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ARTICLE

Freshwater Ecology

Experimental riparian forest gaps and increased sediment loads modify stream metabolic patterns and biofilm composition

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Abstract

Forest management operations greatly influence stream habitats. Canopy clearing and subsequent canopy development during succession, site preparation, and ditching alter the light environment, and increase sediment inputs and nutrient exports from upland and riparian soils to streams. These physicochemical changes affect aquatic biofilms and metabolic rates, and in this study, we tested their individual and combined effects. We used 12 artificial streamside channels, together with a field survey of nine streams in and around clear-cuts, to assess the effects of shading, substrate composition, and nutrient addition on biofilm biomass and composition, as well as metabolic rates. We found that biofilm biomass and gross primary production (GPP) were light limited in channels under 70% canopy shading. Nitrate additions at this shading level only marginally increased autotrophic biomass, while the rates of respiration increased 10-fold when carbon was added. Open (unshaded) channels had three times higher rates of GPP compared with channels with 70% shading, and autotrophic biomass was twice as high, largely caused by the colonization of filamentous green algae. These changes to biofilm biomass, composition, and GPP were caused by differences in light alone, as temperature was not affected by the shading treatment. Notably, higher rates of GPP led to no positive effect on net ecosystem production. Further, fine-grained substrates negatively affected GPP as compared with stone substrates in the experimental channels. In the surveyed streams, the negative effects of fine-grained substrates exceeded the positive influence of light on biofilm biomass. Altogether, our results highlight the need for riparian management that protects headwaters from unwanted stressors by focusing on preventing sediment erosion and carbon transport in clear-cuts, while providing variable shade conditions in second-growth forests.

KEYWORDS
biofilm, buffer, chl *a*, clear-cut, forestry, gross primary production, metabolism, respiration, riparian forest, sediment, shading, stream

INTRODUCTION

Forestry operations, if conducted without careful environmental consideration, can greatly affect stream ecosystems. For example, decreased riparian canopy shading, changes in nutrient inputs, and increased sediment loads are commonly observed after clear-cutting, and especially when riparian protection is compromised (Kuglerová et al., 2021). Shading, nutrients, and sediments all affect the chemical and physical habitats of running freshwaters, which in turn alter ecosystem processes such as metabolic rates (Bechtold et al., 2017). Maintaining riparian forest buffers along streams is a management practice aimed toward decreasing the negative effects of rotational forestry on freshwaters. Designing ecologically meaningful buffers is challenging, partly because one must weigh the cost to the industry for not harvesting commercial trees against the benefit to the environment from those trees. Furthermore, it is not clear what our ecological goals for the stream ecosystems are when designing riparian buffers. In many countries, including Sweden, buffers along forested streams are imposed by law (Swedish Forestry Act, 1979), but there are no prescriptions for specific ecological outcomes and ecosystem processes, including aquatic primary production and ecosystem respiration (ER).

When assessing optimal protection, old-growth forests can serve as templates of ecosystems with structural complexity, tree species diversity, and mosaic of habitat types that include frequent canopy gaps (Stovall et al., 2009; Warren et al., 2017). Streams in old-growth forests often have a wide range of light conditions and coarse-grained substrates, and they generally have tight nutrient cycling with small losses of inorganic forms (Ashkenas et al., 2004; Kaylor et al., 2017; Kortelainen et al., 2006). Such habitats favor aquatic primary production, a diversity of primary producers, and higher trophic levels, as well as disturbance resilience compared with their younger stand counterparts (Warren et al., 2018). In contrast, streams in forests managed by rotational forestry differ from old-growth forests in that they typically experience dramatic changes during and after clear-cutting, with increases in incident light and stream temperatures (Chellaiah & Kuglerová, 2021; Roon et al., 2021; Warren et al., 2013), possible pulses of nutrients (Futter et al., 2010; Kreutzweiser et al., 2008), and increases in sediment loading and suspended particles (Palviainen et al., 2014; Rachels et al., 2020). Streams draining clear-cuts therefore can experience high primary production but low species diversity and low nutritional quality of biofilms—which often make up the base of the food web (e.g., Lowe et al., 1986; Noel et al., 1986), unless limited by nutrients (Johnson et al., 2023) or degraded by high sediment export (Murphy & Hall, 1981). On the contrary, during later successional stages, between 30 and 100 years, streams shift toward highly shaded, low-nutrient conditions, leading to dramatic decreases in aquatic productivity (Burrows et al., 2021; Kaylor et al., 2017; Murphy & Hall, 1981).

In addition to total primary productivity, biofilm community composition is also important to consider when evaluating the potential impacts of forestry on streams. Changes to biofilm community composition can negatively affect macroinvertebrate diversity if filamentous algae are promoted (Tonkin et al., 2014), and the nutritional quality of the biofilm is lowered if heterotrophic species dominate (Jyväsjärvi et al., 2022). Such changes to biofilm community composition have been seen after increased nutrient inputs and sedimentation (Neif et al., 2017), combined light and temperature increases (Noel et al., 1986), and changes to nutrient availability plus acidity (Holopainen & Huttunen, 1992). Generally, green algae are promoted in clear-cuts, but the combination of high nutrient and high light/temperature makes it difficult to separate the individual effects of these habitat factors in field observations. In addition to changes in the autotrophic community, the balance between autotrophs and heterotrophs, which regulates the carbon balance of streams (Roberts et al., 2007) and can affect the nutritional quality of biofilms (Jyväsjärvi et al., 2022), is likely to be affected by forestry-induced stressors. It is easy to assume that autotrophy would increase in clear-cuts due to increased light; however, heterotrophic activity is often fueled by algal exudates (Hotchkiss & Hall, 2015; Romaní & Sabater, 1999), and additionally, they can be strongly promoted by increases in unstable, sandy sediments (Atkinson et al., 2008; Uehlinger et al., 2002) and heterotrophs would therefore also be promoted by clear-cutting. Today we have a limited understanding of how boreal stream biofilm communities and net ecosystem productivity (NEP) respond to individual and simultaneous habitat alterations of light, nutrients, and substrate composition.

