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PHOTOSYNTHETIC RESPONSE OF STREAM PERIPHYTON TO FLUCTUATING LIGHT REGIMES[1]

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An experiment was conducted on intact algal assemblages of stream periphyton to test their response to fluctuating and constant light regimes having the same mean intensity. The light regimes (in $\mu mol \cdot m^{-2} \cdot s^{-1}$) were constant light at 100, light fluctuating between 50 and 150 with a period of 5 min, and light fluctuating between 10 and 460 with periods of either 4:1 or 8:2 min. Compared to the rates measured under 100 in $\mu mol \cdot m^{-2} \cdot s^{-1}$ constant light conditions, fluctuations ranging between 50 and 150 in $\mu mol \cdot m^{-2} \cdot s^{-1}$ with a 5-min period produced a 23% greater rate of photosynthesis. Conversely, fluctuations between 10 and 460 in $\mu mol \cdot m^{-2} \cdot s^{-1}$ led to a 59%–74% decrease in photosynthetic activity. Detailed examination of periphytic algal responses to fluctuating light revealed that higher light intensities produced steeper photosynthesis/time slopes, but it was the combined interaction with lower light intensity that ultimately determined overall photosynthetic rate for a given light regime. This study offers compelling evidence that variable light regimes have important consequences for algal photosynthesis in natural streams.

Key index words: **algal photosynthesis, fluctuating light, stream periphyton, sunflecks, Switzerland**

Algae growing in streams experience a highly dynamic light environment. Passing clouds, sunflecks created by sunlight passing through riparian foliage, ripples on the stream surface, and movement of the periphytic overstory all cause light intensity to fluctuate on time scales that may range from hours to less than a second (Meulemans 1987, Chazdon 1988). Consequently, sunlight reaching stream periphyton can fluctuate by orders of magnitude over brief periods (DeNicola et al. 1992, Hill 1996). In terrestrial systems, patches of sunlight lasting as little as 2 s may represent a vital resource to light-limited forest understory plants, contributing as much as 85% of the total daily irradiance (Chazdon and Pearcy 1991). Some higher plant species appear to have adapted their photosynthetic machinery to utilize these transient bursts of sunlight (Weber et al. 1985, Pfitsch and Percy 1989), but the response of algae to sunflecks remains largely unexplored (but see Marra 1978, Greene and Gerard 1990). Studies that examine the relationship between periphytic photosynthesis and light intensity typically treat light as unvarying except over large-scale cycles (e.g. diurnal or seasonal; McIntire and Phinney 1965, Jasper and Bothwell 1986, Guasch and Sabater 1995). This bias overlooks the potentially important influence that shorter-period light fluctuations may have on periphytic photosynthesis and productivity in streams.

Here we investigate the influence of periodic variations in light intensity of 5 min or less on the photosynthetic rates of intact stream periphyton. Our objective was to compare periphytic photosynthesis at light intensities that differed in period and amplitude but not in total light quanta. We tested the null hypothesis that photosynthetic rates of periphytic algae would not differ significantly between constant and fluctuating light regimes that were within the natural range experienced by the periphyton we tested.

MATERIALS AND METHODS

Periphyton for this study was grown on tiles placed in the Chriesbach, a small, second order stream of the Swiss Plateau draining 25 km^2 of suburban and rural areas. Our study site was located next to the Swiss Federal Institute of Environmental Science and Technology (EAWAG) in the town of Dübendorf, Switzerland (8°36′ E; 47°24′ N; 430 m asl). The Chriesbach receives outflow from a wastewater treatment plant located about 2 km above our study site. Summer nutrient levels in the Chriesbach range from 29 to 51 $\mu g \cdot L^{-1}$ for phosphorus and from 6200 to 7200 $\mu g \cdot L^{-1}$ for nitrate. Diatoms are the most abundant algae and appear to be moderately grazed by *Goera sajanesis* Mart. (Trichoptera) and *Baetis* spp. (Ephemeroptera). Riparian vegetation along the Chriesbach is dominated by alder (*Alnus glutinosa*), maple (*Acer campestre*), and grasses. Light reaching the stream in our study section was partially filtered through riparian foliage and received sunflecks, or ''sunpatches,'' throughout the day, resulting in temporally variable light levels (Fig. 1). On 31 October 1995, 48 ceramic tiles measuring 4.0 × 2.5 × 0.4 cm were attached with silicon sealant to cement blocks and supported 50 cm above the streambed and about 20 cm below the water surface. Heavy growth of *Ranunculus fluitans* Lam. blanketed the stream and filled the water column in 1995, necessitating the re-

