

Characterizing short-term light dynamics in forested headwater streams

Emily D. Heaston^{1,3}, Matthew J. Kaylor^{2,4}, and Dana R. Warren^{1,2,5}

¹Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331 USA

²Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

Abstract: Light controls local- and reach-scale primary production in forested headwater streams. In terrestrial ecosystems, short periods of elevated light beneath canopies (sunflecks) are instrumental in maintaining understory autotrophic production, but sunflecks are unexplored and uncharacterized in stream systems. We described short-term light dynamics in 4 forested headwater streams in the western Cascade Mountains of Oregon. We quantified the prevalence and characteristics of sunflecks, compared the timing of light exposure at stream sites to a sensor in full sun, and evaluated whether sunfleck characteristics differed between stream sections in old-growth vs second-growth forest. Sunflecks were common in streams. A minimum of 3 individual sunflecks/d occurred at each of 47 sensor locations. Short sunflecks were more common than long sunflecks, a result consistent with findings in terrestrial studies. However, streams had longer sunflecks than upland forests in this region, probably because canopy gaps are larger over stream channels than in the forest. In $>1/2$ of the 47 sensor locations, daily light distributions differed between in-stream and full-sun locations, revealing that canopies affect both the total light and the timing of light delivery to understory locations. The timing of peak stream temperature coincided better with light delivery by sunflecks than in full sun. Peak stream temperature was offset by ≥ 3 h from midday peak light in full sun, but beneath the forest canopy at the 4 surveyed streams, 26 to 60% of sunfleck events occurred within 2 h of peak stream temperature. These findings highlight the presence and potential importance to in-stream autotrophy of short-term light events (sunflecks) in forested streams. In a model simulation, a 1-h sunfleck increased stream primary production 5 to 17%, depending on the time of day that sunfleck occurred.

Key Words: sunfleck, transient offset light, stream light, riparian forest, HJ Andrews Experimental Forest, forest age

Light availability is an important factor controlling primary production and, in turn, foodweb dynamics and nutrient processing in many ecosystems. Heavily shaded ecosystems, such as understory plant communities and forested headwater streams, are commonly light limited (DeNicola et al. 1992, Hill et al. 1995, Leahey et al. 2004). In forests, much of the light reaching understory plants occurs in the form of localized, short-duration (min) periods of elevated light flux (sunflecks) that are important promoters of understory plant growth (Canham et al. 1990, Chazdon and Pearcy 1991, Leahey et al. 2004). Forested stream ecosystems are understory environments, but few investigators have characterized or considered the influence of sunflecks on stream ecosystems. Most researchers characterizing and evaluating light availability in headwater streams describe light dynamics at large spatial (10^1 – 10^2 m) or temporal (seasonal, annual) scales (Hill et al. 1995, Guasch and Sabater

1998, Ylla et al. 2007). However, in-stream primary production is a fundamentally local and largely instantaneous process. Thus, the small-scale and short-duration dynamics of stream light flux may have important effects on benthic primary production in forested headwater streams over those shorter time frames.

In terrestrial ecosystems, small-scale and short-duration light events enable understory plants to persist below largely closed canopies that limit light to forest floors (Chazdon and Pearcy 1986, Pearcy and Seemann 1990). Terrestrial plants reach their peak photosynthetic rate only after exposure to irradiance for periods of several minutes because light is needed to activate key photosynthetic enzymes (Walker 1973). Exposure to sunflecks early in the day primes photosynthetic machinery of understory plants for more effective use of subsequent sunflecks by creating stores of activated metabolites and reducing induction requirements (Chaz-

E-mail addresses: ³emily.heaston@oregonstate.edu; ⁴matthew.kaylor@oregonstate.edu; ⁵dana.warren@oregonstate.edu

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don and Pearcy 1991). Thus, the number, duration, timing, and intensity of sunflecks play a crucial role in controlling photosynthetic rates, thereby determining levels of C fixation in these systems. Sunflecks also are likely to occur in forested headwater streams, where canopies (and canopy gaps) create heterogeneous light regimes (Keeton et al. 2007, Warren et al. 2013).

Low light fluxes limit primary production in heavily shaded headwater streams (Boston et al. 1991, Hill et al. 1995). In forested streams, large and relatively uniform changes in light can affect stream autotrophy at the stream-reach scale (Finlay et al. 2011, Hill et al. 2011). For instance, canopy removal via timber harvest increases primary production, stream nutrient cycling, and the abundance and biomass of consumers in stream food webs. These effects suggest that these systems were at least partially light limited prior to canopy alteration (Hansmann and Phinney 1973, Murphy and Hall 1981, Noel et al. 1986, Bilby and Bisson 1992, Sabater et al. 2000). Large-scale changes in canopy cover and light availability also occur in association with seasonal changes in leaf cover. In deciduous-dominated and deciduous-conifer forest systems, canopy development and spring leaf-out can reduce light penetration, which leads to dramatic declines in stream gross primary production (GPP) and shifts headwater streams from net autotrophy to net heterotrophy (Hill et al. 1995, Roberts et al. 2007).

In contrast, fine-scale spatial and temporal heterogeneity in localized light is rarely considered in streams despite its demonstrated importance in terrestrial systems. Patterns of light exposure affected C fixation rates in one of the few studies of the influence of short-term, temporal variation in light regimes on periphyton primary production (Wellnitz and Rinne 1999). In a set of closed, experimental chambers, Wellnitz and Rinne (1999) explored photosynthetic rates of benthic stream algae exposed to 4 light regimes with the same total accumulated photosynthetically active radiation (PAR). When moderately intense ($150 \mu\text{mol m}^{-2} \text{s}^{-1}$) light was delivered in 5-min intervals followed by 5-min intervals of low light ($50 \mu\text{mol m}^{-2} \text{s}^{-1}$), the photosynthetic rate of algae increased by 23% relative to the photosynthetic rate when the same total accumulated light was delivered at a constant rate of $100 \mu\text{mol m}^{-2} \text{s}^{-1}$. These results suggest that patterns of in-stream light delivery, rather than just the total amount of available light, are important for in-stream primary production.

We evaluated fine-scale spatial and temporal variation of in-stream light by quantifying diurnal light patterns at multiple locations in 4 forested headwater streams in the Pacific Northwest region of North America. First, we compared patterns of light exposure in forested, mid-order streams relative to in open (full sun) environments, with a focus on the timing of light throughout the day rather than total accumulated light. Daily patterns of light could be similar in shaded and open streams (whereas magni-

tude would differ), if shading over the stream were spatially uniform (e.g., a shade cloth). However, in natural systems, variability in canopy structure should create spatial and temporal heterogeneity in stream light as the sun angle changes over the course of the day. We hypothesized that patterns of daily light exposure in forested streams would differ from open systems because of the influence of forest canopies on short-term light heterogeneity. Second, we focused on characterizing individual sunfleck events in these systems. We quantified the length, duration, frequency, timing, and proportion of total light from sunflecks within and among streams. To date, no studies in which authors quantified sunflecks or described sunfleck characteristics in stream ecosystems have been published. Therefore, we modeled our description and quantification of stream sunflecks after established terrestrial research (particularly Canham et al. 1990). Last, we evaluated how patterns of daily light and sunfleck dynamics interacted with patterns of daily stream temperature and how these 2 diurnal patterns might differ between stream reaches with riparian forests of differing structural characteristics (old- vs second-growth riparian forests).