Here we evaluate the individual and interactive effects of light levels, substrate composition, and nutrient addition to biofilm biomass and composition, and whole-channel metabolic rates. To separate the individual and interactive effects, we performed a fluvial mesocosm study, using 12 experimental channels where we manipulated light (70% shade vs. no shade), bottom substrates (sand vs. stones), and nutrients (nitrogen and carbon additions). Further, we surveyed biofilm chl *a* levels in nine streams, and this was done upstream, within, and downstream of recent clear-cuts to include dark/light sites and sand/stone sites. We hypothesized that loss of shading would increase biofilm chl *a*, gross primary production (GPP), and nitrogen limitation. Furthermore, we hypothesized that sandy substrates would reduce biofilm chl *a* and GPP, but that ER would increase. Together, this would result in a change in biofilm composition, where the lowest rates of NEP occur in shaded, sandy channels. Finally, we hypothesized that the different shading would result in different algal composition, where open (no shade) channels would have more green algal growth compared with shaded ones.

METHODS

Study site

We used 12 artificial channels at the Svartberget experimental facility (Laudon et al., 2021) in northern Sweden, 60 km west of Umeå. We asked how sandy substrates, decreased riparian shading, and nutrient additions affect biofilms (biomass and metabolic rates) and whole ecosystem metabolic rates (Figure 1). We chose to manipulate these three parameters as they represent typical physicochemical changes that follow final felling and site preparation in Sweden and other countries (Kreutzweiser & Capell, 2001; Kuglerová et al., 2021; Marttila et al., 2020). The artificial channels we used are 15 m long and 20 cm wide, with flow through water from an adjacent, forest stream. Water depth varied from 3 to 11 cm (top to bottom), with a slope of ~0.5 cm m^{-1}. Water discharge was constant at 1–2 L s^{-1} and water velocity was 0.1 m s^{-1}. Water to the artificial stream channels is continuously pumped from the forest stream using a bilge pump (Flygt KS 2610) to a 3000-L water collection tank, from which the water is then led to four 1000-L boxes, each feeding three of the channels (Figure 1). The residence time in the boxes is less than 30 min. This setup ensures that water is well mixed in the tank and boxes so that all channels have similar water flow (discharge) and inlet chemistry (Appendix S1: Table S1). During the experiment, the channel water had high dissolved organic carbon (DOC) concentrations (20–30 mg L^{-1}), low inorganic nutrient concentrations (average dissolved inorganic nitrogen; DIN = 35 μg L^{-1} and PO_4^{3-} = 4 μg L^{-1}), and was cold (average 11°C), conditions typical for forest streams in the region (Laudon et al., 2021). We ran the experiment for 38 days from 1 August to 7 September 2022, with the tarp used to reduce light installed on 3 August.

We coupled our chl *a* results from the artificial channel experiment with a snapshot field survey of chl *a* in nine forest streams, upstream, within, and downstream of recent clear-cuts, in the county of Västerbotten within 1 h driving distance from the city of Umeå, northern Sweden (Table 1). The site conditions around the streams ranged from young (30–40 years) to mature (60+ years) forests in the upstream and downstream sites to clear-cuts. The clear-cuts range in buffer width from essentially no buffers (a few individual trees or high stumps) up to 15-m-wide buffers. Substrate conditions in

