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Interactive Effects of Drought and Shading on Boreal Stream Metabolism and Algal Biomass in Experimental Mesocosms

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ABSTRACT

1. Boreal catchments are experiencing intensified land-use and climate change simultaneously, yet these stressors are seldom addressed in conjunction. It is expected that exposing multiple stressors on an ecosystem will have interactive effects, and here we aimed at testing the effects of drought and loss of shading on stream ecosystem functioning.
2. We exposed natural substrates in experimental, outdoor flumes under a gradient of shading (from 0% to 74%) to a 2-week drought and assessed the effects on benthic algal biomass (chl-α) and whole channel metabolic rates (Gross Primary Production, GPP and Ecosystem Respiration, ER) for 5 weeks pre and 2 weeks post-drought.
3. Drought and shading had interactive effects on all response variables, but the magnitude varied over the course of the experiment. Chl-α was initially strongly negatively correlated with shading level, but the drought and onset of autumn conditions post-drought together diminished the shading effects. The drought effect on chl-α was only significant for 1 week post-drought, after which algae in some channels had recovered. However, for metabolic rates, the effect of drought was sustained during the whole 2-week period post-drought, and we did not see recovery.
4. We show that streams in this boreal setting, with a lack of sufficient shading (<43%) grow an algal community dominated by fast growing, filamentous algae which promote high respiration rates and that fail to recover post-drought. Algae in the most heavily shaded streams (74%) were not filamentous, and they recovered in biomass (chl-α) post-drought, but they had low metabolic rates both pre- and post-drought. This interaction of shading and drought has implications for how we manage our forested streams and highlights the susceptibility of streams with limited shade to drought.

1 | Introduction

Global change is reshaping ecosystems worldwide, encompassing multiple interacting pressures such as intensified land use and climate change (Mantyka-Pringle et al. 2012). Boreal headwater streams play a critical role in biogeochemical cycles, as well as in supporting unique communities (Soininen et al. 2016; Sponseller et al. 2016). Yet, these ecosystems are increasingly subjected to intensified land use, particularly forestry, and co-current climate-induced alterations such as flow regime changes (Yonce et al. 2021). The impacts of forestry and climate-induced stressors, with rising temperatures and altered precipitation patterns, have so far mostly been studied in isolation (but see Truchy et al. 2020) or in nutrient-rich, temperate conditions (Nelson et al. 2023; Zlatanović et al. 2018). These studies show that responses of community respiration and periphytic algae to drought and low flow in temperate streams can be dependent on secondary stressors, specifically shading and sediment structure

(Zlatanović et al. 2018), or nutrient pollution and sedimentation (Baattrup-Pedersen et al. 2020). Consequently, it is becoming evident that these co-current pressures may lead to interactive effects (Murdoch et al. 2020) and that the increasing occurrence of drought in an otherwise wet boreal setting can exacerbate underlying pressures and result in unexpected effects on the freshwater ecosystem (Teutschbein et al. 2015; Wang et al. 2014). It is therefore imperative to investigate how drought interacts with other underlying pressures in boreal streams, specifically those caused by intense forestry practices.

In boreal forest streams, intense clearcut forestry without adequate riparian protection often leads to clearing of riparian vegetation and, consequently, a loss of shading (Jyväsjärvi et al. 2020; Ring et al. 2022). Shading levels directly influence light availability, but also stream temperatures (Myrstener, Greenberg, Lidberg, and Kuglerová 2025), altering stream ecosystem functions, including algal growth and metabolic rates (Weaver and Jones 2022). In addition, these boreal stream functions are mediated by nutrient availability (Burrows et al. 2021; Johnson et al. 2023) and disturbance regimes (Holopainen and Huttunen 1992). Loss of shading can lead to fast-growing filamentous algae outcompeting slower-growing communities (Noel et al. 1986; Myrstener et al. 2023), risking negative effects on food webs (Tonkin et al. 2014), and changing the overall seasonality of primary production (Breuer et al. 2016). Increasing light levels to streams can additionally promote heterotrophic activity due to its close connection to primary production (Demars et al. 2020; Hotchkiss and Hall 2015), yet in temperate streams it has been found that this effect will vary with differences in bottom sediment (Marcarelli et al. 2015) and nutrient availability (Weaver and Jones 2022). Nevertheless, how altered light regimes affect boreal stream biofilm and metabolic responses to other types of disturbance (Warren et al. 2018), including changes in the flow regime, is less explored.

Co-currently with intense forestry, boreal forests are experiencing increased frequency and intensity of drought events because of climate change (Teutschbein et al. 2015; Wang et al. 2014). Although little attention has traditionally been given to drought in boreal waters, due to its limited occurrence in comparison to temperate and arid zones, it has become a topic of concern in the last decade with frequent drought of headwaters (Tiwari et al. 2022). While total river discharge is predicted to increase in most boreal zones, on an annual scale (Teutschbein et al. 2015), summer droughts are predicted to increase (Liu et al. 2023). Drought drastically alters stream hydrology, leading to reduced water flow, and in extreme cases, complete drought of streambeds. This is likely to reduce periphytic biomass (Truchy et al. 2020) and increase concentrations of DOC (Harjung et al. 2019; Tiwari et al. 2022) and heterotrophic activity (Zlatanović et al. 2018). The reduction in water volume during droughts also concentrates nutrients and pollutants in pools, potentially leading to algal blooms and oxygen depletion (Gómez-Gener et al. 2020).

Given that boreal stream metabolic rates and algal biomass vary depending on shading regimes (Myrstener, Greiser, and Kuglerová 2025; Weaver and Jones 2022), mediated by nutrient availability (Burrows et al. 2021), the effects of drought might differ depending on the shading level (Barthès et al. 2015). Furthermore, drought effects can vary depending on the types of benthic algae (Peterson 1987; Falasco et al. 2020), which in turn are shaped by shading regimes. Ultimately, it is very hard to predict drought effects on biofilms in boreal, headwater streams, as they might be less adapted to drought, in contrast to intermittent streams, where drought-rewetting occurs often, and most studies have been done (Colls et al. 2019; Steinman and McIntire 1990). Understanding these interactions is crucial for developing effective management and conservation strategies to mitigate the impacts of simultaneous land-use and climate changes on boreal stream ecosystems.