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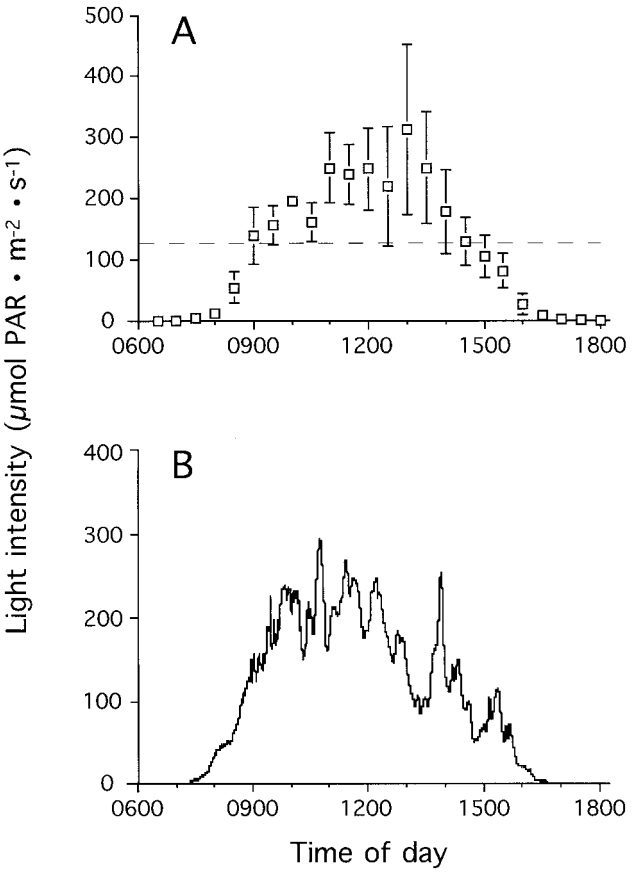

FIG. 1. Photosynthetically active radiation (PAR) levels in the Chriesbach. (A) Mean ± 1 SD irradiance from 19 to 29 November 1995 showing variability in hourly light levels. Values are based on hourly averages for the 10-day period. Average daily irradiance at tile depth during the colonization period was 121 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (dotted line). (B) Irradiance recorded throughout the day at 10-s intervals on 20 November 1995 showing fine-scale variability in PAR.

moval of macrophytes from a 3-m section of the stream before tile placement. The tiles were left in the stream for 26–28 days to be colonized by periphytic algae. Overcast skies were common during this period, and heavy rain on 16–17 November caused substantial turbidity within the water column, decreasing mean light levels to less than 100 $\mu mol \cdot^{-2} \cdot s^{-1}$ on these 2 days. Throughout the colonization period, two Li-Cor™ quantum sensors placed about 1 m upstream and downstream of the tiles and at the same depth measured photosynthetically active radiation (PAR) at 10-s intervals.

Tiles and their associated periphyton were collected from the stream, six tiles at a time, on days 26–28. The tiles were chosen randomly, removed from their supporting block, and immediately transported to the laboratory in stream water. Rates of algal photosynthesis were assessed under constant and fluctuating light with an apparatus called the ''phototron,'' based on a design by Rai and Krambeck (1992). The phototron controlled temperature and light regime while simultaneously measuring dissolved oxygen in six replicate chambers. Each cylindrical, frosted glass chamber (0.85 cm depth × 0.40 cm I.D.) has a temperature probe, an oxygen sensor, and a motor-driven stirrer to cause turbulent mixing. Oxygen concentrations were recorded at 2-s intervals, and measurements within each chamber were independent of one another. A liquid cooling system maintained chamber temperatures at 11° C, the average daytime water temperature in the Chriesbach during tile collection. Light from a halogen lamp (OSRAM Decostar 35, 35 W) entered through the bottom of each chamber, and computer-controlled baffles regulated light intensity. Each periphyton-covered tile was placed in the chamber with its upper surface facing down to intercept light from the lamps. The tile's edges rested against the chamber wall such that its surface was oriented at a 60° angle to the light source. This orientation created a space where water could circulate over the periphyton covering the tile's surface. Light levels in each chamber were determined using a flat, underwater Li-Cor™ PAR quantum sensor. Cosine-corrected irradiance values were used to account for the angle of incidence and determine actual irradiance striking periphyton. There were no significant differences (ANOVA, $F = 0.49$, $P = 0.78$, df = 5,30) in photosynthetic response when periphyton samples were exposed to 1 h of constant light (100 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in the morning or afternoon during each of the 3 days of the experiment, so we assumed that time of measurement did not influence our results.