We expected more frequent deviation from full-sun patterns in reaches with old-growth (complex canopy structure) than with second-growth riparian forests (limited canopy complexity) (Franklin et al. 2002, Franklin and Van Pelt 2004). We also expected the characteristics of sunflecks to differ between streams with old-growth and with second-growth riparian forest canopies. Specifically, we expected the duration and intensity (total PAR accumulation) of sunflecks to be greater in old- than in second-growth forested streams, leading to more daily accumulated PAR in reaches with old-growth riparian forests than in reaches with second-growth riparian forests.

METHODS

Study site

We conducted our study in July and August 2014 in 4 streams in and adjacent to the HJ Andrews Experimental Forest (HJA) in the Western Cascade Mountains of Oregon (lat 44.2°N, long 122.2°W; Fig. 1). Each stream had 2 reaches (100–300 m apart) with contrasting riparian forest stand age/structure. One reach of each stream was bordered by 50- to 60-y-old second-growth forest and the other reach was bordered by structurally complex old-growth forest. Thus, we had a total of 8 study reaches. This paired study design allowed us to characterize and compare light patterns between riparian forest types while controlling for inherent stream-to-stream variability in aspect and topographical shading. Our study reaches were Upper McRae Creek, Lower McRae Creek, Mack Creek, and Cook Creek (Fig. 1). We sampled upper McRae Creek twice during summer 2014 (mid-July and mid-August) and all other streams once. Upper McRae Creek, Lower McRae Creek, and Mack Creek are

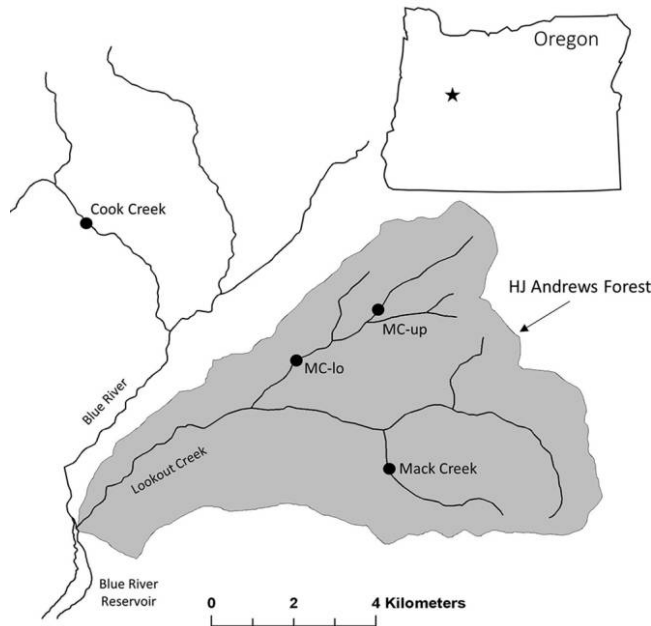


Figure 1. Map of study sites and the HJ Andrews Experimental forest (HJA). Each dot represents a pair of reaches, one in old- and the other in second-growth riparian forest. MC-up = Upper McRae Creek, MC-lo = Lower McRae Creek.

all in the Lookout Creek drainage basin of the HJ Andrews Experimental Forest. Cook Creek is in the Blue River drainage basin adjacent to the Lookout Creek drainage basin. The streams ranged from 3rd- to 4th-order with mean bankfull widths ranging from 6.3 to 10.5 m (Table 1). The Pacific Northwest has a Mediterranean climate, characterized by wet winters and dry summers. Summer days from July to August are rarely cloudy, and we quantified light at all streams on ≥ 1 cloudless, full-sun day.

Old-growth forests in the western Cascades of Oregon are dominated by Douglas fir (*Pseudotsuga menziesii*),

western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*), and can have dominant canopy trees >400 y old. Mid-seral second-growth forests typically are dominated by Douglas fir and often have high abundances of hardwood species, primarily red alder (*Alnus rubra* Bong.) and vine maple (*Acer circinatum* Pursh). Forest structure varied among the second-growth reaches we surveyed. Riparian forests at Upper McRae Creek and Cook Creek were composed of Douglas fir and red alder. The forest at Lower McRae Creek was harvested only on the west side, leaving the east side as old-growth (all other streams had second-growth forest on both stream banks). The harvested section of this reach has regrown with a mix of red alder, vine maple, and Douglas fir. The canopy of the second-growth reach of Mack Creek has not closed despite nearly 50 y of regeneration (~32% open; MJK, unpublished data).

Light data collection

We deployed 10 Odyssey PAR sensors (Dataflow Systems, Christchurch, New Zealand) at 47 locations throughout July and August 2014 (Table 1). These sensors recorded accumulated PAR calibrated to mol/m² over time intervals of 5, 10, or 15 min, depending on the stream. We deployed all 10 PAR sensors at a given stream on the same day and left them for 1 to 3 d (depending upon weather and logistic constraints in retrieving sensors). To characterize and compare summer light dynamics at multiple locations within and among streams, we selected a single cloudless 24-h period within the deployment period for analysis. To compare light consistently across all streams, we used 98% of total light (PAR) recorded in the 24-h period in analyses. Daylight lengths (98% of total light) ranged from 9 to 12 h, with the earliest beginning at 0700 h and the longest lasting until 1900 h. We attached sensors to rebar positioned in the center of the stream channel and secured just above the water surface. We calibrated sensors relative

Table 1. Physical habitat metrics of each stream sampled. MC-up = Upper McRae Creek, MC-lo = Lower McRae Creek, OG = old-growth, SG = second-growth. Dates are formatted m/dd/yyyy. – = not measured.

Stream	Date	Forest age class	Stream order	Bankfull width (m)	Gradient (%)	% canopy cover	Reach length (m)	Number of sensors
MC-up	7/1/2014	OG	3	6.9	6.8	77.8	80	5
		SG	3	6.3	6.8	91.6	80	5
MC-up	8/8/2014	OG	3	6.9	6.8	77.8	80	5
		SG	3	6.3	6.8	91.6	80	4
Mack	8/7/2014	OG	3	9.8	9.5	76.1	150	5
		SG	3	9.3	9.9	67.8	150	5
MC-lo	8/26/2014	OG	4	10.4	7.6	71.0	90	5
		SG	4	8.6	4.0	67.3	90	5
Cook	7/14/2014	OG	3	10.5	4.6	76.2	100	5
		SG	3	8.6	4.0	95.2	100	3

to the HJ Andrews Central Meteorological (CENMET) station meter (Model LI190SB; Li-COR PAR Sensor; Li-COR, Lincoln, Nebraska; lat 44.23°N, long 122.14°W) in late June 2014. The HJA meter is situated in an open-canopy environment and served as a full-sun reference against which to compare stream sensors and to calculate % full sun for each day on which we measured PAR. This meter records PAR in 15-min intervals, and we set the PAR meters to record at the same interval as the reference CENMET station (15-min intervals). However, we also were interested in quantifying higher-resolution light exposure in at least one stream, so PAR meters at Upper McRae Creek were set to record at 5-min intervals. Data from Upper McRae Creek were used most extensively in comparing stream light regimes to terrestrial work in the HJA by Canham et al. (1990).