This study aims to assess the interactive effects of loss of shading and drought on stream ecosystem functioning, focusing on algal biomass and whole channel metabolism (gross primary production: GPP and ecosystem respiration: ER). We tested this in artificial, outdoor channels using a gradient in shading levels from 0% to 74% and 2 weeks of little to no flow, with a following 2-week recovery period. We dried half our channels for 2 weeks in September, which is within normal ranges for drought duration and timing for Northern Sweden (Teutschbein et al. 2022) and in line with a Finnish drought experiment by Truchy et al. (2020). We hypothesized that drought would promote ER over GPP. We further hypothesized that drought would decrease algal biomass and that the effect would be strongest in the low shading treatments due to low drought tolerance of the algal community that developed under low shading conditions.

2 | Methods

2.1 | Experimental Design

In this study, we tested the interactive effects of shading and drought on algal biomass and ecosystem metabolism. We used 12 outdoor, artificial channels with shade cloths to mimic differences in canopy cover, and in addition, we induced a 2-week drought. The experiment ran from August 4 to October 3. We established bare, uncolonized stream substrates (sand and cobbles) and shade cloths on August 7. The biofilms grew for 1 month before the drought was implemented on September 5. First, the water discharge was lowered by 90% for 1 week, and after that, the water was turned off completely for another week. This timing and duration of drought is within normal ranges for drought duration, magnitude, and timing for Northern Sweden (Gómez-Gener et al. 2020; Teutschbein et al. 2022). The water was started again on September 19.

The artificial channels (or flumes, Figure 1) are located at Svartberget field station in northern Sweden (Laudon et al. 2021). There are 12 individual flumes, each 15 m long and 0.2 m wide and water depth varied from 0.003 to 0.01 m (top to bottom), with a slope of ~0.005 m m^{-1}. Water discharge was constant at 1–2 L s^{-1} and velocity was 0.1 m s^{-1}, which is representative of summer (June–August) and early autumn (September–October) base flow conditions in the surrounding headwater streams (Krycklan Catchment Study 2025). Water to the flumes was continuously pumped from an adjacent forest stream using a bilge pump (Flygt KS 2610) to a 3000 L water collection tank, from which the water flows to four 1000 L boxes, each feeding three of the channels (Figure 1). The residence time in the boxes is

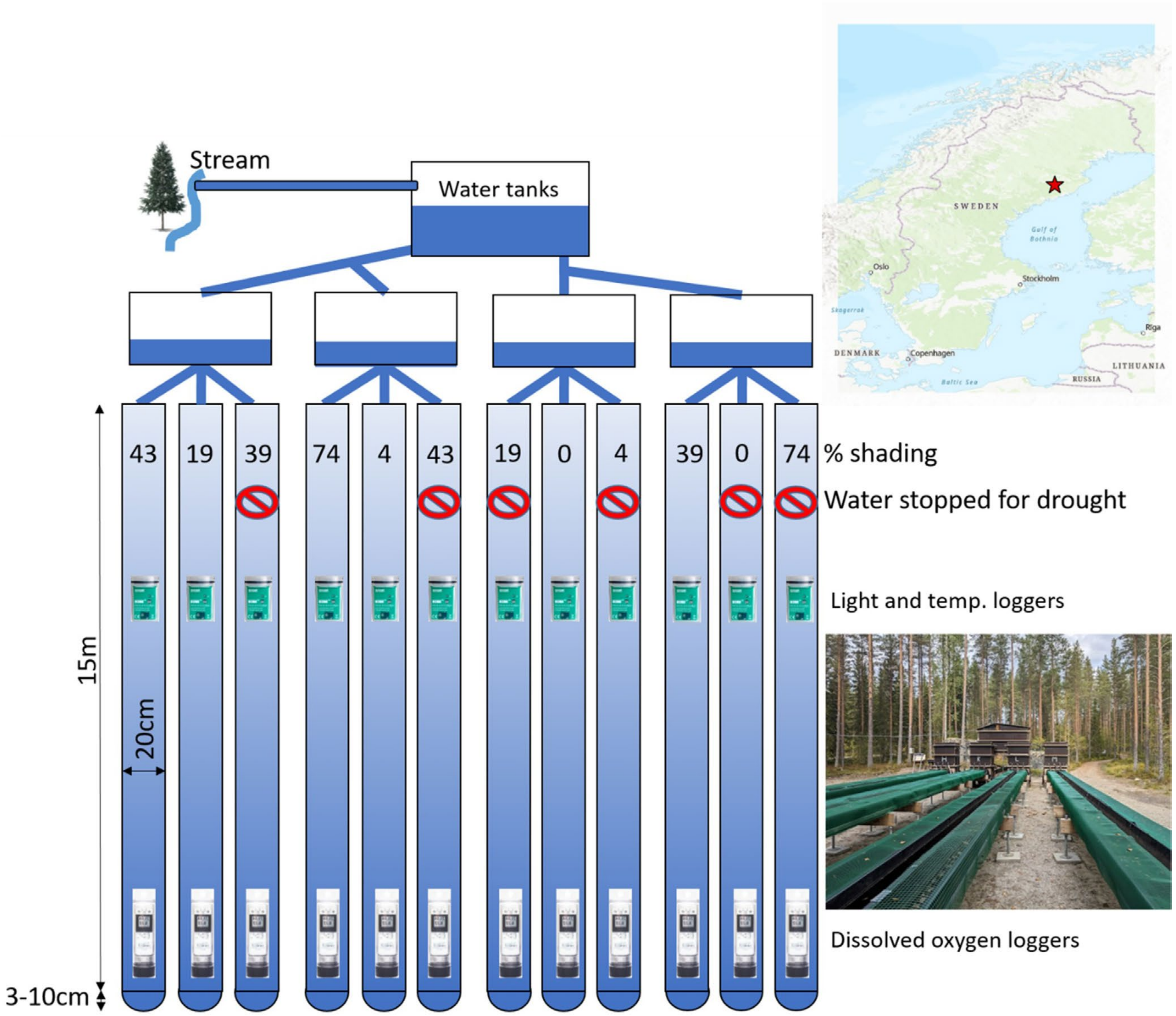

FIGURE 1 | Experimental set-up of the flumes showing shading and drought treatments. Photo by Maria Myrstener.

less than 30 min. This setup ensures that water is well mixed in the tank and boxes so that all flumes have similar chemistry (Myrstener et al. 2023). The bottom substrates in all flumes were made up of a 1–2 cm layer of finer sediments (majority being sand) on the bottom, with one layer of coarser substrates on top (pebbles, cobbles) from a nearby quarry, representing local, natural material, dominated by gneiss and granite.