Four different light regimes (one constant, three fluctuating) were tested. The four light regimes (in $\mu mol \cdot m^{-2} \cdot s^{-1}$) were constant light at 100, light fluctuating between 50 and 150 with a period of 5 min, and light fluctuating between 10 and 460 with periods of either 4:1 or 8:2 min (Fig. 2). Six replicate tiles were tested simultaneously for each light regime, and each light regime experiment was conducted once. Regardless of the regime, the average light quanta received by the periphyton on the tiles was the same: 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 2 h. Daytime light levels in the Chriesbach (Fig. 1A) averaged 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$, so we considered 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ an appropriate value for mean photon flux. The light regimes used in this study were a compromise between what the periphyton experienced in nature and those that the phototron could produce.

Immediately following the photosynthesis assay, periphyton was removed from tiles with a razor blade and toothbrush and rinsed into a beaker with a squirt bottle containing deionized water. The collected slurry was filtered (Schleicher and Schuell GF 6 glass-fiber filter), and chl *a* was extracted in hot 90% ethyl alcohol and analyzed using a Krontron Instruments high-performance liquid chromatograph following the procedures outlined in Meyns et al. (1994).

On day 28, five randomly chosen tiles were collected for determination of composition, density, and biovolume of periphytic algal species. Periphyton was removed from tiles as described previously and preserved in 2% formalin solution. Density and biovolume estimates were based on counts of intact, protoplast-containing (i.e. live) cells using an inverted phase-contrast Leitz microscope. Cell density and species composition were estimated by counting at least 300 cells from each sample. Large algal cells were counted at 125× magnification; cyanobacteria and small diatoms were counted at 1250×. Diatom species identifications were made at 1250× magnification on Hyrax-mounted slides from material cleared in 30% hydrogen peroxide before mounting. Cell dimensions were measured with an ocular micrometer, and cell volume was estimated by applying average dimensions of a minimum of 20 cells per species per sample to the geometric shape best approximating the cell shape of each species (Wetzel and Likens 1991).

Net photosynthesis was measured in terms of oxygen evolved over time. Oxygen production curves for each replicate tile were standardized by the amount of chl *a* extracted from the tile at the end of the assay (Table 1). Values used for statistical analysis were the slopes of the lines for oxygen produced per unit chl *a* over 2 h. For each treatment regime, we assumed a linear response of oxygen production to light intensity (Fig. 4). The effects of light regime on photosynthetic rate were analyzed with a one-way analysis of variance (ANOVA) using the multiple ANOVA (MANOVA) module in Statistica™ (StatSoft Inc., Tulsa, Oklahoma). Data were square-root-transformed prior to analysis so that they fit homogeneity of variance and normality assumptions (Zar 1984). Multiple contrasts were made using the Newman-Keuls test in Statistica™.

RESULTS

Periphyton scraped off tiles contained 29 species of algae of which diatoms, especially *Achnanthes lan-*