Comparison of in-stream vs full-sun daily light patterns

To evaluate whether the pattern of light exposure at a given location in the stream differed from that of an open, full-sun system, we compared proportional cumulative distributions of PAR over the day between in-stream sensor locations and the full-sun sensor with Kolmogorov–Smirnov tests in R (version 3.1.3; R Project for Statistical Computing, Vienna, Austria). We measured the time interval over which 98% of total daily light exposure occurred at the full-sun sensor on each deployment date to establish clear start and stop times for stream PAR data collection and to reduce the influence of low-light tails associated with dusk and dawn. Total daily accumulated PAR will always be less in a forested stream than a full-sun reference site because of stream canopy cover and shading, but we were focused on the *pattern* of light rather than total accumulated PAR values for this analysis. Therefore, we standardized the full-sun and in-stream sensor data relative to the total PAR accumulated during the set time interval. All data sets included values from 0 at the start of the day to 1 at the end of the day, with analysis conducted on the patterns in these proportional changes of PAR over the day (i.e., proportional cumulative distributions). We evaluated the number and proportion of sensor locations that exhibited a distribution of light accumulation that differed from that of the full-sun reference site (Kolmogorov–Smirnov test, $p < 0.05$).

Light event (sunfleck) characterization

Identification of a sunfleck was subjective in most terrestrial studies in which sunfleck characteristics were quantified. In a few widely cited studies, researchers identified sunflecks as “brief pulses of predominantly direct radiation in contrast to the relatively constant levels of background diffuse radiation” (Chazdon and Pearcy 1991) or as “a continuous excursion above some threshold just above the background diffuse light level or some physiologically relevant level” (Way and Pearcy 2012). We used a prescribed

deviation from background diffuse light patterns to identify the start and end of a sunfleck. We distinguished pulses of high-irradiance light from background light by graphing daily PAR data over time and removing all high-light events. The initiation of a high-light event was identified as an increase in stream light $>0.005 \text{ mol m}^{-2} 15 \text{ min}^{-1}$ above the baseline estimate of diffuse light reaching the stream surface. The duration of the high-light event encompassed the sum of successive time intervals over which PAR continued to be $>0.005 \text{ mol m}^{-2} 15 \text{ min}^{-1}$ above the diffuse light baseline. Authors of some studies considered a light event lasting $>1 \text{ h}$ to be something more than a sunfleck, but we use the term sunfleck to characterize all high-light events of any duration. The PAR sensors recorded accumulated PAR within the time interval set initially, so a short-duration but high-intensity event could cause the whole interval to be classified as a sunfleck, even if the event was shorter than the interval. We addressed this potential shortcoming by applying a shorter interval (5 min) to the Upper McRae Creek sensors and focused in the other streams on patterns in sunfleck characteristics relative to each other and to terrestrial systems. Longer integrated time intervals would have reduced our ability to identify shorter sunflecks, but we did not expect these longer intervals to strongly affect our comparison of sunfleck characteristics among streams or between riparian forest types within the same stream when evaluating overall trends across multiple sensors because these comparisons were made of data collected with the same time-interval constraints and were applied to both reaches.

At each of the 47 sensor locations, we measured total daily accumulated PAR, % PAR from all sunflecks, % daily PAR from the largest sunfleck, % of day experiencing sunflecks, number of sunflecks, and mean, median, and maximum sunfleck duration. Analysis for each stream and riparian forest type within a stream was based on the aggregate or mean value (depending on the metric) across all sensor locations in each stream and forest type.

To assess whether overall patterns of in-stream sunfleck characteristics differed from patterns in terrestrial coniferous forests, we compared the number and duration of sunflecks on both dates at Upper McRae Creek to data collected by Canham et al. (1990) at a conifer forest in the HJA. The Upper McRae Creek data set included 19 sensor records of accumulated light in 5-min intervals, which we used to recreate the analysis conducted by Canham et al. (1990) characterizing the frequency of sunflecks of varying duration. We created histograms of the frequency of sunflecks classified by duration for all 4 streams.

Temperature also can be an important limiting factor to primary production in streams, so we evaluated how daily stream temperature trends interacted with light patterns to estimate the degree to which periods of peak light exposure aligned with or were offset from periods of peak stream

temperature in these systems. We recorded stream temperature over a 2-wk period in each stream using HOBO Pro v2 temperature data loggers (Onset, Bourne, Massachusetts) for 1 wk before and 1 wk after deploying the PAR meters at each stream). Mean temperature was calculated over this time period in 15-min intervals throughout the day in each stream, and we used these data to create a mean mid-summer daily stream temperature profile for each stream. We evaluated this temperature profile relative to daily PAR profiles from the full-sun sensor and the in-stream sensors. First, we compared the timing of peak light at the full-sun sensor to the timing of peak in-stream temperature. Temperature profiles are asymmetric in these systems (Fig. 2), so we evaluated the number of sunflecks that occurred within the period when temperature was within 0.2 and 0.5°C of peak daily in-stream temperature. We also counted the sunflecks that occurred over 2- and 4-h time periods centered on the time of peak daily in-stream temperature.

Sunflecks in a stream ecosystem model

We used the stream ecosystem model (McIntire and Colby 1978, McIntire et al. 1996) to assess potential periph-

yton response to changes in timing, duration, and intensity of daily light regimes. The stream ecosystem model was developed at HJA based on biotic and abiotic data collected in small headwater streams from the same basin in which we conducted our study. It estimates stream benthic GPP based on periphyton standing stock, temperature, light, and nutrient availability. The model uses a 1-h time step, and light may be changed at this temporal scale over the 16 h of daylight used in the model. This flexibility allowed us to manipulate hourly light intensity to test for the influence of a relatively short period of elevated light. We input a set of light-regime scenarios based on light data from our study. In all cases, we used the default photosaturation levels. We ran the model for 10 consecutive days and focused on cumulative estimated periphyton GPP (g/m^2) over those 10 d to compare scenario outcomes. We used 1 d of diffuse light values without sunflecks from the second-growth reach of Upper McRae Creek (1 July 2014) in the model simulations. We also used characteristics of sunflecks (timing, duration, and intensity) to simulate sunflecks in the model. This stream experienced a sunfleck at 1200, 1300, and 1500 h. Not all sunflecks were 1 h long, but the constraints of the model required that we apply full 1-h events.