We created a gradient of shading using shade cloths (from polypropen) with 0 (no cloth), 4%, 19%, 39%, 43%, and 74% shading. This shading was supposed to mimic different canopy cover, with the highest shading (74%) representing a stream surrounded by mature forest dominated by spruce and the lowest shading representing a stream in a harvest site. The gradient in between reflects different levels of riparian protection (Chellaiah and Kuglerová 2021). Each shading treatment was replicated twice to facilitate drought of one channel per shading treatment during the second half of the experiment. Shading and drought treatments were assigned randomly (Figure 1). We ran the experiment with shade cloths for 5 weeks, and on September 5th; we gradually turned off the water inlet to half of the channels (one replicate of each shading level) for 2 weeks, until September 18. During the first week of the drought, water was decreased by 90%, and during the second week, we turned the water off completely to mimic a gradually occurring drought. During the week when the water was fully turned off, there was still moisture on the bottom of the channel bed, but elevated rocks were completely dry (Figure 2). On September 18, water to the dry channels was turned back on, and we continued the experiment for another 2 weeks to capture recovery. We stopped the experiment on October 3 coinciding with high flows in surrounding streams because of increased precipitation.

2.2 | Water Temperature, Light and Chemistry

We recorded incident light in lux and water temperature in celcius every 15 min using two Hobo pendant loggers (Onset Computer Corporation, Borne, U.S.A.) per channel. We did not estimate lux or temperature in the dry channels during the

FIGURE 2 | Photo showing a close-up of the wet versus the onset of the drought treatment. Stones were dry during the drought, while the sand below was moist and with ~0.5 cm of standing water in some places. Photo by Maria Myrstener.

drought period (as this would have recorded air temperature and lux). Lux was converted to photosynthetically active radiation (PAR), using a conversion factor of 0.0185 according to Thimijan and Heins (1983) and presented as daily photon flux (DPF, mol photons m^{-2} day^{-1}). Loggers were cleaned from algal growth and debris 1–2 times per week. We sampled water from the boxes and from the downstream end of each channel three times to measure concentrations of nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}) and dissolved organic carbon (DOC). This was done at the start of the experiment (2023-08-07), pre-drought (2023-09-05), and immediately after turning the dry channels back on (2023-09-18). Dissolved inorganic nitrogen (DIN) hereafter represents the sum of NO_3^- and NH_4^+. Water was filtered (0.45 μm) on site and kept refrigerated (DOC) or frozen (DIN and PO_4^{3-}) before colorimetric analysis of NO_3^--N (Method G-384-08), NH_4^+-N (Method G-171-96), and PO_4^{3-} (Method G-297-03) with an Auto Analyser 3 Spectrophotometer (Omniprocess).

2.3 | Chlorophyll-α

We used chl-α as a proxy for the standing stock of periphytic algal biomass on the natural bottom substrate (cobbles and sand) of the channels. Chl-α standing stocks were estimated by using a BenthoTorch (Moldanke BBE). The BenthoTorch is a handheld instrument that analyses chl-α pigments in situ by fluorescence. The BenthoTorch measures an area of 1.1 cm^2 and we systematically measured each channel once per week using established transects from top to bottom with 10 measurements per channel and sampling occasion. The BenthoTorch enables frequent and non-destructive estimates of chl-α, which we could not accomplish using ceramic tiles or other sub-sampling of the channel bottom.

2.4 | Ecosystem Metabolism

Details on metabolic calculations in this facility are presented in Myrstener et al. (2023), in short, one miniDOT logger (Precision Measurement Engineering Inc., USA) was placed at the downstream end of each channel to record dissolved oxygen at 10-min intervals. We recorded oxygen throughout the experimental period (August 7 to October 4), except in the dry channels during the drought, as these did not have water during that time. Ecosystem metabolism was estimated using the single-station diel oxygen method where gross primary production (GPP) and Ecosystem Respiration (ER) were estimated using Bayesian inverse modelling. We used time series of dissolved oxygen (DO), water temperature, light (from lux loggers), as well as a constant gas exchange rate coefficient (K) and channel depth (z). The main equation for GPP and ER was:

$$\mathrm{dDO} / \mathrm{dt} = (\mathrm{GPP} + \mathrm{ER}) / \mathrm{z} + \mathrm{K}(\mathrm{DOsat} - \mathrm{DO})$$

The change in oxygen over time (O_2 m^{-3}) equals all oxygen produced by photosynthesis (GPP, g O_2 m^{-2} d^{-1}) minus all oxygen consumed by respiration of both autotrophs and heterotrophs (ER, g O_2 m^{-2} d^{-1}) and the rate of gas exchange between the water and air (K, d^{-1}). We modelled GPP and ER and used constant K based on nighttime regression analysis. Usually, K is modelled based on a K ~ discharge relationship because these variables co-vary. As Q is stable in the channels, we used the same K for the whole period, and this K was based on nighttime regression from the channels. We divided the experimental period into four periods and presented the metabolic rates as the average daily rates over each period. As water is well mixed in the boxes and in the inlet of the channels, we expect little influence of the box and upstream water on the channel metabolism. In any case, all channels have the same background input.