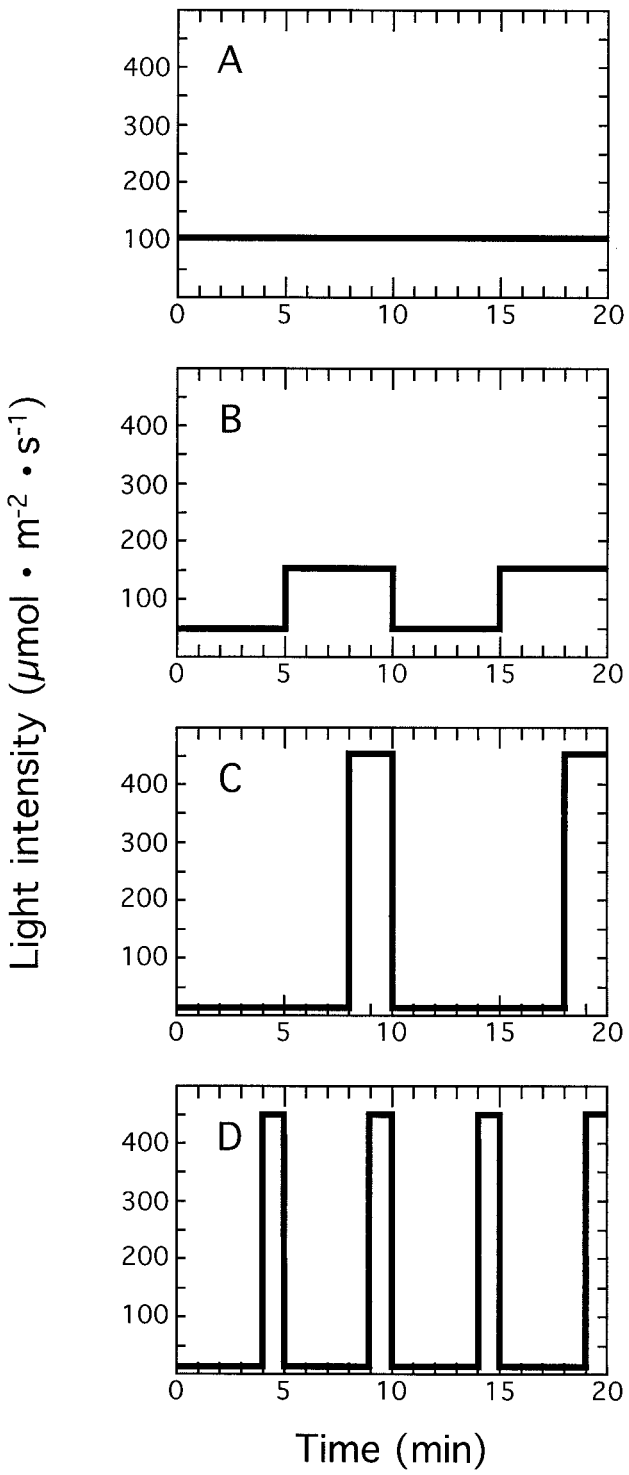

FIG. 2. Experimental light regimes. Intact periphytic assemblages from the Chriesbach were exposed to four light regimes: (A) constant light at 100 μmol·m^{-2}·s^{-1}, (B) light fluctuating between 50 and 150 μmol·m^{-2}·s^{-1} with a period of 5 min, (C) light fluctuating between 10 and 460 μmol·m^{-2}·s^{-1} with a period of 8:2 min, and (D) light fluctuating between 10 and 460 μmol·m^{-2}·s^{-1} with a period of 4:1 min. Actual measurements of irradiance did not differ noticeably from the desired exposures. In each case the total light quanta received by the periphyton on the tiles was the same: 100 μmol·m^{-2}·s^{-1} for 2 h. Note that only 20 min of the 2-h sequence are shown.

TABLE 1. Intensity and period of irradiance for four light regimes, the number of replicate chambers for each trial, and the mean (±1 SD) amount of chlorophyll *a* removed from the tiles from each trial. Oxygen production in the chambers was standardized by the amount of chlorophyll *a* per tile.

Light intensity (μmol·m^{-2}·s^{-1})	Light period (min)	Replicates (chambers)	Chlorophyll *a* (μg·cm^{-2})
100	constant	6	4.22 ± 0.81
50–150	5:5	6	3.67 ± 0.45
10–460	8:2	6	2.03 ± 0.23
10–460	4:1	6	3.17 ± 0.25

ceolata, A. minutissa, Cocconeis placentula, and *Gomphonema parvulum,* were the most abundant (Table 2). Twelve species of Bacillariophyta made up 87% of the algal biovolume on tiles, two species of Chlorophyta made up 9%, and one cyanobacterium, *Chamaesiphon* sp., made up just 4% of the total biovolume.