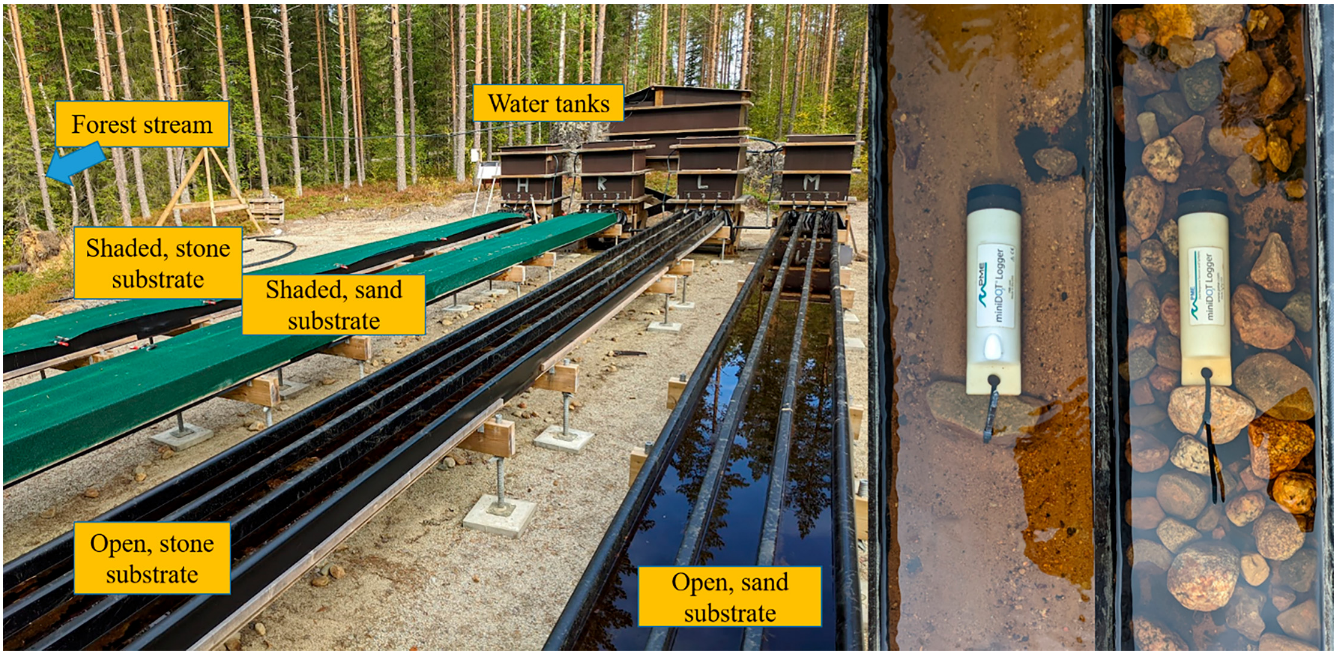

FIGURE 1 Setup of the experimental channels and a view of the sand and stone substrates with deployed oxygen loggers. Photo credit: Maria Myrstener.

TABLE 1 Coordinates (in WGS84) and background data of surveyed streams.

Site	Year of clear-cut	Coordinates (WGS84)	DIN concentration (μg L^{-1})	Temperature range (average °C)	Average PAR (μmol m^{-2} s^{-1})
1	2015	63.75254, 19.60335	96	13.4–15.3	9–80
2	2019	63.80009, 19.88431	61	12.7–13.1	18–84
3	2017	63.7937, 19.65494	24	12.4–12.8	13–68
4	2016	63.63104, 19.29214	21	13.3–13.9	7–34
5	2014	64.16962, 19.38988	33	11.9–12.8	6–36
6	2017	63.7644, 19.79955	56	11.7–12.0	10–83
7	2018	64.2011, 19.79091	37	12.5–13.0	15–114
8	2020	64.0918, 19.9764	39	12.2–13.0	14–58
9	2017	63.79328, 19.4781	21	11.4–11.9	6–61

Note: Dissolved inorganic nutrient concentration (DIN, NO_3^- + NH_4^+) was sampled three to four times during open water season in 2021 and represents an average of all sites (upstream, clear-cut, and downstream). Temperature and light (lux, converted to PAR) were recorded from July to October in 2021 and represent the range in average temperature and light between stream sites (upstream, clear-cut, and downstream).
Abbreviations: DIN, dissolved inorganic nitrogen; PAR, photosynthetically active radiation.

the surveyed streams varied from no sand present to stream bottoms dominated by fine-grained particles. The sites were clear-cut between 2014 and 2020 (Table 1).

Channel experiment setup

We used a 2 × 2 factorial design, with three replicates of each treatment. The two factors were substrate (sand vs. stones as bottom substrate) and light (70% shading tarp or no tarp; Figure 1). The sand (median diameter 0.2 mm) and stones (median diameter 8 cm) came from a nearby quarry, representing local, natural material, dominated by gneiss and granite. The substrate treatment tests for effects on biofilm growth and metabolism, but it does not test for disturbance effects such as burrowing or scouring because the bottoms were stable throughout the experiment. The sand sediment had no effect on the nutrient concentration of the water in the channels (Appendix S1: Table S2) unlike in, for example, Pérez-Calpe et al. (2021). The tarp mimics stream light conditions in a mature forest stand or a wide buffer (>15 m; Chellaiah & Kuglerová, 2021; Jyväsjärvi et al., 2022). There was no effect of the tarp on water temperature, and the average temperature was 11.0 (±0.06) in the shaded channels and 11.1 (±0.04) in the open channels. This enabled us to test for light effects without any confounding temperature effects, which is hard to achieve in natural streams as the two are closely coupled. For ease of installment and access to the channels, we fixed the tarp over three channels side by side instead of fixing it randomly, on individual channels. Nevertheless, each channel is treated as an independent replicate because the setup delivers well-mixed water from the same source to each channel separately and the starting conditions for all channels did not differ (see Appendix S1: Table S1 and further below).

Physicochemical parameters in the channels

We recorded incident light in lux and water temperature in degrees Celsius every hour using two Hobo pendant loggers (Onset Computer Corporation, Borne, USA) in each channel. 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, in micromoles of photons per square meter per day). Loggers were cleaned one to two times per week. We sampled water from the boxes and from the downstream end of each channel to measure the concentrations of nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), and DOC. DIN represents the sum of NO_3^- and NH_4^+. Water was filtered (0.45 μm) on site and kept refrigerated (DOC) or frozen (DIN + PO_4^{3-}) before analysis. Results are available in Appendix S1: Tables S1 and S2.

Biofilm biomass and species composition in the channels

We estimated biofilm biomass as chl *a* (in micrograms per square centimeter) once per week, based on 10 measurements in each channel. For all chl *a* estimates, we used a BenthoTorch, an in situ, handheld fluorometric instrument (bbe Moldaenke, Germany). The

BenthoTorch estimates chl *a* and distinguishes between diatoms, green algae, and cyanobacteria, which often dominate stream biofilms (Allan & Castillo, 2007). Estimates of total chl *a* from a BenthoTorch compare well with conventional spectrophotometric methods when biofilms are relatively thin, as in our situation. However, when quantifying community composition, the BenthoTorch has been shown to overestimate the abundance of diatoms (Kahlert & McKie, 2014), yet the instrument performs well in factory calibrations against standards. Still, we only used the community composition results to note the presence or absence of green algae in the channels. All statistical analyses used the sum of diatoms, green algae, and cyanobacteria (i.e., total chl *a*).