2.5 | Data Analysis

2.5.1 | Light, Temperature and Water Chemistry

Water chemistry, more precisely DOC, phosphate, ammonium, and nitrate, is presented for all three sampling rounds. Averages in water chemistry are summarised for dry and wet channels per sampling round and the differences in the post-drought measurements are compared using *t*-tests for phosphate (log-transformed), ammonium, and nitrate and a *U*-test for DOC.

2.5.2 | Effects of Shading Level and Drought

The effects of shading level and drought on chl-α, GPP, and ER were analysed using a linear mixed-effects ANOVA model. The models included chl-α, GPP, and ER respectively, as the dependent variable, and drought (dry vs. wet) and shading (gradient from 0% to 74%) as the fixed factors, with their interaction (drought × shading) modelled to assess their combined effect. Shading was treated as a continuous variable because we saw a linear relationship between shading level and the dependent variables. Channel ID was included as a random effect to account for channel-specific variability in measurements. The model was fitted using the lme function from the nlme package (Pinheiro et al. 2021) in R. Specifically, the model was expressed as (example with GPP):

$$\mathrm{GPP} \sim \mathrm{Drought}^{*}\mathrm{Shading1} + \mathrm{Drought}^{*}\mathrm{Week} + \mathrm{Shading1}^{*}\mathrm{Week},\ \mathrm{random} = \sim 1 \,|\, \mathrm{Channel}$$

To assess the effects of drought and shading for each week of the experiment, we used estimated marginal means (emmeans package, Lenth 2023) and performed pairwise contrasts within each week. Statistical significance was determined using F-tests from joint tests and the multiple comparisons were adjusted using Tukey's Honestly Significant Difference test.

3 | Results

3.1 | Light, Temperature and Water Chemistry

Light varied strongly among channels with the daily photon flux in open channels nearly five-fold higher compared to the highly shaded channels (Table 1). Water temperatures were generally similar between wet and dry channels (Table 1).

Water chemistry varied substantially over time with DOC, phosphate, ammonium, and nitrate all decreasing between their initial levels and the start of the drought (Table 2). Post-drought, the dried channels had significantly lower levels of DOC ($p = 0.01$, *U*-test/Wilcoxon rank sum test, Table 2), ammonium ($p = 0.05$, $t = -2.26$, *t*-test, Table 2), and nitrate ($p = 0.02$, $t = -2.92$, *t*-test, Table 2) compared to the wet channels. There was no difference in phosphate concentrations between the dry and wet channels post-drought ($p = 0.29$, $t = -1.16$, *t*-test).

3.2 | Chlorophyll-α

Over the full experiment, chl-α averaged 3.3 μg cm^{-2}, with 3.6 in the wet channels and 2.9 in the dry channels (Figure 3A) and a significant effect of both shading ($F_{1,8} = 18.9$, $p < 0.01$) and drought ($F_{1,8} = 5.9$, $p = 0.04$), and with a significant interaction between the two ($F_{1,8} = 4.5$, $p < 0.01$). The effect of shading and drought varied over the course of the experiment, and the shading effect was strongest before the drought began ($F_{1,8} = 27.0$, $p < 0.01$) with chl-α being 5.8 μg cm^{-2} in the lowest shading and 1.6 μg cm^{-2} in the highest shading (Figure S1). The first sampling post-drought showed no effect of either shading or drought and chl-α averaged 5.0 μg cm^{-2} in the wet channels and 5.2 μg cm^{-2} in the dry channels, compared to 4.9 and 3.8 μg cm^{-2} respectively in the last sampling pre-drought. After the drought, chl-α decreased and averaged only 3.3 μg cm^{-2} in total (4.4 in wet and 2.2 in dry channels, $F_{1,8} = 15.7$, $p < 0.01$). When the experiment ended, 2 weeks after the drought period, there was no clear effect of either shading or drought on chl-α (Figure 3C). The change in chl-α between 1 week pre-drought and 2 weeks post-drought was significantly correlated with shading level

TABLE 1 | Summary of daily photon flux (DPF) and temperature in the experimental flumes.

Channel nr.	Mean DPF (excl. Drought) Mol m^{-2} day^{-1}	Max DPF (excl. Drought) Mol m^{-2} day^{-1}	Mean Temp. (excl. Drought) °C	Mean Temp (incl. Drought, only wet flumes) °C	Max. Temp. °C	Min. Temp. (excl. Drought) °C	Min. Temp (incl. Drought, only wet flumes) °C	Shade	Drought treatment
1	2.63	5.85	10.9	10.5	14.6	6.98	6.17	43%	Wet
2	3.34	7.36	10.9	10.4	14.7	6.88	6.06	19%	Wet
3	2.28	6.77	10.9		14.6	7.08		39%	Dry
4	1.19	2.41	10.9	10.5	14.4	6.98	6.06	74%	Wet
5	4.05	10.07	10.9	10.5	15.2	6.88	6.17	4%	Wet
6	2.62	5.60	10.9		15.4	6.98		43%	Dry
7	4.12	8.78	10.9		15.1	6.98		19%	Dry
8	5.02	10.88	10.9	10.5	15.8	6.98	6.06	0%	Wet
9	4.73	11.48	10.9		15.6	6.98		4%	Dry
10	3.42	6.93	10.8	10.4	15.0	6.88	6.06	39%	Wet
11	4.24	9.15	10.9		15.0	6.98		0%	Dry
12								74%	Dry

Note: Mean and maximum of DPF, and mean, minimum and maximum temperatures are presented for individual channels. Data excludes the drought period, but separate columns provide mean and minimum values for the wetted channels over the entire experiment including the drought. The data for flume 12 is missing as the logger malfunctioned.

TABLE 2 | Summary of water chemistry.