Periphytic photosynthesis responded differently to fluctuating light regimes compared to constant light ($F = 36.39$, $P < 0.0001$, df = 3,17; Fig. 3). Compared to the rates measured under 100 μmol·m^{-2}·s^{-1} constant light conditions, fluctuations ranging between 50 and 150 μmol·m^{-2}·s^{-1} with a 5-min period produced rates of photosynthesis that were about 20% greater than constant light (Newman-Keuls test, $P < 0.03$). Conversely, fluctuations between 10 and 460 μmol·m^{-2}·s^{-1} resulted in less photosynthetic activity. This was true whether the period was 8:2 or 4:1 min; both showed lower pho-

TABLE 2. Species composition of algae taken from tiles (n = 5) colonized 28 days in the Chriesbach. Twenty-nine species were encountered. The mean (±1 SE) density and biovolume of the 15 most abundant species are shown below. These species made up 88% of the total algal biovolume on tiles.

Algal species	Density (cells·mm^{-2})	Biovolume (μm^3·mm^{-2} × 10^{-4})
Bacillariophyceae		
Achnanthes lanceolata (Bréb.) Grun.	3181 ± 349	114 ± 24
Achnanthes minutissima Kütz.	24,741 ± 1773	114 ± 27
Cocconeis pediculus Ehr.	84 ± 66	30 ± 22
Cocconeis placentula Ehr.	435 ± 135	102 ± 34
Cymbella minuta Hilse. ex Rabh.	147 ± 45	4 ± 1
Fragilaria ulna (Nitz.) Lange-Bertalot	10 ± 10	6 ± 5
Gomphonema olivaceum Lyng.	318 ± 241	6 ± 5
Gomphonema parvulum (Kütz.) Cl.	1812 ± 329	118 ± 29
Melosira varians Ag.	15 ± 15	5 ± 5
Navicula erifuga Lange-Bertalot	81 ± 19	7 ± 2
Navicula lanceolata (Donk.) Cl.	115 ± 70	47 ± 27
Navicula minuscula Grun.	1161 ± 826	8 ± 5
Chlorophyta		
Monostroma sp.	4713 ± 1751	43 ± 16
Stigeoclonium sp.	439 ± 301	15 ± 9
Cyanobacteria		
Chamaesiphon sp.	7913 ± 1412	28 ± 7
Total	45,165	677

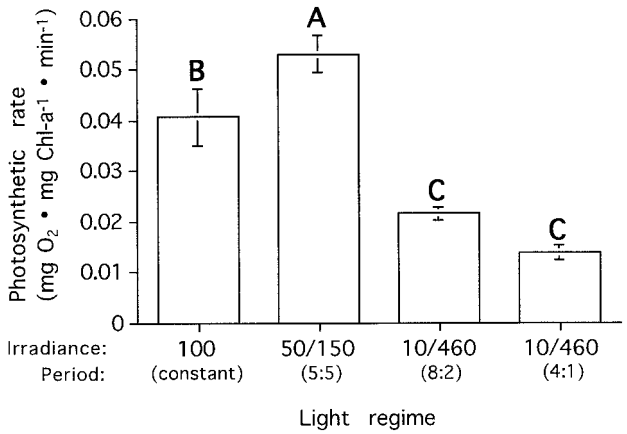

FIG. 3. Mean (±1 SE) photosynthesis under one constant and three fluctuating light regimes. From left to right, the bars show photosynthetic rates under constant light at 100 μmol·m^{-2}·s^{-1}, light fluctuating between 50 and 150 μmol·m^{-2}·s^{-1} with a period of 5 min, light fluctuating between 10 and 460 μmol·m^{-2}·s^{-1} with a period of 8:2 min, and light fluctuating between 10 and 460 μmol·m^{-2}·s^{-1} with a period of 4:1 min. Bars with the same letter did not differ significantly ($P > 0.05$, Newman-Keuls test).