Nitrate and carbon addition experiment in the channels

We conducted a resource addition experiment using nutrient diffusion substrates (NDS) to grow microbial biofilms (following Tank et al., 2006) in each of the channels. Each NDS consists of a 30-mL plastic cup, filled with 2% agar solution, and a 30-mm-diameter cellulose sponge top. The cellulose tops agree well with results using ceramic tops for chl *a* but cellulose tops perform better for heterotrophic activity (Myrstener et al., 2018), which is why we chose a cellulose surface so that we could analyze both chl *a* and community respiration (CR) using only one surface. NDS cups were enriched with either 0.5 M $NaNO_3$ (N treatment), $C_2H_3NaO_2$ (acetate, C treatment) or kept unamended as controls. We use N additions and not P because a previous study conducted in close vicinity to our study site showed no responses of biofilms to P additions (Burrows et al., 2021). Three replicates of each treatment were randomly attached to an L-bar and placed in each channel. NDS were deployed for 20 days, starting on 10 August and ending on 29 August. Upon removal, we placed surfaces individually in 50-mL Falcon centrifuge tubes and stored at 4°C until analyses the following day.

All NDS surfaces were incubated in the laboratory for estimates of CR and after that analyzed spectrophotometrically for chl *a*. Incubations were conducted 24 h after collection using the modified dark bottle method (Johnson et al., 2009), where tubes are filled with oxygen-saturated stream water, and dissolved oxygen (DO) saturation (YSI Pro ODO, Yellow Springs, USA) is measured before and after incubation. NDS surfaces were incubated for 3 h in the dark at 12°C, with an additional three blanks, treated the same way as the NDS samples, which were used to correct for any water column changes in DO. CR (in micrograms of O_2 per square centimeter per hour) was calculated as the background-corrected DO consumption during dark incubations:

$$\mathrm{CR} = (\Delta \mathrm{DO} \times V)/(t \times A),$$

where ΔDO is the difference in DO concentration before and after incubation, V is the volume of the Falcon tubes, t is the exact incubation time, and A is the area of the NDS surface. After incubations, all NDS surfaces were frozen. Chl *a* was later estimated following Steinman et al. (2017), including correction for pheophytins, using a JENWAY 6405 UV/Vis spectrophotometer (Sheung Wan, Hong Kong). NDS surfaces were thawed and put in centrifuge tubes with 90% acetone for 24 h prior to analysis of the extract.

Whole-channel metabolic estimates of GPP and ER

Each channel was equipped with a miniDOT (Precision Measurement Engineering, USA) to record DO at 10-min intervals. Metabolism was estimated using the single-station diel oxygen method approach where GPP and ER were estimated using Bayesian inverse modeling (Hall & Hotchkiss, 2017). We used time series of DO, water temperature, light (from lux loggers), as well as a prior for gas exchange rate coefficient (K) and channel depth (z). The main equation for GPP and ER is as follows:

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

The change in oxygen over time (in O_2 per cubic meter) equals all oxygen produced by photosynthesis (GPP, in grams of O_2 per square meter per day) minus all oxygen consumed by respiration of both autotrophs and heterotrophs (ER, in grams of O_2 per square meter per day) and the rate of gas exchange between the water and air (K, per day). We modeled two parameters (GPP and ER) and used prior K based on nighttime regression analysis (following Rocher-Ros et al., 2020). We used an average K from nighttime regressions instead of daily values because these channels have stable flow and depths. Finally, we filtered data for erroneous model days using the mean average error between the observed and the modeled DO concentrations. All days with a mean average error larger than 0.2 were removed (Lupon et al., 2019). When GPP is very low, a poor model fit can still produce a small error, thus all remaining days were also visually inspected to further exclude erroneous estimates. Following these guidelines, we removed 40% of analyzed days across all channels. We are aware that the footprint of the oxygen loggers might incorporate signals from the water tanks and/or the stream that feeds the channels, but the water is well mixed after being pumped through two different water tanks. If there still was a signal from the tanks, it would be the same for all channels and therefore it does not affect the treatment effects. We analyzed metabolic rates on the first days of the experiment (when there was no biofilm developed in the channels) and it revealed no GPP signal and only a weak ER signal (0–0.4 g O_2 m^{-2} day^{-1}). Nevertheless, absolute values of GPP and ER are not important for this study and should be used with caution if compared among studies. Metabolic rates are presented as cumulative rates based on the days where there were data from at least one channel from each treatment (12 days out of 30).

Field survey of chl *a* in streams

During the field survey, we estimated chl *a* on two occasions in each of the nine streams using a BenthoTorch. The first survey was on 1 September and the second was on 19 October 2022. In the September survey, we had transects in the clear-cut part of the stream, and in the October survey, we added transects upstream and downstream of the clear-cuts to include both open and closed canopy sites. At each site, we had six to eight transects, with three measurements taken from the bottom along each transect, for a total of 18–24 measurements per site. In the streams, we measured chl *a* only from sand and stone substrates, so the setup was not fully random (i.e., avoiding wood, gravel, and leaves).

Statistical analyses

Channel experiment

Treatment effects (substrate and shade) on chl *a* in the channel experiment were evaluated using estimated chl *a* values after four weeks of accrual, using a mixed-effects model (r package lme4, function lmer; Bates & Maechler, 2009) with substrate and shading as fixed effects (individually and in interaction) and channel ID (1–12) as a random effect (each channel had 10 estimates of chl *a*). To evaluate the effects of substrate and shade (and their interaction) on GPP, ER, and NEP, we used the cumulative rates (based on 12 days over the whole experimental period) in a fixed-effect ANOVA model.

