al.* Scale-dependent groundwater contributions influence patterns of winter baseflow stream chemistry in boreal catchments. *J Geophys Res-Bioge* **120**, 847–858, doi:10.1002/2014jg002878 (2015).
 35. Lavonen, E. E., Gonsior, M., Tranvik, L. J., Schmitt-Kopplin, P. & Kohler, S. J. Selective Chlorination of Natural Organic Matter: Identification of Previously Unknown Disinfection Byproducts. *Environ Sci Technol* **47**, 2264–2271, doi:10.1021/es304669p (2013).
 36. Geris, J., Tetzlaff, D. & Soulsby, C. Resistance and resilience to droughts: hydrogeological controls on catchment storage and run-off response. *Hydrological Processes* **29**, 4579–4593, doi:10.1002/hyp.10480 (2015).
 37. Karlsen, R. H. *et al.* The role of landscape properties, storage and evapotranspiration on variability in streamflow recessions in a boreal catchment. *J Hydrol* **570**, 315–328, doi:10.1016/j.jhydrol.2018.12.065 (2019).
 38. Fork, M. L., Sponseller, R. A. & Laudon, H. Changing Source-Transport Dynamics Drive Differential Browning Trends in a Boreal Stream Network. *Water Resour Res* **56**, doi:10.1029/2019WR026336 (2020).
 39. Crowther, T. W. *et al.* Quantifying global soil carbon losses in response to warming. *Nature* **540**, 104–+, doi:10.1038/nature20150 (2016).
 40. Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P. & Dosio, A. Will drought events become more frequent and severe in Europe? *Int J Climatol* **38**, 1718–1736, doi:10.1002/joc.5291 (2018).
 41. Kaiser, K., Canedo-Oropeza, M., McMahon, R. & Amon, R. M. W. Origins and transformations of dissolved organic matter in large Arctic rivers. *Sci Rep-Uk* **7**, doi:10.1038/s41598-017-12729-1 (2017).
 42. Laudon, H., Sponseller, R. A. & Bishop, K. From legacy effects of acid deposition in boreal streams to future environmental threats. *Environ Res Lett* **16**, doi:10.1088/1748-9326/abd064 (2021).
 43. Ledesma, J. L. J. *et al.* Riparian zone control on base cation concentration in boreal streams. *Biogeosciences* **10**, 3849–3868, doi:10.5194/bg-10-3849-2013 (2013).

44. Oni, S. K. *et al.* Long-term patterns in dissolved organic carbon, major elements and trace metals in boreal headwater catchments: trends, mechanisms and heterogeneity. *Biogeosciences* **10**, 2315–2330, doi:10.5194/bg-10-2315-2013 (2013).
45. Karlsen, R. H. *et al.* Landscape controls on spatiotemporal discharge variability in a boreal catchment. *Water Resour Res* **52**, 6541–6556, doi:10.1002/2016wr019186 (2016).
46. Laudon, H. *et al.* The Krycklan Catchment Study-A flagship infrastructure for hydrology, biogeochemistry, and climate research in the boreal landscape. *Water Resour Res* **49**, 7154–7158, doi:10.1002/Wrcr.20520 (2013).
47. Laudon, H., Kohler, S. & Buffam, I. Seasonal TOC export from seven boreal catchments in northern Sweden. *Aquat Sci* **66**, 223–230, doi:10.1007/s00027-004-0700-2 (2004).
48. Tiwari, T., Sponseller, R. A. & Laudon, H. Extreme Climate Effects on Dissolved Organic Carbon Concentrations During Snowmelt. *J Geophys Res-Bioge* **123**, 1277–1288, doi:10.1002/2017jg004272 (2018).
49. Fellman, J. B., D'Amore, D. V., Hood, E. & Boone, R. D. Fluorescence characteristics and biodegradability of dissolved organic matter in forest and wetland soils from coastal temperate watersheds in southeast Alaska. *Biogeochemistry* **88**, 169–184, doi:10.1007/s10533-008-9203-x (2008).
50. Hunt, A. P., Parry, J. D. & Hamilton-Taylor, J. Further evidence of elemental composition as an indicator of the bioavailability of humic substances to bacteria. *Limnol Oceanogr* **45**, 237–241, doi:10.4319/lo.2000.45.1.0237 (2000).
51. Kindler, R. *et al.* Dissolved carbon leaching from soil is a crucial component of the net ecosystem carbon balance. *Global Change Biol* **17**, 1167–1185, doi:10.1111/j.1365-2486.2010.02282.x (2011).