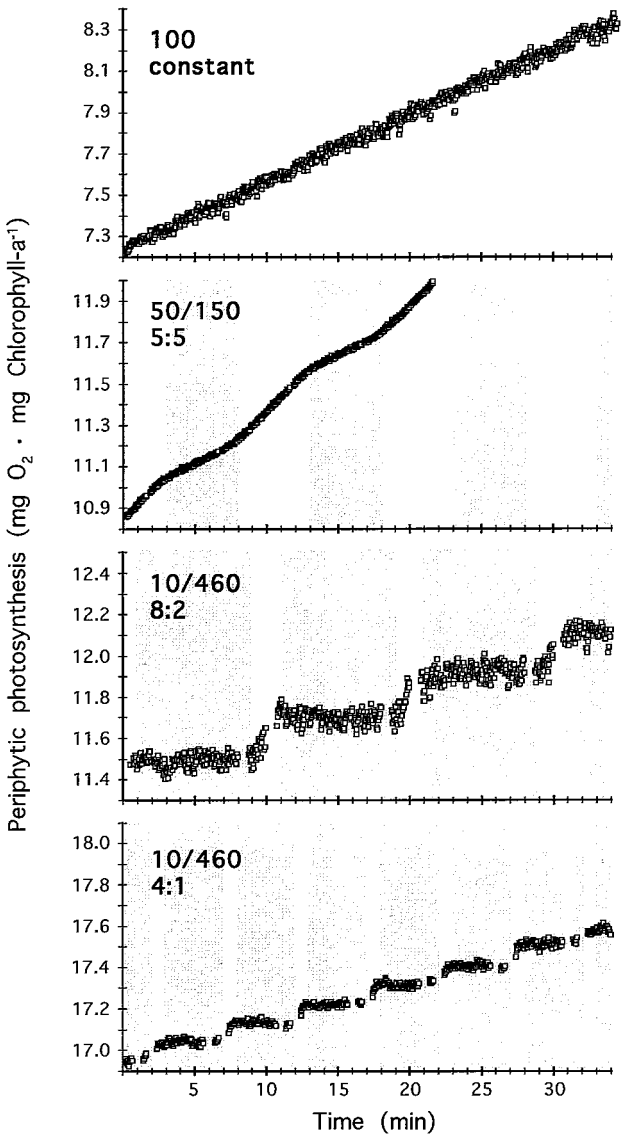

FIG. 4. Detail of periphytic response to light regimes. Data are oxygen production rates recorded for individual chambers from each treatment during 34 rain periods. All periods were taken from the first hour of exposure. Time scale is marked to indicate 5-min intervals, and shaded bands represent low-light periods in the fluctuating regimes. Note that only 34 min of the 2-h sequence are shown.

tosynthetic rates than either constant light or light fluctuating between 50 and 150 μmol·m^{-2}·s^{-1} (Newman-Keuls test, $P < 0.001$ for each comparison). Photosynthesis did not differ statistically between the two 10–460-μmol·m^{-2}·s^{-1} regimes (Newman-Keuls test, $P = 0.09$).

Measuring photosynthesis/time slopes for discrete light intensities within each light regime revealed that higher light intensities always produced steeper slopes (i.e. 460 > 150 > 100 > 10 μmol·m^{-2}·s^{-1}; Fig. 4). However, it was the combined interaction with the lower light intensity that ultimately determined the overall photosynthetic rate for a given light regime. For example, under the 460/10-μmol·m^{-2}·s^{-1} regimes, photosynthetic rates were 0.08 mg O_2·mg chl a^{-1}·min^{-1} or greater during the 460-μmol·m^{-2}·s^{-1} light phase, the highest rates recorded, but photosynthesis leveled out under 10 μmol·m^{-2}·s^{-1}, giving the response-time curve a ''stepped'' appearance and producing the lowest overall rates of photosynthesis recorded.

DISCUSSION

Our experiment yielded significantly different production rates for constant and fluctuating light regimes with the same mean intensity. Brief, intense light periods of 460 μmol·m^{-2}·s^{-1} produced greater photosynthesis/time slopes than did 50, 100, or 150 μmol·m^{-2}·s^{-1}, but it was the complete light regime that determined photosynthetic rates for the 2-h period. Although periphyton did utilize the 1- and 2-min sunflecks produced by the 10–460-μmol·m^{-2}·s^{-1} regimes, the integrated photosynthetic rates for these two light regimes were the lowest recorded. By contrast, the 50–150-μmol·m^{-2}·s^{-1} fluctuating regime yielded the highest rates of photosynthesis seen, exceeding constant-light photosynthesis by 23%.