In the nutrient limitation experiment, we assessed results using both absolute values and response ratios (Elser et al., 2007), which are calculated as the treatment response divided by the unamended control. We tested whether light and sediment had an effect on the N response using an ANOVA model (aov r function) with the N response ratios (RR_N).

Stream field survey

Differences in chl *a* between substrates (sand vs. stone) and light conditions (dark vs. light) in the stream field survey were evaluated using a mixed-effects model with substrate and light (and their interaction) as fixed factors and stream ID (1–9) and survey month as a random factor. The light versus dark sites were grouped based on summer light data from 2021 and an average PAR of 40 μmol m^{-2} s^{-1} (3.5 mol m^{-2} day^{-1}) was used as the cutoff between groups based on the light limitation threshold presented in Warren et al. (2017). This separated most clear-cut sites into the light group (7 sites, 254 chl *a* estimates) and all upstream, downstream, and two clear-cut sites with wide buffers in the dark group (20 sites, 428 chl *a* estimates). All statistical analyses were done in RStudio (R Core Team, 2020).

RESULTS

Light treatment

Shaded channels received an average DPF of 1.5 mol m^{-2} (±0.3) while open channels (unshaded) received a four times higher photon flux of 6.1 mol m^{-2} (±0.8). The shaded channels peaked at 3.1 DPF and the open channels at 11.5 DPF on the first day of measurements.

Biofilm chl *a*

Biofilm chl *a* estimated with the BenthoTorch was below detection limit in all channels at the start of the experiment. Biofilms developed evenly in all treatments during the first two weeks, averaging 0.25 μg chl *a* cm^{-2} (SD ±0.09). After three weeks, green algae colonized the open channels (unshaded), and after four weeks, open channels had 1.7 times higher biofilm biomass compared with shaded ones, 0.58 versus 1.03 μg cm^{-2} (est = 0.435, $t = 1.742$, df = 1, $p < 0.01$; Figure 2; Appendix S1: Table S3). The effect of substrate was not significant on its own (est = 0.43, $t = 1.74$, df = 1, $p = 0.4$), nor was the interaction with light (interaction term: est = −0.58, $t = -1.63$, df = 1, $p = 0.1$), although open channels with stone substrates had on average 1.6 times higher chl *a* (1.27 μg cm^{-2}) than open channels with sand substrate (0.79 μg cm^{-2}). Green algae comprised <1% of total chl *a* in the shaded channels and 73% in the open channels

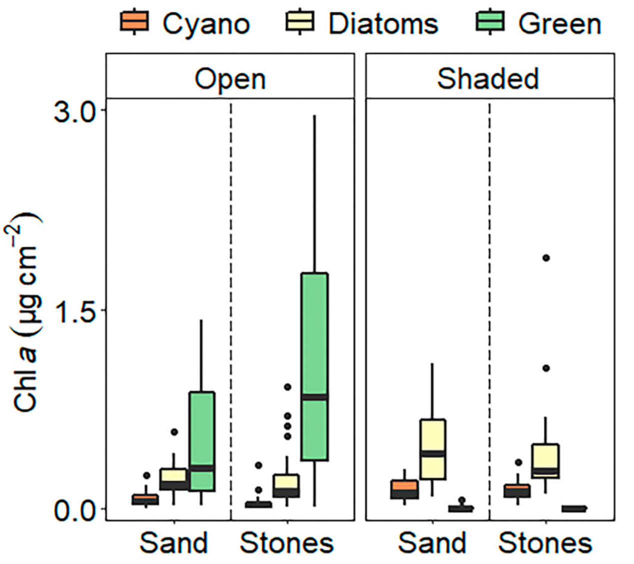

FIGURE 2 Chl *a* standing stocks in the experimental channels after four-week colonization, estimated with the BenthoTorch directly on the bottom substrates. Each box represents three channels with 10 estimates from each channel. The box shows first and third quartiles, the line in the box is the median, and the lower whiskers are first quartile − 1.5 × inner quartile range, and the upper whiskers are third quartile + 1.5 × inner quartile range. Solid circles are outliers beyond the whisker values.

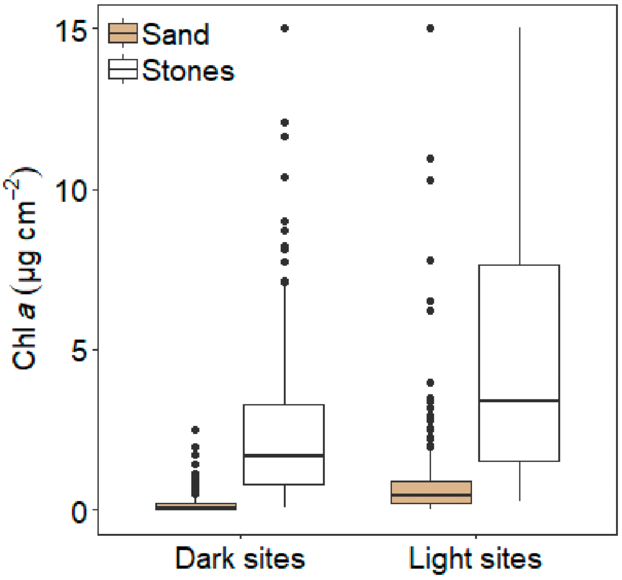

FIGURE 3 Chl *a* standing stocks measured using the BenthoTorch in the field-surveyed streams on 1 September and 18–19 October. The light threshold separating dark from light sites is 3.5 mol day^{-1}. The box shows first and third quartiles, the line in the box is the median, and the lower whiskers are first quartile − 1.5 × inner quartile range, and the upper whiskers are third quartile + 1.5 × inner quartile range. Solid circles are outliers beyond the whisker values. Note that 15 µg cm^{-2} is the highest detection level of the BentoTorch and this was reached on a few of the stones of the light sites.

after four weeks. The colonization of green algae was patchy (see error bars in Figure 2).