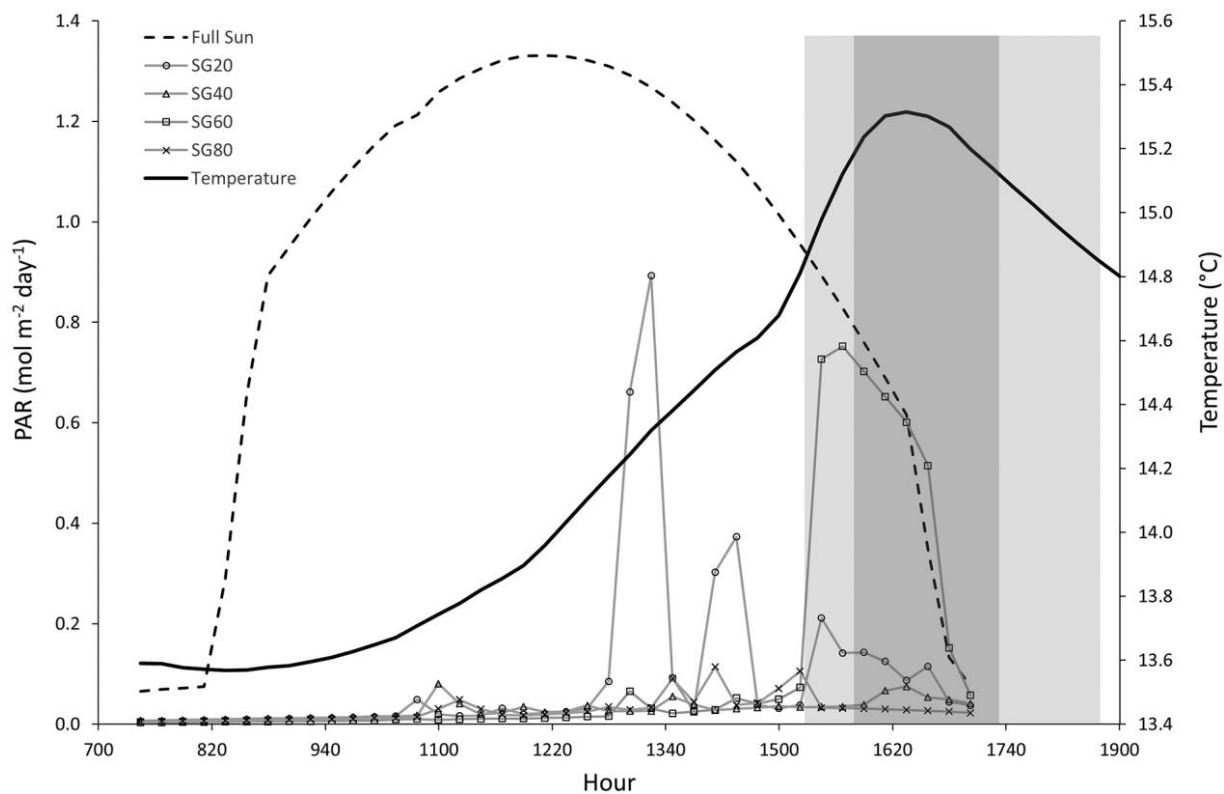


Figure 2. In-stream temperature, photosynthetically active radiation (PAR) in a full-sun reference sensor (HJ Andrews CENMET station), and PAR recorded by 4 in-stream light sensors deployed at the second-growth reach of lower McRae Creek (MC-lo) over a 24-h period. Light shading represents period of time within 2°C (1545 to 1730 h) of peak in-stream temperature and dark shading represents period of time within 5°C (1515 to 1845 h) of peak in-stream temperature.

Modeled daily light patterns included a base level with diffuse values consistent with the baseline at the Upper McRae Creek location with no sunflecks. We then applied 6 scenarios modifying light. First, we evaluated 3 scenarios with one 1-h sunfleck during the day (at 1000, 1300, and 1500 h). Next, we evaluated a scenario with two 1-h sunflecks during the day (one at 1300 and one at 1500 h) and a scenario with one 2-h sunfleck beginning at 1200 h. Last, we evaluated a scenario in which we increased light 40% above baseline for 16 h, which reflected the total accumulated light intensity that occurred when we applied each short-term, high intensity sunfleck scenario (magnitudes based on data from the field). In a final step, we calculated the uniform increase in accumulated light that would be needed to yield a GPP response comparable to the largest sunfleck response of GPP that was observed.

RESULTS

Comparison of in-stream vs full-sun daily light patterns

In 3 of the 4 streams and 4 of the 5 sampling events, ≥ 1 sensor recorded a daily light regime pattern that differed significantly from standard diel pattern of light observed at the full-sun sensor (Kolmogorov–Smirnov test of proportional cumulative distributions, $p < 0.05$; Table 2). Light measurement at Upper McRae Creek (bankfull width = 6.6 m) included 2 separate sampling dates with different PAR sensor locations for each data set (for all but 1 sensor location). On the 1st sampling date at Upper McRae Creek (7 July), 80% of sensor locations differed from full sun. On the 2nd sampling date at Upper McRae Creek (8 August), only 30% of sensor locations differed from full sun (Table 2). At Cook Creek (bankfull width = 9.6 m), 0 of 8 sensor locations differed from full sun. However, 60% of sensor locations at Lower McRae Creek (bankfull width = 9.5 m) and 50% of sensor locations at Mack Creek (bankfull width = 9.5 m) differed from full sun. The number of sensor locations that differed from full sun did not differ between old- and second-growth forest.

Sunfleck analysis

Light availability in the streams was not uniform throughout the day. None of the 47 sensors recorded < 3 sunflecks, and on average across all streams, sensors recorded 5.7 sunflecks/d in the study streams (Table 3). Between 64.2 and 89.4% of the mean total daily PAR in each stream occurred during sunflecks (Table 3). Mean sunfleck duration at each stream ranged from 23.6 to 56.6 min (medians: range = 12.5 to 49.5 min). At all streams, short-duration sunflecks were more common than long-duration sunflecks. Most sunflecks were < 20 min, but all streams had ≥ 1 sunfleck/light event > 1 h (Fig. 4), and longer sunflecks generally contributed more PAR to daily available light.

We found limited support for the hypothesis that accumulated PAR would be greater in old- than in second-

Table 2. Results of the Kolmogorov–Smirnov analysis comparing daily in-stream light distributions collected across 5 sampling dates and 4 streams to those of a full-sun reference sensor (HJ Andrews CENMENT station). MC-up = Upper McRae Creek, MC-lo = Lower McRae Creek, OG = old-growth, SG = second-growth. Dates are formatted m/dd/yyyy. Bolded values are totaled values for each pair of SG and OG reaches in each stream, and italicized values are the percent of samples that differed from full sun.