It is important to note that the light regimes generated by the phototron used in this study only approximated natural conditions. In the stream, periphyton was exposed to sunflecks that were more variable in their extent, duration, and intensity. By contrast, those produced by the phototron had a regular period, fixed intensities, and a set duration. The light regimes chosen were constrained by the requirement that each treatment produce the same mean irradiance and also by limitations imposed by the phototron. For example, the phototron was not

able to create sunflecks of less than 1 min duration, although sunflecks lasting only a few seconds are common in nature (Chazdon and Pearcy 1991). Thus, our experiment examined only a subset of the types of sunflecks to which periphyton is exposed. Nevertheless, our data indicate that sunflecks of 1–5 min duration can have important consequences for periphytic photosynthesis. This was made strikingly clear by the result that fluctuations between 50 and 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with a 5-min period produced greater photosynthetic rates than did constant light at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Echoing these results were similar findings made by Marra (1978) for a marine diatom exposed to long period fluctuations of about 2 h. Marra showed that fluctuating light superimposed on a diurnal regime increased rates of photosynthesis and raised the threshold for light saturation. Put together, these studies and others (e.g. Greene and Gerard 1990; see the following discussion) suggest that the way in which light is ''packaged'' may have important implications for short-term algal photosynthesis.

We suggest two possible mechanisms to explain why the periphytic communities in this study showed greater net photosynthesis under moderate fluctuations (i.e. 50–150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) compared to constant light. One possibility is that the ratio of algal respiration/photosynthesis was different between constant and fluctuating light treatments. In their study of the marine alga *Chondrus crispus* Stackh., Greene and Gerard (1990) showed that growth rates of this macroalga were higher under fluctuating light than under constant light, a difference that was caused by decreased algal respiration. Under fluctuating light, *C. crispus* channeled more photosynthate into synthesis of new tissue than it did into catabolic respiration. Growth rates for *C. crispus* were higher under fluctuating light despite the fact that gross photosynthesis was actually lower compared to algae grown in constant light. Thus, the 50–150- $\mu mol \cdot m^{-2} \cdot s^{-1}$ regime may have produced greater photosynthetic rates by lowering algal respiration relative to the other light regimes. However, we did not assess algal or periphytic respiration, so we cannot confirm that this occurred in our study. Moreover, this explanation does not readily account for lower O_2 production rates seen under the two more extreme fluctuating regimes of 10–460 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

A second possibility may be that periphytic taxa within any given assemblage have different photosynthetic optima. This phenomenon has been demonstrated for species in pure culture (Dubinsky et al. 1986, Falkowski and LaRoche 1991) and for entire assemblages grown under high or low irradiance (Boston and Hill 1991, Hill and Boston 1991, Hill et al. 1995), and it may also occur *within* a periphytic assemblage. Were this the case, only some fraction of algae would attain high rates of photosynthesis under constant light. However, fluctuating regimes would present a range of light intensities that would bracket the photosynthetic optima of several taxa. Thus, assemblage-wide photosynthetic response would depend in part on how well the intensities of a fluctuating regime matched the optima of the constituent algal species. Of course, regimes having extreme fluctuations in intensity may fail to yield high photosynthetic rates. For example, under the two 10–460-$\mu mol \cdot m^{-2} \cdot s^{-1}$ regimes, 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was probably limiting and insufficient to support high rates of photosynthesis, whereas 460 $\mu mol \cdot m^{-2} \cdot s^{-1}$ may have caused photoinhibition among ''shade-adapted'' taxa (Hill et al. 1995).

Variable light regimes appear to be the rule rather than the exception in many natural stream habitats (Hill 1996). The accumulating evidence that sunflecks are an important energy source for understory terrestrial plants suggests that greater attention should be paid to the effects of sunflecks and other classes of fluctuating light on stream periphyton. Estimates of primary productivity in streams based on constant, mean hourly irradiance may misrepresent actual rates of carbon fixation and photosynthesis in streams in which fluctuating light levels are common. Even if sunflecks prove to be too brief to make substantial contributions to whole-stream photosynthesis, these transient bursts of light may help to explain photosynthetic variability in streams.

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