In the field-surveyed streams, standing stocks of biofilm chl *a* varied from 0 to 15 µg cm^{-2} (15 µg cm^{-2} is the maximum detection limit of the BenthoTorch), with the median being 0.80 µg cm^{-2} (Figure 3). The largest effect was that of substrate, and chl *a* was about 5.7 times higher on stone substrates, averaging 3.40 µg cm^{-2}, than on sand substrates, which averaged 0.59 µg cm^{-2} (est = 2.82, $t = 26.45$, df = 1, $p < 0.01$). Further, we grouped sites based on incoming light, where light sites received a daily average above 3.5 mol m^{-2} day^{-1} and dark sites received less than 3.5 mol m^{-2} day^{-1}. Standing stocks of biofilm chl *a* were higher in light sites (average 3.5 µg cm^{-2}) than in dark sites (average 1.5 µg cm^{-2}, est = 1.09, $t = 8.24$, df = 1, $p < 0.01$), and biofilm chl *a* was lowest on sand in dark sites (interaction term: est = −0.81, $t = -4.45$, df = 1, $p < 0.01$).

Whole ecosystem metabolism in the experimental channels

There were no measurable rates of GPP during the first week of the experiment in any of the channels. During the following three weeks of the experiment, GPP stayed below 0.15 µg O_2 m^{-2} day^{-1} in the shaded channels. GPP peaked at 0.4 µg O_2 m^{-2} day^{-1} in the open, sandy channels and at 0.7 µg O_2 m^{-2} day^{-1} in the open, stony channels. Both sandy substrate ($F = 5.9$, df = 1, $p = 0.04$) and shading ($F = 25.9$, df = 1, $p < 0.01$) had a significant negative effect on cumulative GPP (as based on 12 days; Figure 4), but the interaction between the tested parameters was not significant ($p > 0.05$). ER varied from 0.2 to 11 µg O_2 m^{-2} day^{-1}, and all channels were net consumers of oxygen throughout the experiment (Figure 4). The average rate of ER on the first day was 0.4 µg O_2 m^{-2} day^{-1}, likely a signal from the water tanks or the stream that supplied the tanks. There was no treatment effect (individual or interaction) on ER (Figure 4) or NEP (Appendix S1: Figure S1) over the four weeks ($p > 0.11$).

Nutrient limitation test

Biofilm chl *a* on the nutrient diffusion surfaces (measured with spectrophotometry) was on average 5.1 times higher for the N treatment than for the unamended NDS, and the C treatment was twice as high as the unamended NDS (Figure 5). Unamended NDS had low values of chl *a* (range 0.06–0.33 µg cm^{-2}). There was a positive

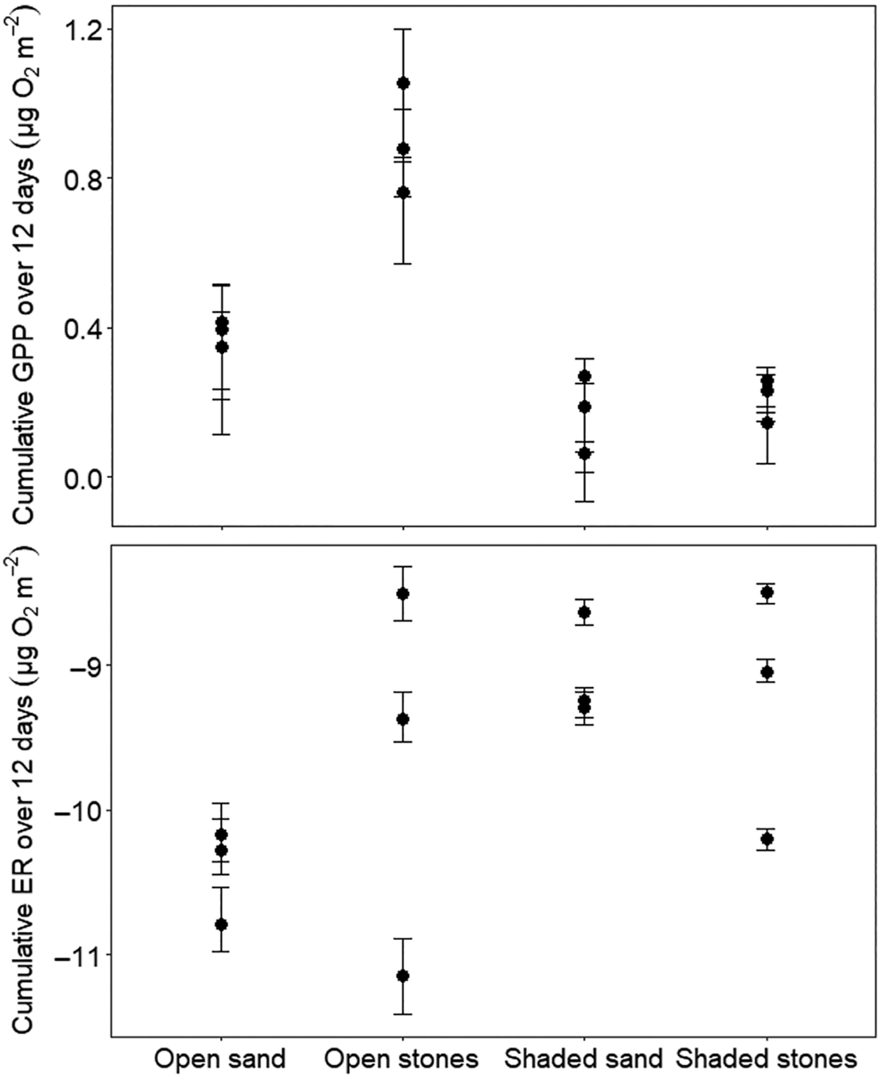

FIGURE 4 Cumulative gross primary production (GPP) and ecosystem respiration (ER) over 12 days during the experiment. Not all days of the experiment were included due to insufficient model fits. The 12 days were chosen to include at least one channel with a good model fit from each treatment. Error bars represent the uncertainty of parameter estimation reported as 95% credible intervals.