	Date	Channels	N	Mean	SD	Min	Max
DOC (mg L^{-1})	2023-08-07	All	12	49.6	0.4	49.1	50.2
	2023-09-05	All	12	41.5	0.5	40.6	42.1
	2023-09-18	Dry	6	23.3	4.0	16.3	27.3
	2023-09-18	Wet	6	30.2	0.5	29.6	30.8
NH_4 (μg L^{-1})	2023-08-07	All	12	19.8	4.8	15.7	29.8
	2023-09-05	All	12	13.1	0.8	12.2	14.6
	2023-09-18	Dry	6	13.5	4.1	8.3	18.5
	2023-09-18	Wet	6	19.9	5.6	14.7	28.3
NO_3 (μg L^{-1})	2023-08-07	All	12	11.9	1.8	10.0	15.8
	2023-09-05	All	12	10.3	0.4	9.7	10.9
	2023-09-18	Dry	6	8.5	2.0	5.5	11.2
	2023-09-18	Wet	6	11.6	1.5	10.3	13.5
PO_4 (μg L^{-1})	2023-08-07	All	12	5.0	0.4	4.3	5.5
	2023-09-05	All	12	4.2	0.2	3.9	4.6
	2023-09-18	Dry	6	3.9	2.3	2.5	8.5
	2023-09-18	Wet	6	4.4	0.3	3.9	4.8

Note: Averages, standard deviations, and extremes are reported for each sampling occasion of DOC, NH_4, NO_3, and PO_4. For the final sampling date of 2023-09-18, data has been split between the dried and wetted channels. The shading only distinguishes rows with data from all channels and rows with data from either dry or wet channels.

with the largest decrease in chl-α in the low shading channels and no change or an increase in chl-α in the highly shaded channels ($r^2 = 0.53$, $p < 0.01$, Figure 3B).

3.3 | Ecosystem Metabolism (GPP and ER)

Patterns in GPP were similar to chl-α in that there was a significant effect of both shading ($F_{1,8} = 87.4$, $p < 0.01$), drought ($F_{1,8} = 105.9$, $p < 0.01$), and the interaction between the two ($F_{1,8} = 39.4$, $p < 0.01$, Figure 4C). Over the full experiment, average GPP was 0.1 μg O_2 m^{-2} day^{-1}, with 0.15 in the wet channels and 0.04 in the dry channels (Figure 4A). GPP peaked at 0.86 μg O_2 m^{-2} day^{-1} in the low shading, wet channel (Figure S2). For GPP, there was less recovery post-drought, as compared to chl-α, and the drought effect was still significant when the experiment ended 2 weeks post-drought ($F_{1,8} = 130.5$, $p < 0.01$). There was a stronger drought effect on GPP in the unshaded channels as compared to shaded ones, and the delta change in GPP pre- and post-drought showed a weak linear relationship to shading level ($r^2 = 0.54$, $p = 0.059$, Figure 4B) where the least shaded streams lost the most biomass post-drought.

ER showed a similar pattern to GPP, being significantly affected by both shading ($F_{1,8} = 13.2$, $p = 0.01$) and drought ($F_{1,8} = 18.7$, $p < 0.01$), and there was a significant interaction between shading and drought ($F_{1,8} = 24.5$, $p < 0.01$, Figure 5C). The average ER over the whole experiment was −0.85 μg O_2 m^{-2} day^{-1}, with −0.98 μg O_2 m^{-2} day^{-1} for the wet and −0.68 μg O_2 m^{-2} day^{-1} for the dry channels (Figure 5A). The highest ER was recorded in the wet channel with 4% shading at −7.33 μg O_2 m^{-2} day^{-1} (Figure S3). In line with GPP, ER did not recover within the remaining 2 weeks of the experiment after the drought, and drought still had a significant effect on ER at the end of the experiment ($F = 119{,}0$, $p = 0.01$).

Overall, the channels were heterotrophic with an NEP averaging −0.74 μg O_2 m^{-2} day^{-1}. The wet channels were more heterotrophic (NEP = −0.82 μg O_2 m^{-2} day^{-1}) than the dry channels (NEP = −0.63 μg O_2 m^{-2} day^{-1}), with the lowest NEP recorded in the wet channels with the low shading (Figure S4). The difference between the wet and dry channels was largest in the final week of the experiment (Δ = 1.18, wet = −1.99, dry = −0.81 μg O_2 m^{-2} day^{-1}).

4 | Discussion

In this study we combined a continuous shading gradient with a 2-week drought, which enabled us to examine how the strength of drought effects varied across shading levels in boreal outdoor experimental channels. We showed that both shading and drought have significant and interactive effects on primary production and aquatic metabolism. Moderate to high shading levels (43%–74%) supported balanced metabolic conditions, while reduced shading (< 43%) promoted algal overgrowth and more heterotrophy, ultimately decreasing net ecosystem productivity. Drought had strong negative effects on GPP and ER under low shading, with algal biomass showing less pronounced responses, particularly in more shaded channels.