Site	Date	Riparian stand age class	Locations sampled	Number different from full sun ($p < 0.05$)
MC-up	7/1/2014	OG	5	5 (100%)
		SG	5	3 (60%)
		All	10	8 (80%)
MC-up	8/8/2014	OG	6	2 (33%)
		SG	4	1 (25%)
		All	10	3 (30%)
Mack	8/7/2014	OG	5	2 (40%)
		SG	5	3 (60%)
		All	10	5 (50%)
MC-lo	8/26/2014	OG	5	3 (60%)
		SG	5	3 (60%)
		All	10	6 (60%)
Cook	7/14/2014	OG	2	0
		SG	6	0
		All	8	0

growth reaches. Reaches bordered by old-growth riparian forests had greater accumulated PAR than reaches bordered by second-growth forest in Upper McRae Creek (both dates) and in Cook Creek. However, accumulated PAR was similar between old- and second-growth reaches at Lower McRae Creek, and at Mack Creek accumulated PAR was greater at the second- than at the old-growth reach (Table 3).

The pattern of sunfleck frequency relative to sunfleck duration in Upper McRae Creek, where we had the highest-resolution light measurements, was broadly consistent with the patterns observed by Canham et al. (1990). The shortest duration sunflecks occurred most frequently, but the pattern of sunfleck durations differed notably at the tail of the distribution (Fig. 3). Longer duration sunflecks were more common in this stream than in the upland forest understories assessed by Canham et al. (1990) at the same Long-term Ecological Research site. The longest period of assessment conducted by Canham et al. (1990) was 1 h, and they found no sunflecks lasting > 35 min. In contrast, we found many examples of sunflecks > 1 h at Upper McRae Creek (Fig. 3). Across the full range of streams, 34 (12.5%) of 271 total sunflecks recorded had durations > 1 h (Fig. 4A–E).

Table 3. Characterization of 271 sunflecks based on data collected from 47 locations in old-growth (OG) and second-growth (SG) reaches of 4 streams and 5 sampling events. n = number of sensors, accumulated PAR = mean (SD) total photosynthetically active radiation, % total daily light = mean (SD) percent of total available (full-sun) daily PAR reaching the stream, MC-up = Upper McRae Creek, MC-lo = Lower McRae Creek, OG = old-growth, SG = second-growth. Dates are formatted m/dd/yyyy. Bolded values are total values for each pair of SG and OG reaches.

Site	Date	Forest age	n	Accumulated PAR (mol m ⁻² d ⁻¹)	% total daily light (accumulated PAR)	Mean number of sunflecks	% PAR from sunflecks	Sunfleck duration (min)		
								Mean	Median	Maximum
MC-up	7/1/2014	OG	5	9.6 (5.3)	24.7 (13.6)	6.8	89.2	31.3	20.0	78.0
		SG	5	3.1 (1.6)	8.0 (4.4)	8.2	70.6	15.9	10.0	40.0
		All	10	6.4 (5.1)	16.4 (13.0)	7.5	79.9	23.6	12.5	59.0
MC-up	8/8/2014	OG	5	5.9 (3.7)	16.1 (10.1)	5.7	89.4	40.8	29.2	90.8
		SG	4	1.8 (1.6)	5.0 (4.4)	6.8	70.7	14.9	11.3	38.8
		All	9	4.2 (3.6)	11.6 (9.9)	6.1	86.2	30.5	22.0	70.0
Mack	8/7/2014	OG	5	2.7 (2.1)	7.5 (5.7)	4.0	76.6	47.7	40.5	79.0
		SG	5	5.4 (3.3)	15.1 (9.1)	2.8	84.5	65.5	58.5	49.0
		All	10	4.1 (3.0)	11.3 (8.2)	3.4	80.6	56.6	49.5	64.0
MC-lo	8/26/2014	OG	5	3.0 (3.0)	8.3 (8.2)	4.8	64.2	33.2	22.5	69.0
		SG	5	3.1 (1.8)	8.5 (4.9)	4.6	69.6	34.8	24.0	75.0
		All	10	3.0 (2.3)	8.4 (6.4)	4.7	66.9	34.0	23.3	72.0
Cook	7/15/2014	OG	5	7.3 (3.1)	20.0 (8.3)	5.6	69.3	40.2	27.0	86.0
		SG	3	3.7 (1.4)	10.1 (3.8)	8.3	64.9	35.0	30.0	66.7
		All	8	6.0 (3.1)	16.3 (8.4)	6.6	67.7	38.3	28.1	78.8

Sunflecks occurred throughout the day and their timing relative to peak stream temperature was widely variable (Table 4). Change in diurnal temperature was between 0.7 and 1.7°C over the daylight time intervals assessed in our study. Peak light at the full-sun sensor was offset from the time of peak daily in-stream temperatures by an average of ~4 h across all streams. Stream temperature at peak light (solar noon) was, on average, ~0.8°C lower than the peak daily in-stream temperature. Nearly 26% of the 271 sunflecks recorded occurred within 1 h and ~40% occurred within 2 h of the time of peak in-stream temperature. Overall, 1/3 of all observed sunflecks occurred when stream temperature was within 0.2°C and nearly 1/2 occurred when stream temperature was <0.5°C of peak stream temperature (Table 4).

Sunflecks in a stream ecosystem model

Stream ecosystem modeling provided an estimate of how daily short-term variation in light dynamics, including intensity and timing, might alter stream GPP. The simulated sunfleck light regimes demonstrated that the timing of a sunfleck can affect daily autotrophic productivity. A regime in which a 1-h sunfleck occurred daily at 1000 h, when baseline light was low, resulted in a 20% increase in GPP over 10 d. However, regimes in which a 1-h sunfleck of equal magnitude and duration occurred at 1500 h, when baseline light

was higher, increased GPP by only 5% over 10 d. A regime in which a 1-h sunfleck occurred at 1200 h when baseline light was at its maximum (and comparable to a sunfleck documented from our empirical light assessments) yielded a 6% increase in GPP over 10 d.

Duration of sunflecks also influenced simulated GPP. Longer-duration sunflecks resulted in larger increases in GPP. Even though the total change in light intensity was similar to that generated by 1-h sunflecks, a regime in which a 2-h moderately high-light sunfleck occurred at 1300 resulted in a 17% increase in GPP, whereas a regime in which a 1-h sunfleck began at the same time increased GPP by 6%. Increasing light uniformly to yield the same total increase in accumulated light (~40%) resulted in the largest increases in GPP, but 1 regime with a sunfleck occurring at 1000 h resulted in the same change in GPP as a uniform increase of 20% in daily sunlight intensity.