effect of light on the response to nitrate addition (RR_N in light 7.9 vs. RR_N in shaded 2.4, $F = 79.2$, $p < 0.01$), but no substrate effect ($p = 0.7$). CR on the other hand showed strong C responses (RR = 10.6) and smaller nitrate responses (RR = 1.7), with no effect of either substrate or shading (Appendix S1: Figure S2).

DISCUSSION

Effect of different light levels

One of the primary goals of retaining riparian buffers in forestry is to maintain shading over water surfaces (Richardson et al., 2012) to prevent strong temperature increases and detrimental algal blooms. On the other hand, intensive forest management in Sweden converted many riparian forests into even-aged, conifer-dominated stands with higher levels of shading when compared with old-growth or unmanaged forests (Bechtold et al., 2017; Hasselquist et al., 2021; Lundqvist, 2022). Too much shading hinders primary production, with consequences for the entire food web (Kaylor & Warren, 2017), and therefore, the appropriate level of shading has recently been discussed (Hasselquist et al., 2021). Our experimental results show that 70% shading (average 1.5 mol m^{-2} day^{-1}) led to rates of GPP that were only just above detectable levels and average biofilm chl *a* was consistently below 1 μg cm^{-2}, even when supplied with extra nitrogen. The stream survey showed that the average light levels of 3.5 mol day^{-1}, that is, our cutoff value between dark and light sites, are indeed still limiting for

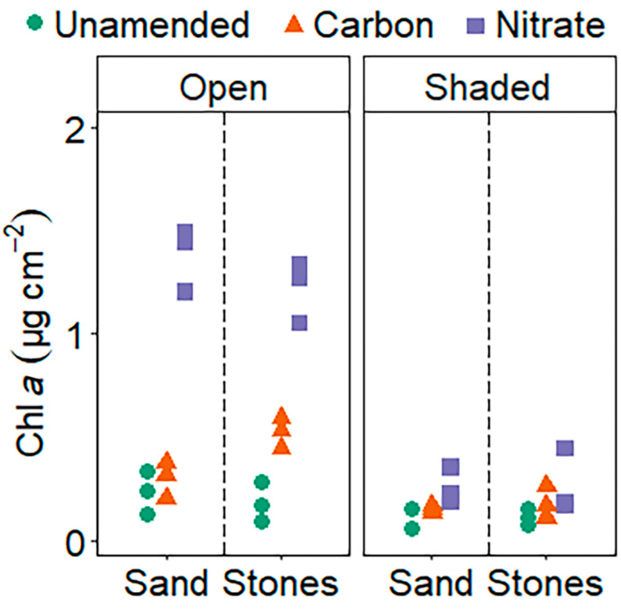

FIGURE 5 Chl *a* on nutrient diffusion substrates (NDS) in the experimental channels. Each point represents three NDS surfaces from one channel.

stream biofilms (Warren et al., 2017), but that biofilm accrual was not completely hampered (see dark sites in Figure 3). ER was also low under 70% shading, but showed strong responses to carbon additions, which suggests that respiration can be promoted in highly shaded streams if they experience carbon leakage from, for example, clear-cutting.

The open (unshaded) channels had a threefold higher level of GPP and twice as high primary producer biomass than the shaded channels, without confounding increases in temperature or nutrients. Similarly, biofilm biomass in the natural streams was two times higher in the light sites than in the dark sites. This difference in biomass between shaded and open channels was higher than reported from a similar study in Finland (Jyväsjärvi et al., 2022) and Oregon, USA (Johnson et al., 2023). This is likely due to the observed increase in filamentous green algae in our clear-cut sites and unshaded channels, in line with, for example, Lowe et al. (1986). Filamentous algae are not always captured by artificial tiles, such as those used by Jyväsjärvi et al. (2022), and growth of green algae was not promoted in Johnson et al. (2023). Ultimately, large increases in filamentous algae can negatively affect macroinvertebrate diversity (Tonkin et al., 2014). Here, we show that GPP and filamentous algae can be promoted by high light alone, without the influence of temperature or nutrients. The lack of a temperature increase in our channel experiment is of fundamental importance, because disentangling the effects of light and temperature is normally extremely difficult to do in natural streams, where temperature is strongly related to incident light, particularly in clear-cuts (Roon et al., 2021; Swartz et al., 2020). Our combined experimental and observational results show the importance of reaching appropriate light levels, which promote primary producers without leading to complete shifts in species dominance (i.e., filamentous algae).

The 70% shading used in our study represents the higher end of light conditions in many headwaters flowing through managed, second-growth, spruce forests (Chellaiah & Kuglerová, 2021; Hasselquist et al., 2021), whereas the open channels represent a situation where buffers are missing or composed of sparse individual trees, a typical situation for many clear-cut streams in Sweden (Kuglerová et al., 2020). Our experimental channel results show that 70% shading limits primary production, indicating that this is not an optimal shading level to be maintained homogenously over streams if we want to promote primary production. In old-growth forests, canopy cover varies across small spatial scales from ~30% to 90% due to the structural complexity of the canopy (Bechtold et al., 2017; Kaylor et al., 2017; Lundqvist, 2022). Our results suggest that such variation should be promoted also in managed, second-growth forests. It is important to note here that we studied only two light levels: highly shaded and not shaded. We therefore cannot make conclusions about light thresholds that promote primary producers but prevent the dominance of one species, a matter that should be the subject of future studies.