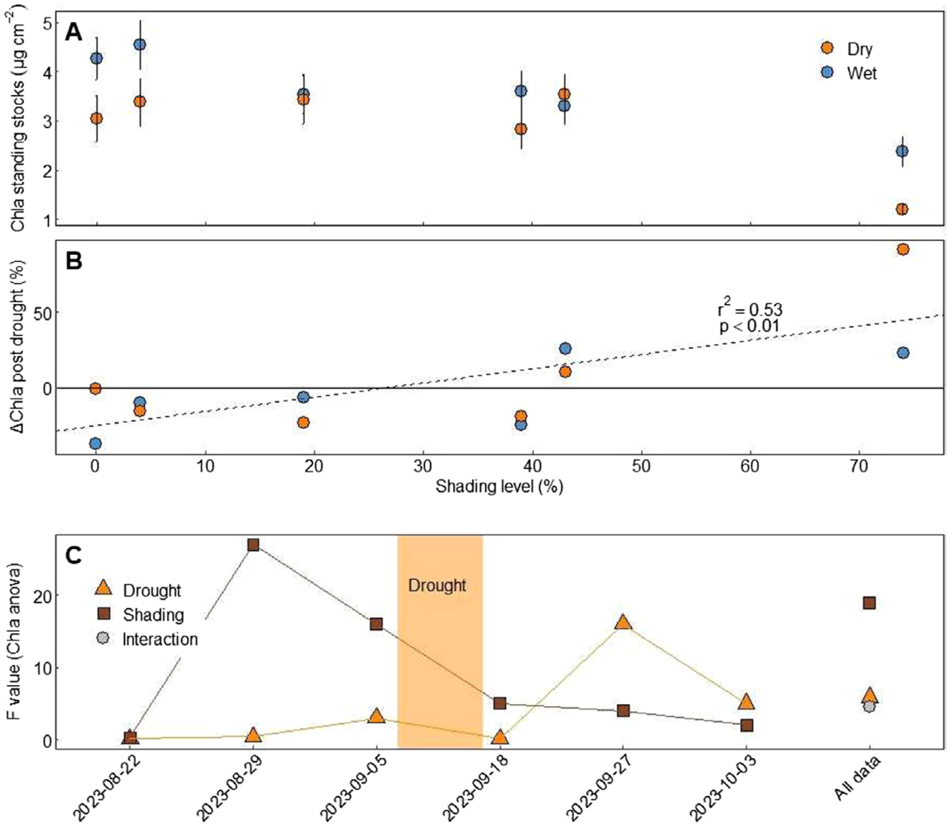

FIGURE 3 | (A) Average (±SE) chl-α standing stocks (μg cm^{-2}) over the whole experiment in the different shading levels with eight estimates per channel and sampling occasion (64 estimates total per point). Wet channels were not exposed to drought while dry channels experienced a 2-week drought. (B) Change in chl-α pre- (2023-08-27 to 2023-09-05) and post- drought (2023-09-19 to 2023-10-02) in the different shading levels. A linear regression between delta chl-α and shading level of both dry and wet channels is presented with r^2 and p value. (C) F values from a linear mixed effect ANOVA on effects of drought and shading on chl-α standing stocks analysed weekly.

4.1 | Effects of Shading

Primary productivity in boreal streams flowing through mature forest stands is often nutrient (Burrows et al. 2021) and/or light limited (Weaver and Jones 2022). Light limitation can be enhanced by intensive forest management that results in dense and even-aged coniferous riparian forests, as compared to older, unmanaged forests (Bechtold et al. 2017; Kuglerová et al. 2025). Removal of shading as a consequence of forest harvesting often results in increased metabolic rates, as well as increased algal biomass, but the effects depend on the remaining riparian buffer and other local stream habitat factors (Burrows et al. 2021; Melody and Richardson 2007; Myrstener, Greiser, and Kuglerová 2025). Here we isolated the effect of a range of shading levels (0%–74%) on chl-α, ER, and GPP, without confounding effects of temperature or nutrients. There was generally a very strong negative linear relationship between both chl-α and GPP with shading level, and at shading levels less than 43%, we saw that channels grew large amounts of green, filamentous algae, in line with Hill et al. (2009). Notably, the growth in low shading channels stopped before the experiment ended. All wet channels (i.e., those that were not exposed to drought) that received less than 43% shading showed a marked decrease in algal biomass in the final weeks of the experiment. This contrasted with the highly shaded channels where biomass growth was sustained for the entire experiment (also post-drought). Seasonal differences in algal growth under high versus low light are well known in temperate streams and are driven by differences in the temperature and light optima of algae (Breuer et al. 2016). Similar patterns have also been recorded in northern Swedish clear-cut streams (Myrstener, Greiser, and Kuglerová 2025). In our study, we show that this negative effect in autumnal (September–October) growth occurs at summer shading levels below 43% boreal headwaters, or light levels above 2.6 mol photons m^{-2} day^{-1}. Even though biomass growth in the highly shaded channels was sustained throughout autumn, GPP remained low in these channels, likely due to the lack of light (Hill et al. 2009; Warren et al. 2017) and low nutrient availability (Baattrup-Pedersen et al. 2020).

Regarding ER, dense algal growth under low shading promoted heterotrophs to the point that net ecosystem productivity in fact was lower under high light availability than under low light availability. This is in stark contrast to the notion that high light availability decreases heterotrophy, at least in highly productive waters (Nebgen and Herrman 2019). Yet, similar tight coupling between GPP and ER has been found multiple times in nutrient poor, boreal headwaters (Myrstener, Greiser, and Kuglerová 2025), likely caused by strong nitrogen and carbon limitation of heterotrophic activity (Burrows et al. 2015; Demars et al. 2020). One possible explanation for decreased net ecosystem productivity under low shading could be priming of fresh autochthonous carbon from algae that increases the heterotrophic use of more recalcitrant DOC