Tables

Table 1. The regression coefficient of Drought and Post-drought responses of DOC, LMW DOC, and CN ratio in the sub-catchments used in this study

Sites	Drought			Post-drought		
	DOC	LMW DOC	CN ratio	DOC	LMW DOC	CN ratio
C1	0.42	0.20	0.25	0.33	0.24	0.14*
C2	0.29	0.37	0.27	0.39	0.56	0.50
C4	0.41	0.45	0.43	0.65	0.64	0.44
C5	0.33	0.28	0.47	0.07*	0.36	0.58
C6	0.36	0.02*	0.31	0.42	0.36	0.20
C7	0.51	0.14*	0.39	0.67	0.27	0.40
C9	0.43	0.20	0.27	0.58	0.17*	0.36
C10	0.52	0.04*	0.20	0.60	0.21	0.43
C12	0.65	0.02*	0.37	0.45	0.45	0.59
C13	0.30	0.01*	0.29	0.12*	0.59	0.14*
C14	0.60	0.40	0.41	0.28	0.31	0.46
C15	0.52	0.54	0.13*	0.20*	0.35	0.33
C16	0.39	0.50	0.30	0.31	0.39	0.31

All values significant at $p < 0.05$ except *

Figures

Figure 1

Variation in discharge from C7 in the Krycklan catchment showing summer low flow days $<0.1 \text{ mm day}^{-1}$ (a), and the distribution of discharge over the years with 0.1 mm day^{-1} thresholds (b). The jitter dots are actual discharge values for each year from which the ridgeline distribution curve was estimated in panel B.

Figure 2

Changes in DOC concentrations across 13 nested sub-catchments over 17 years in relation to summer low flows showing (a) Drought (r^2 range 0.29-0.65, $p < 0.05$) and (b) Post-drought (r^2 range 0.28-0.67, $p < 0.05$). The points represent the changes in concentration of each summer fitted with regression lines for individual catchments. The red horizontal line indicates zero change while the vertical grey line indicates average low flow days (18 days). Note differences in y-axis scales.

Figure 3

Monthly variation in DOC changes relative to the long term means from 2003-2019 in the Krycklan sub-catchments showing the long-term DOC mean (black line) and the years with the high number of low flow days (above the 90th percentile) (blue line), years with the lowest number of low flow days (orange) and the years with average low flow days (grey dots) in Krycklan. The loess regression curves show the average DOC change in years with the high number of low flow days (blue) and low number of low flow days (orange)

Figure 4

The Drought and Post-drought effects of LMW DOC (a: where r^2 range 0.20-0.54, $p < 0.05$ and, b: where r^2 range 0.21-0.64, $p < 0.05$ respectively) and CN ratio (c: where r^2 range 0.27-0.47, c: where r^2 range 0.2-0.59, $p < 0.05$) of 13 boreal sub-catchments stream chemistry. Data for the CN ratio for the driest summer (2006) is missing because sampling started in 2007. Additionally, for some of the larger sites (C10, C12, C14, C15), sampling stopped in 2017 hence data for 2018 and 2019 were unavailable.

Figure 5

Drought and post-drought effects on groundwater DOC (a, b), LMW DOC (c, d), and CN ratio (e, f). Riparian wells values were obtained from averages of samples at depths of 0.1-0.65 m while values from the mire wells were obtained from averages of sampling at depths 2-2.5, which is consistent with the dominant flow paths for the two catchments (Laudon et al. 2013).

Figure 6

DOC slope responses to summer low flows, modeled using the best predictor (catchment size) during (a) Drought and (b) Post-drought. Note only significant values were used in the models

Figure 7

Conceptual responses of DOC, LMW DOC, and CN ratio to summer low flow conditions at different time intervals representing our predictions for (a) the Drought effects during summer, and (b) the Post-drought effects after the first rewetting in relation to long-term averages normalized to seasons.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementary.docx](#)