DISCUSSION

Our results demonstrate that light regimes in forested streams are spatially and temporally variable and that sunflecks are common. In streams, the timing of light exposure was highly variable and proportional cumulative distributions of PAR often differed from that recorded at a full-sun sensor. All 47 sensors recorded ≥3 sunflecks/d. Overall, characteristics of in-stream sunflecks were relatively con-

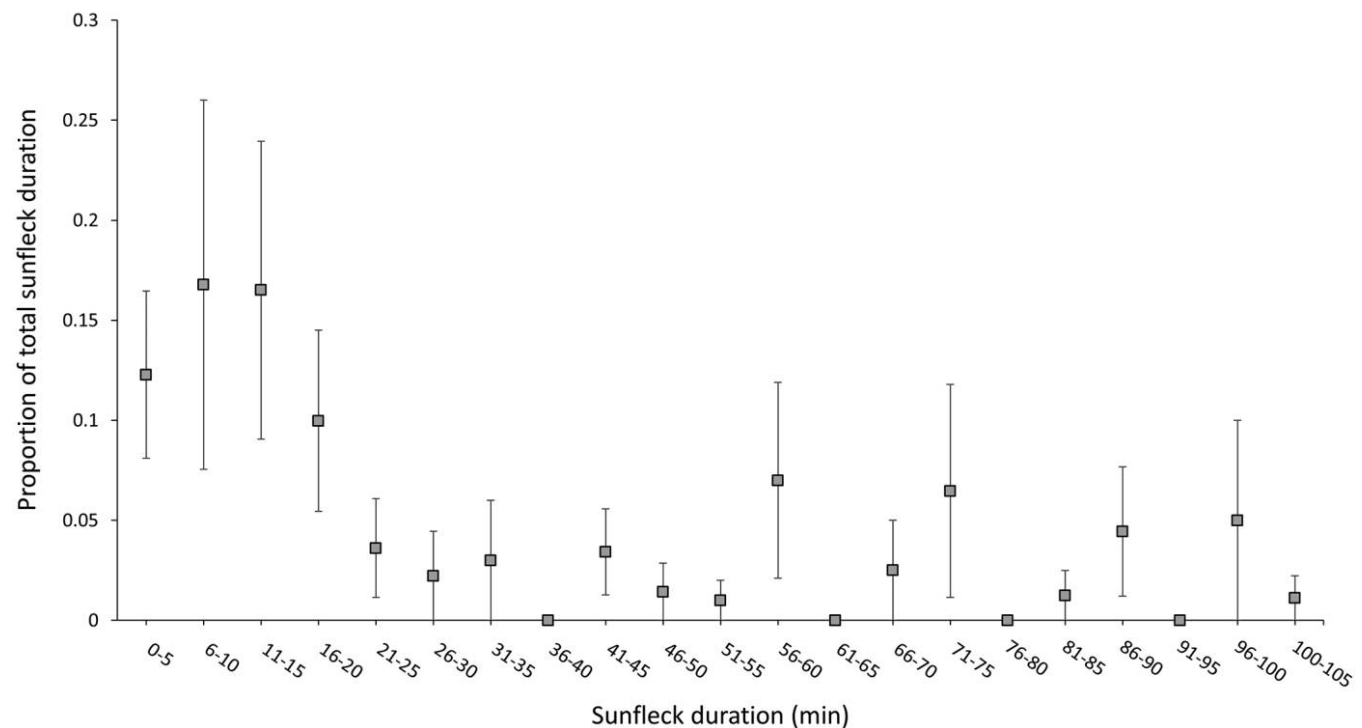


Figure 3. Mean (\pm SE) proportion of sunfleck duration in 5-min bins. Sunfleck data were aggregated from 19 light sensors deployed over 2 sampling dates throughout old-growth forested stream reaches of Upper McRae Creek in the HJ Andrews (HJA) Experimental Forest. This figure is comparable to fig. 2 by Canham et al. (1990) showing mean (\pm SE) proportion of sunfleck duration (in 2-min bins) in the HJA upland old-growth forests.

sistent with those previously observed in upland forests, but streams had more long-duration (>1 h) sunflecks than the upland forest sites, probably because of the larger canopy gaps created by the stream channel.

Comparison of in-stream vs full-sun daily light patterns

Proportional cumulative distributions indicated that the pattern of stream light exposure through the day deviated from that in full sun in slightly $>1/2$ of the light sensor locations. This finding suggests that the timing of light exposure in forested headwater streams may not be well represented by a standard diurnal light pattern with peak light exposure at solar noon. The potential for light patterns to differ between forested headwater streams and open systems is clearly present and warrants consideration in extrapolating results. However, we observed considerable variability among the streams, and our results do not allow us to completely reject the null hypothesis that light patterns do not differ between stream locations and open sun. For example, in Cook Creek, light patterns did not differ from the pattern in full sun. For this stream, we clearly were unable to reject our null hypothesis. In contrast, in Lower McRae Creek, light patterns at 6 of 10 sensor locations differed significantly from the pattern in full sun, and rejection of the null hypothesis was warranted.

The influence of forest age class on daily patterns of in-stream light exposure was also inconsistent. We expected riparian forest canopies to be more uniformly closed in second- than in old-growth forests and that canopy gaps characteristic of old-growth forests would result in more spatial and temporal variability in light availability. Thus, we expected a greater proportion of old- than second-growth forest reaches to exhibit distributions in daily light exposure that differed from full sun. However, this expectation was met at only 1 stream (Upper McRae Creek). At 2 streams, the number of sensor locations with patterns that deviated from full sun did not differ between second- and old-growth locations, and at 1 stream (Mack Creek), patterns at more old- than second-growth forest sensor locations differed from full sun.

The small number of replicate stream reaches restricted our ability to draw further inference related to differences in daily light patterns in second- and old-growth forested streams. Nevertheless, our results highlight the spatial variability of light patterns in these streams and suggest that caution is needed before making blanket assumptions about the influence of riparian forests on stream light patterns; i.e., riparian forests influence both the *amount* and the *timing* of light reaching streams. The duration of the sampling interval also was a shortcoming of our data set and limited inference of the Kolmogorov–Smirnov analysis. Our analy-