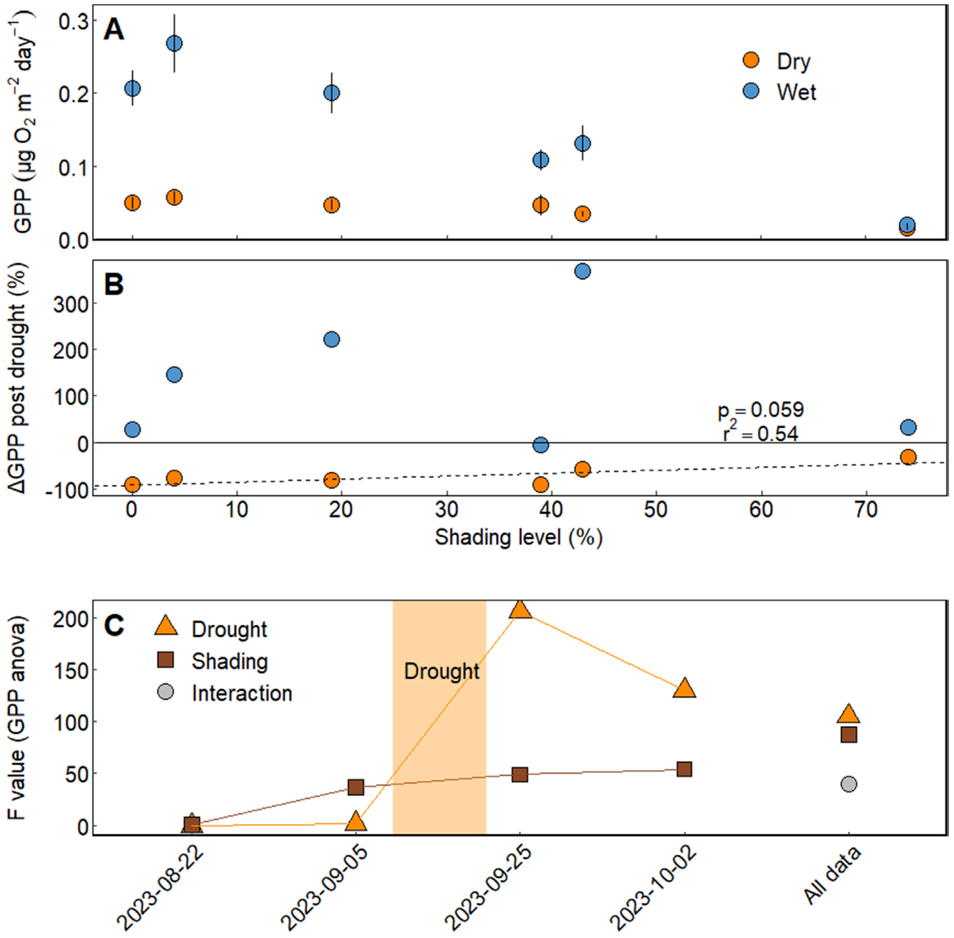

FIGURE 4 | (A) Mean (±SE) Gross Primary Production (GPP, μg O_2 $m^{-2}day^{-1}$) over the whole experiment in the different shading levels (0%–74%). Wet channels were not exposed to drought while dry channels experienced a 2-week drought. (B) percent change in average daily GPP pre (2023-08-27 to 2023-09-05) and post drought (2023-09-19 to 2023-10-02) in the different shading levels. A linear regression between delta GPP and shading level of dry channels is presented with r^2 and p value. (C) F values from the linear mixed effect ANOVA on effects of drought and shading on average daily GPP over 2-week periods.

(Hotchkiss et al. 2014). Overall, our results suggest that shading, with some variability between 43% and 74%, will promote balanced metabolic activity in the nutrient limited headwaters typical for the boreal north.

4.2 | Effects of Drought

Hydrological droughts, or drought and rewetting cycles, are expected to become more frequent in the future (IPCC 2014; Spinoni et al. 2018), including in boreal headwaters (Teutschbein et al. 2015). Drought in large perennial rivers can promote GPP due to less turbidity and increasing temperatures (Hosen et al. 2019). Smaller, perennial, boreal streams, on the other hand, run the risk of complete drought, which causes desiccation of biofilms and potentially anaerobic metabolism (Gómez-Gener et al. 2020). In our channels, the 2-week drought had a strong, negative effect on GPP and ER, while the effect was less strong on chl-α. The relatively small effect of drought on chl-α that we found contrasts with Truchy et al. (2020) that conducted a similar flume experiment; however, it is hard to compare algal biomass growth on natural substrates (sand and cobbles in our case) with accrual on ceramic tiles like in Truchy et al. (2020). Furthermore, the sand substrate in our experiment likely holds some moisture and therefore it mimics a less severe drought as compared to completely dried up ceramic tiles. In addition, growth of algal mats protects the bottom layer from drought (Nelson et al. 2023). As algal growth in our study (1 month of accumulation before drought) was one order of magnitude higher than that on tiles in Truchy et al. (2020), it is likely that some insulation from complete drought of the surfaces was provided. Furthermore, chl-α is quantifiable from dead biomass (its degradation products, Steinman et al. 2017) which can cause an overestimation when using the BenthoTorch.

Finally, the drought had a stronger proportional effect on GPP than ER, in line with studies from subalpine and temperate streams (Harjung et al. 2019; Nelson et al. 2023), likely because algae are less resistant to drought than heterotrophic organisms (Acuña et al. 2015). Yet, because absolute ER was much higher than GPP, the drought caused an overall increase in NEP in channels with low shading. In highly shaded channels, results were more in line with previous studies that show decreasing NEP after drought (Gómez-Gener et al. 2020). This clearly shows that shading is an important factor to include when making predictions about effects of drought on metabolic balance in small boreal forest streams.