Effects of sandy substrates

Increased sediment transport and deposition on stream bottoms after clear-cutting or site preparation have been reported for managed forests (Futter et al., 2016; Kreutzweiser & Capell, 2001). The negative impact of sedimentation on stream carbon balance and autotrophic productivity works through several mechanisms, including burial and scouring (Kuglerová et al., 2021), and promotion of heterotrophic taxa in the biofilm (Erdozain et al., 2018). Yet factors such as increased light can potentially overwhelm the negative effects of substrate after forest operations, depending on the size of the fine sediment and the slope of the stream (Murphy & Hall, 1981). We found support for our hypothesis that whole-channel GPP was lower on sandy substrates than on stones, even without the effects of sediment suspension or abrasion, and this has not been shown before. Our field study confirms that fine-grained sediments were detrimental for biofilm growth even under high light conditions, although under the right circumstances (such as low flow and low gradient streams), sandy substrates certainly can accrue thick biofilms (see outliers in Figure 3 and Atkinson et al., 2008). Strikingly, the negative effect of sand also overwhelmed differences between streams in terms of nutrient concentration, which together with light limitation has been highlighted as the main controlling factors on stream primary production in northern Sweden (Burrows et al., 2021) and in streams in general (Hill et al., 2009; Mulholland et al., 2001; Myrstener et al., 2022). This is a very important finding in combination with the light effects we found; if management strategies attempt to increase light in streams through targeted tree removal (mimicking canopy gaps), that effort can be hampered if sediment transport to the streams is not prevented.

We did not see any difference between sandy substrates and stone substrates in relation to ER or NEP, contrary to what we hypothesized. Sand substrates do not necessarily have higher ER than stone substrates (Hoellein et al., 2009), and in our channel experiment, the sand bottom was thin and undisturbed during the experiment, which contrasts with the mature sediments with large pools of carbon that can stimulate heterotrophic activity (Gerull et al., 2012; Hoellein et al., 2009; Rier & King, 1996). The rates of ER were low overall, likely due to the strong C limitation we found (also in line with Burrows et al., 2017), and this likely dampened shading and substrate effects. Low bioavailability of boreal DOC has been shown before (Soares et al., 2017) and highlights the importance of algal exudates (Hotchkiss & Hall, 2015; Romaní & Sabater, 1999) for heterotrophic activity. We conclude that the main limiting factor for heterotrophic activity in these managed, boreal forests is likely carbon availability.

Management implications

Sustainable management of forests for timber is important in reaching Intergovernmental Panel on Climate Change (IPCC) goals to reduce the use of greenhouse gas-intensive products (IPCC, 2023). However, intensely managed forests, which lack ecological consideration, such as those in Sweden, are detrimental for local stream habitats. During final felling, incoming light abruptly increases if riparian buffer zones are too narrow (Kuglerová et al., 2020) and this is followed by heavy shading during subsequent successional stages (30–80 years), we show that both these situations are problematic for primary production. First of all, we show that large gaps with no shading can cause growth of unwanted filamentous algae, even in the absence of temperature or nutrient increases. We can further confirm that 70% shading in second-growth production forests diminishes primary production (Bechtold et al., 2017). As such, the Swedish forest authorities' recommendation of 50%–70% shading in riparian buffers (Andersson et al., 2013) may be inadequate if applied homogenously throughout second-growth riparian forests. We suggest that to increase light conditions in second-growth forests, buffers can be managed by, for example, partial harvest of larger trees or clusters of trees to create canopy gaps within the riparian zone. Small canopy gaps with lower (but not 0) shading within riparian buffers can locally promote primary production in streams (Bechtold et al., 2017) without the negative effects of increased temperatures. Further, such a management strategy would better balance environmental and economic goals because trees harvested from canopy gaps can compensate for the necessary increase in buffer width along streams in clear-cuts (Davies & Nelson, 1994; Kuglerová et al., 2020, 2023).

Furthermore, increases in fine-grained substrates are common after forest harvest, site preparation, and ditching, and we show that if protective measures fail to reduce sediment transport, the benefits of increased light for aquatic primary consumers might disappear. For example, the current management of riparian buffers in Sweden leads to enormous blow-downs of trees and root wads right at the stream edges (Kuglerová et al., 2023), leading to increased light, but also to increased sediment loading from the damaged stream banks. From our study, we can conclude that the combination of the two does not have a positive effect on the primary production of forest streams.

This study highlights the need for riparian buffer zones that protect headwaters from unwanted stressors by focusing on preventing sediment and nutrient transport, while providing varied shade. Such a management strategy will require riparian buffers that are wider than the current common practice of 5–7 m (Davies & Nelson, 1994; Kuglerová et al., 2020; Ring et al., 2022) and that are managed within and through the entire forest rotation.

AUTHOR CONTRIBUTIONS

Maria Myrstener, Lenka Kuglerová, and Larry A. Greenberg conceived the ideas. Maria Myrstener designed the methodology, collected and analyzed the data, and led the writing of the manuscript with support from Lenka Kuglerová. All authors contributed critically to the manuscript drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Myrstener, 2023) are available from the Swedish National Data Service: https://doi.org/10.5878/xvy7-q004.

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SUPPORTING INFORMATION

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

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