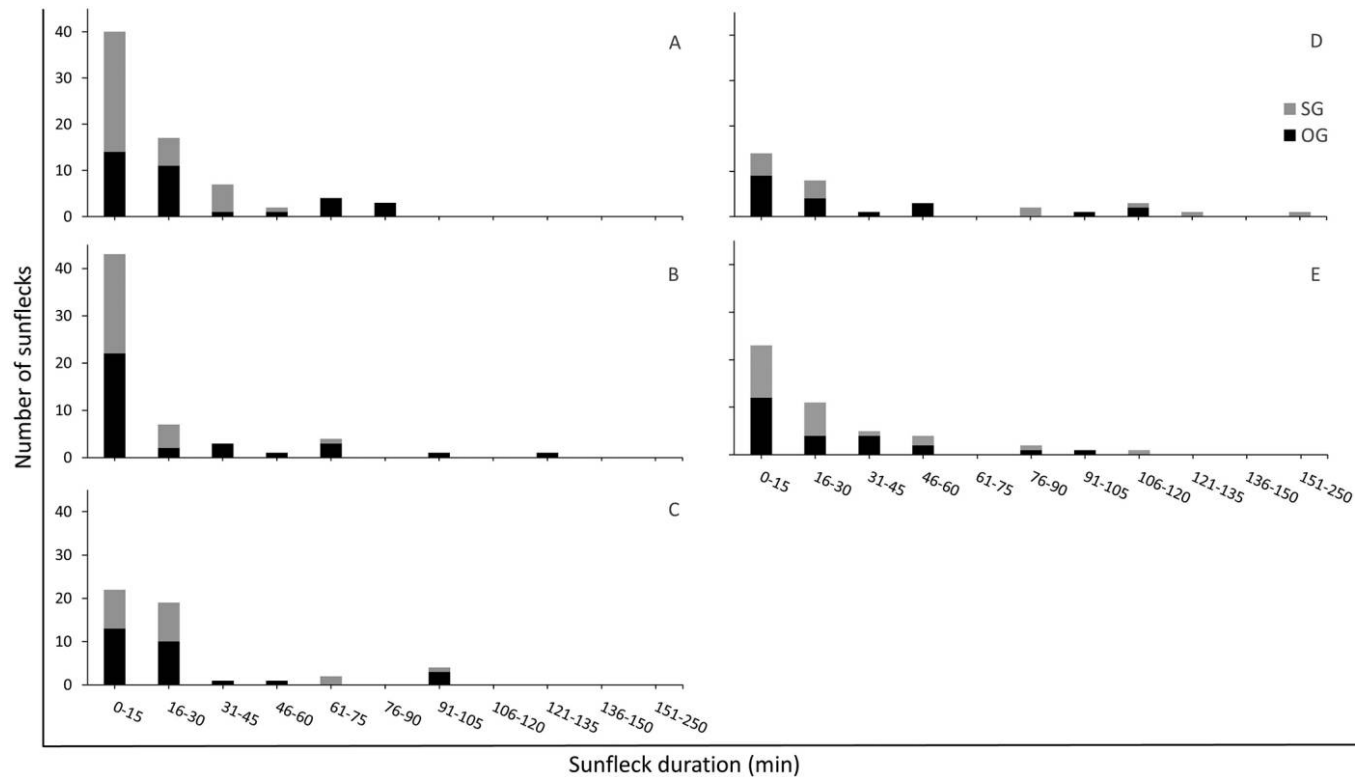


Figure 4. Frequency distribution of sunfleck duration in 15-min bins at Upper McRae Creek in July (A) and August (B), Cook Creek (C), Mack Creek (D), and Lower McRae Creek (E). OG = old-growth reach, SG = second-growth reach.

sis of daily light patterns and the comparison of daily light patterns between riparian forest age classes were limited by the 15-min sampling time interval, which was too large to detect the fine-scale distributions of sunflecks throughout the day. A greater number of higher temporal-resolution light measurements are recommended for future work exploring this question.

Investigators have considered a standard pattern of diel variation when modeling light dynamics (Julian et al. 2008). However, incorrect assumptions about the uniformity of light fluxes and the interaction of light with temperature could influence estimates of stream primary production. Hall et al. (2015) demonstrated the importance of variability in daily stream light as a control of variation in benthic GPP. At shorter time scales, light availability was determined by cloud cover and turbidity, whereas at seasonal time scales, insolation and weather events had much larger effects on the amount of light reaching the water's surface (Hall et al. 2015). Hall et al. (2015) demonstrated that lower light availability at both time scales had notable negative effects on GPP that exceeded the effects of water temperature on GPP under the conditions evaluated. The effects of seasonality on stream GPP has been detailed many times (Rosemond 1994, Guasch and Sabater 1995, Roberts et al. 2007, Lupon et al. 2016), but our understanding of how short-duration, localized changes in light affect in-stream

process within a season is relatively unexplored. Moreover, the ability to estimate how daily light patterns might differ between a forest canopy and full sun is particularly useful when modeling light and associated in-stream ecosystem processes for laboratory experiments focused on recreating stream conditions in natural forest.

Sunfleck analysis

Sunflecks were an important part of the daily in-stream light budget in forested streams, where light can limit GPP (Hill et al. 1995, Cashman et al. 2013). Despite variability in stream size, aspect, riparian forest structure, and the duration of light measurement intervals, ≥ 1 sunfleck was observed at every sensor location. Sunflecks on the stream surface can be as low as 2% of the total daily light exposure in full sun, and sunflecks accounted for as much as 90% of the total flux. The high percentage of light occurring as sunflecks is consistent with results of studies of understory light characteristics of terrestrial environments (Canham et al. 1990, Chazdon and Pearcy 1991, Way and Pearcy 2012).

Sunflecks were not uniform throughout the surveyed sites, demonstrating that light regimes can be highly variable at small spatial scales in forested streams. Sunfleck characteristics did not appear to be related to most abiotic stream characteristics we evaluated (Table 1). However, we did see

Table 4. Characteristics of in-stream temperature (T) and daily light regimes. Peak mean temperature (PMT) at the full-sun sensor occurred at solar noon (data from CENMET station). In-stream PMT is the average peak in-stream temperature over a 1-mo period from 2 wk before to 2 wk after the sampling date. Full-sun analysis includes the number of hours between 1200 h (time of peak daily light at the full-sun sensor) and in-stream PMT (time offset from solar noon) and the number of °C between T at solar noon at the full-sun sensor and in-stream PMT (T offset from solar noon). Sunfleck time offset analysis includes the number (and % total) of sunflecks occurring within 1 and 2 h of PMT. Sunfleck temperature offset analysis includes the number (and % of total) sunflecks occurring within 0.2 and 0.5°C of in-stream PMT. MC-up = Upper McRae Creek, MC-lo = Lower McRae Creek, OG = old-growth, SG = second-growth. Dates are formatted m/dd/yyyy. Dashes represent repeated values at the same sample location because light was sampled in Upper McRae Creek on 2 separate dates, but temperature was averaged across 2 summer months (August, September) of continuous data collection.