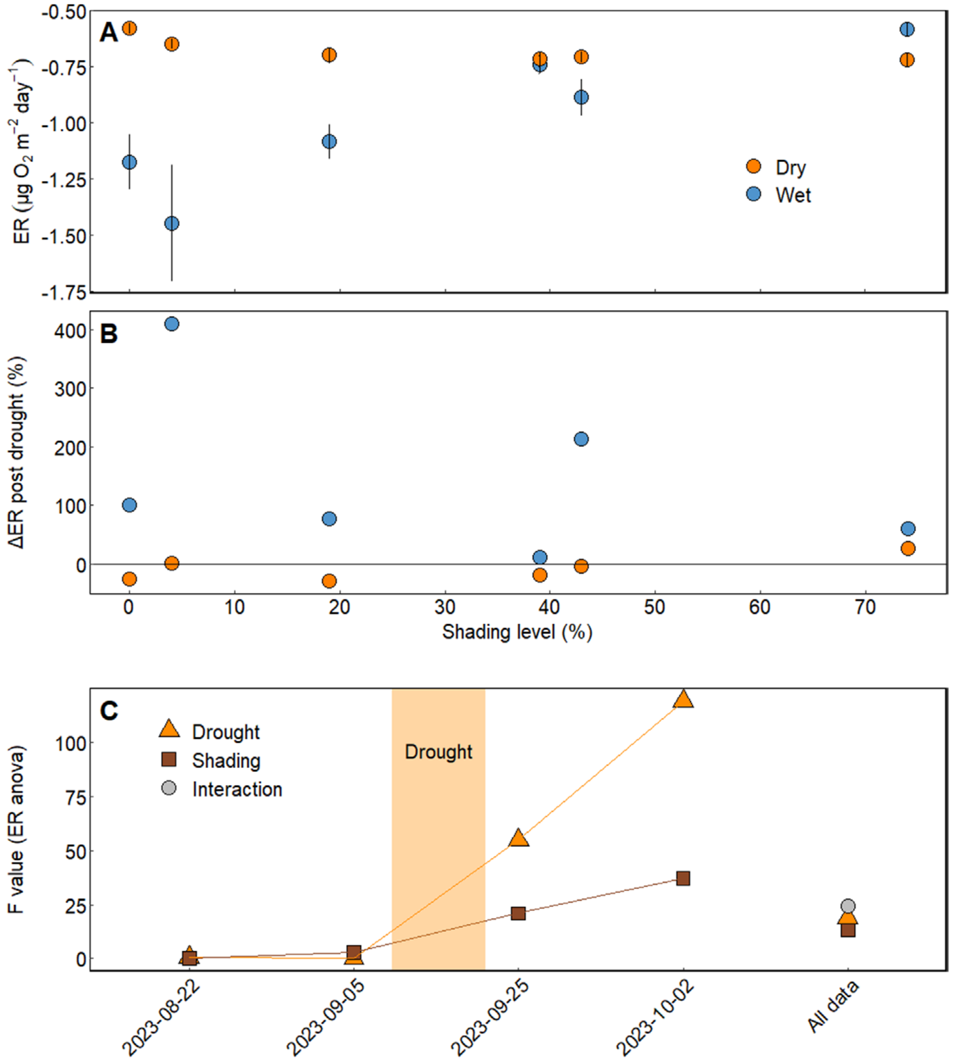

FIGURE 5 | (A) Mean (±SE) Ecosystem Respiration (ER, µg O_2 $m^{-2} day^{-1}$) over the whole experiment in the different shading levels (0%–74%). Wet channels were not exposed to drought while dry channels experienced a 2-week drought. (B) percent change in average daily ER pre (2023-08-27 to 2023-09-05) and post drought (2023-09-19 to 2023-10-02) in the different shading levels. (C) F values from the linear mixed effect ANOVA on effects of drought and shading on average daily ER over 2-week periods.

4.3 | Interactive Effects of Shading and Drought

Even though small streams have low rates of GPP, they dominate total network GPP due to their high cumulative length (Diamond et al. 2021), and small streams are highly susceptible to drought because of low discharge. We hypothesized that large changes to the biofilm community caused by loss of shading (from e.g., removal of riparian trees) would affect the responses to other pressures (Barthès et al. 2015). As hypothesized, we found interactive effects of shading and drought evident by the strong, negative drought effect on all parameters in low shading, and in fact, no measurable effect of drought on ER or chl-α in the 74% shading. As both shading and drought independently affected metabolic rates and chl-α negatively, their combined effect under high shading was antagonistic in nature (less negative than predicted additively, Folt et al. 1999). This antagonistic effect of drought and shading has not been previously found. The effects shown here are a result of drought and the onset of autumn in boreal forests, with colder and darker conditions and therefore, the two cannot be fully separated. It is possible that low shaded algal communities (dominated by filamentous, green algae) are less adapted to both drought and autumn conditions (Peterson 1987; Sabater et al. 2016). This was supported by the chl-α in the wet channels, where low shaded channels did not grow at the end of the experiment, while slow accrual continued throughout the experiment in the channels with 74% shading. In environments with conditions more favourable for fast growing algae (more nutrient rich), these algae tend to have a faster recovery post-drought (Zlatanović et al. 2018; Baattrup-Pedersen et al. 2020). It is also possible that a higher moisture level is kept under the shade cloth that prevents the most extensive desiccation of biofilms under the highest shading (74%). This protective effect of microclimate mimics wide riparian buffers, as compared to narrow ones, after clearcutting (Rykken et al. 2007). Altogether, our results show the presence of interactive effects from drought and shading loss in boreal headwater streams. The study highlights the need for riparian protection across small streams, as loss of shading increased the negative response to drought.

5 | Conclusions

Our results demonstrate that drought and shading interact to shape ecosystem functioning in boreal headwater streams, as inferred from experimental, outdoor flumes with natural substrates. Low shading amplified the negative effects of drought on algal biomass and metabolism, while higher shading buffered these impacts. This highlights the vulnerability of small boreal streams to the combined pressures of forestry and climate change. Future work should test whether these experimental patterns hold in natural stream networks, where multiple pressures co-occur and vary across space and time. From a management perspective, our findings emphasise the importance of maintaining riparian buffers that provide sufficient and variable shading (43%–74%). Such buffers can reduce the risk of algal overgrowth, mitigate shorter drought impacts, and support more balanced ecosystem functioning. Including broadleaved tree species, such as birch, rowan and/or alder, with lower water demands during dry periods may further enhance the buffering capacity of riparian forests, compared to the current tree species composition dominated by Norway spruce (Gutierrez Lopez et al. 2021).

Author Contributions

Conceptualization and developing methods: M.M., R.B.H., L.K. Data analysis, preparation of figures and tables, and conducting the research: M.M., R.B.H. Data interpretation: M.M. Writing: M.M., R.B.H., L.K.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data is available online through the Swedish National Database https://doi.org/10.5878/fk59-8024.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Chl-a (μg cm^{-2}) estimated using the BenthoTorch each week with 10 measurements in each channel. The "dry channels" were subject to a 2week drought between the sampling points 2023-09-05 and 2023-09-18. The water was turned back on right before sampling on 2023-09-18. Error bars represent standard error. **Figure S2:** Daily GPP (μg O_2 m^{-2}day^{-1}) estimated based on the open channel method using oxygen loggers. The "dry channels" were subject to a 2week drought between the sampling points 2023-09-05 and 2023-09-18. Error bars represent uncertainty of parameter estimation reported as 95% credible intervals. **Figure S3:** Daily ER (μg O_2 m^{-2}day^{-1}) estimated based on the open channel method using oxygen loggers. The "dry channels" were subject to a 2-week drought between the sampling points 2023-09-05 and 2023-09-18. Error bars represent uncertainty of parameter estimation reported as 95% credible intervals. **Figure S4:** Mean NEP (μg O_2 m^{-2}day^{-1}) over time whole experiment for the different shading levels (0%–74%). Error bars represent standard error. The "dry" channels were subject to a 2-week drought between 2023-09-05 and 2023-09-18.