			In-stream temperature			Full sun		Sunfleck time offset		Sunfleck T offset	
Stream	Date	Reach	Time of PMT (h)	PMT (°C)	T at noon (°C)	Time offset from noon (h)	T offset from noon (°C)	Sunflecks within 1 h	Sunflecks within 2 h	Sunflecks within 0.2°C	Sunflecks within 0.5°C
MC-up	7/1/2014	OG	1615	12.4	11.6	4.3	0.8	14 (41.2%)	16 (47.1%)	15 (44.1%)	21 (61.8%)
		SG	1600	12.6	11.9	4.0	0.7	15 (36.6%)	24 (58.5%)	11 (26.8%)	23 (56.1%)
MC-up	8/8/2014	OG	—	—	—	—	—	8 (22.9%)	12 (34.3%)	11 (31.4%)	17 (48.6%)
		SG	—	—	—	—	—	6 (22.2%)	10 (37%)	5 (18.5%)	10 (37%)
Mack	8/7/2014	OG	1615	13.8	13.4	4.3	0.3	1 (5%)	6 (30%)	12 (60%)	15 (75%)
		SG	1500	14.3	13.6	3.0	0.7	5 (35.7%)	8 (57.1%)	6 (42.9%)	9 (64.3%)
MC-lo	8/26/2014	OG	1645	15.0	14.0	4.8	1.0	8 (33.3%)	10 (41.7%)	6 (25%)	13 (54.2%)
		SG	1630	15.3	13.9	4.5	1.4	3 (13%)	6 (26.1%)	3 (13%)	6 (26.8%)
Cook	7/15/2014	OG	1500	14.4	13.6	3.0	0.8	6 (21.4%)	9 (32.1%)	8 (28.6%)	10 (35.7%)
		SG	1530	14.3	13.3	3.5	0.9	6 (24%)	10 (40%)	11 (44%)	9 (36%)
Average			—	—	—	4.0	0.8	6.2	9.6	7.8	11.9
Total			—	—	—	—	—	74 (25.9%)	115 (40.2%)	94 (32.9%)	143 (50%)

some predictable results when comparing mean accumulated PAR between riparian forest age classes. Mean accumulated PAR was greater in old- than in second-growth reaches in 3 of 5 streams/dates. Streams that did not follow this trend were Mack Creek and Lower McRae Creek. Mack Creek is north-facing, and thus, more topographically shaded than other streams in our study. However, we suggest that the primary reason for greater light in the second-growth section of this stream is the rate of riparian forest regeneration in the cut-over reach. The riparian canopy had not yet fully re-established in the second-growth reach at Mack Creek. Few trees fully shaded the stream. Thus, canopy cover was similar between the 2 reaches. Percent canopy cover also was similar between old- and second-growth reaches of Lower McRae Creek. Differences in stand regeneration dynamics between streams illustrates the importance of localized sampling and localized processes when considering the influence of light availability on system productivity.

In our study and in the terrestrial study by Canham et al. (1990), short-duration sunflecks were more common than longer-duration sunflecks. The ability of an autotroph to respond to light depends on its induction state or readiness

to use dissolved CO₂. Photosynthetic induction is increased by prior exposure to light and the intensity of that light. High-intensity, short-duration sunflecks can directly influence autotrophic photosynthetic efficiency in terrestrial systems (Chazdon and Pearcy 1991, Way and Pearcy 2012). This phenomenon has not been explored extensively in stream environments, but the results of a study by Wellnitz and Rinne (1999) suggest the potential for a priming effect of light on benthic algae in streams. They measured a higher photosynthetic rate when light was supplied by alternating 5 min of high light with 5 min of low light than by 3 other light regimes. These results provide empirical support for use of a 5-min interval to measure sunflecks and their effect on autotrophic production. This interval will enable easier comparison to terrestrial sunfleck research. Moreover, measurements over short periods can be summed to 15- or 60-min intervals if needed, but it is much more difficult to shorten a duration after data collection.

Algal photosynthetic rates respond to temperature changes in a positive relationship between light availability, thermal energy, and C fixation (Morin et al. 1999, Larned 2010). Light interacts with temperature to influence primary production and directly affects stream temperature,

particularly in small streams with limited light availability (Graham et al. 1995, DeNicola and Hoagland 1996). Therefore, short-duration light events could have a substantial effect on photosynthesis with respect to the availability of enzymes (activated by light) and thermal energy. Light wavelengths that directly influence temperature differ from those used in photosynthesis, but irradiance and PAR are highly correlated in direct sunlight (DeNicola et al. 1992). Mulholland et al. (2006) found that NO_3^- uptake rates increased by 56 and 54% between predawn and midday measurements in 2 streams because of increases in stream temperature of 3.7 and 4.3°C, respectively. The stream with higher mean daily PAR also had consistently higher nutrient uptake rates throughout the day than the stream with lower mean daily PAR (Mulholland et al. 2006). We found that ~40% of all sunflecks occurred within 2 h of peak stream temperature and ~50% of sunflecks occurred within 0.5°C of maximum daily stream temperature. Thus, a substantial number of sunflecks can occur near maximum temperature. Small changes in temperature and the interaction of temperature and light could influence mid-summer benthic primary production.

Sunflecks in a stream ecosystem model

Modification of light regime in the stream ecosystem model demonstrated the potential for the timing of sunflecks to affect biotic responses. Sunflecks that occurred early in the day, even at a moderate intensity, led to disproportionate increases in GPP when compared to sunflecks of equal magnitude that occurred later in the day. This result may be partially explained by assumptions of fixed photosaturation values in the model. Sun angle and background light values are lower earlier in the day than at midday. Thus, a sunfleck that occurs earlier in the day has greater potential to influence GPP than one that occurs later in the day when the difference between background light and the photosaturation value is smaller. The model may have demonstrated a compounding effect, whereby higher levels of light intensity reached earlier in the day result in a net increase of GPP that accumulates throughout the rest of the day. Sunflecks that increased total daily light by ~40% increased GPP by 5 to 20% depending on the timing of sunflecks, whereas a constant 20% increase in light resulted in a 20% increase in GPP. This result probably was caused by the fixed photosaturation values in the model. High-intensity sunflecks exceeded photosaturation values, so not all light influenced GPP, whereas a consistent and uniform increase in light throughout the day was much less likely to cause photosaturation. Sunflecks simulated in this model would occur at a different range of temperatures in a natural system, but the effect of temperature on the biotic response to changes in light was constrained by the model. Temperature was limited to a daily average and, therefore, the model negated the positive effects of asymmetric diel fluxes

in temperature on primary production later in the day. Moreover, nutrient concentrations can affect photosaturation values (Hill et al. 2009). Sunflecks may have a smaller effect on GPP in streams with low than with high nutrient availability.

Conclusions

Most studies of light in streams and its influence on associated stream ecosystem processes have focused on reach-scale light dynamics with little consideration of localized and short-term light regimes. Our results indicate that stream light availability is spatially and temporally dynamic in headwater streams on daily time scales, which is generally assumed, but has not been quantified. Sunflecks have received considerable attention in terrestrial environments, where they support understory plants, and at least one laboratory study indicated that temporal patterns of light may have a direct effect on benthic primary production in streams (Wellnitz and Rinne 1999). Local forest composition and management history, topography, and latitude all affect stream light and sunfleck dynamics, and our study provides the first broad quantification of stream sunflecks from multiple streams and highlights their prevalence. Sunflecks present an interesting new realm of field research in stream ecology that may enhance our understanding of spatial and temporal dynamics of benthic primary production and our understanding of how riparian forest disturbances that change the patterns and duration of sunfleck events can affect stream ecosystems (Franklin et al. 2002).

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