

Comparing streambed light availability and canopy cover in streams with old-growth versus early-mature riparian forests in western Oregon

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Abstract Light availability strongly influences stream primary production, water temperatures and resource availability at the base of stream food webs. In headwater streams, light is regulated primarily by the riparian forest, but few studies have evaluated the influence of riparian forest stand age and associated structural differences on light availability. In this study, we evaluated canopy cover and streambed light exposure in four second-order streams within paired reaches of primary old-growth versus second-growth mature riparian forests. Stand age class was used as a proxy here for canopy complexity. We estimated stream canopy cover using a spherical densiometer. Local streambed light exposure was quantified and compared within and between reaches using fluorescein dye photodegradation. Reaches with complex old-growth riparian forests had frequent canopy gaps which lead to greater stream light availability compared to adjacent reaches with simpler second-growth riparian forests. We quantified light exposure at relatively high resolution (every 5 m) and also found greater variability in stream light along the reaches with old-growth riparian forests in three of the four streams. Canopy gaps were particularly important in creating variable light within and between reaches. This work

demonstrates the importance of the age, developmental stage, and structure of riparian forests in controlling stream light. The highly variable nature of light on the stream benthos also highlights the value of multiple measurements of light or canopy structure when quantifying stream light.

Keywords Riparian forest · Stream light · PAR · Solar radiation · Canopy gap · Sunfleck

Introduction

Forested headwater streams are important landscape features with tightly coupled aquatic-terrestrial linkages (Fisher and Likens 1973; Wallace et al. 1997). In addition to well-established influences of riparian forests on allochthonous carbon inputs and stream structural characteristics (e.g. large wood) (Wallace et al. 1997; Sabater et al. 2000; Bott et al. 2006; Warren et al. 2007), riparian forests strongly influence autotrophic production and temperature in streams by regulating light availability (Johnson 2004; Bott et al. 2006; Julian et al. 2008; Kreutzweiser et al. 2009). Light availability is a fundamental organizing feature in both aquatic and terrestrial ecosystems, and the factors controlling light can have both direct and indirect influences on a range of ecosystem processes. In headwater streams specifically, light is a key factor limiting primary production (Boston and Hill 1991; Hill et al. 1995; Von Schiller et al. 2007; Julian et al. 2011).

Most studies quantifying the influence of riparian forests on stream light and temperature dynamics have focused on the presence or absence of forests within the riparian area with limited consideration for the age, developmental condition, disturbance history, or structural complexity of the riparian forest when present (Noel et al. 1986; Bilby

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and Bisson 1992; Hill et al. 1995; Stone and Wallace 1998; Sabater et al. 2000). There is increasing recognition, however, that variation among forest developmental stages, with associated differences in stand structure characteristics, in the riparian zone can strongly affect stream light and associated ecosystem processes (Valett et al. 2002; Nislow and Lowe 2006; Stovall et al. 2009; Brooks et al. 2012). In this study, we use the well-documented history of a USFS experimental forest in the Cascade Mountains of western Oregon to identify four replicate streams where we could establish a case study of paired stream reaches in close proximity to one another but with riparian forest dominated by either structurally complex, old growth forest or more structurally simple mature, riparian cover. By comparing light between the paired reaches in each stream, we evaluated whether differences in riparian forest stand structure translate to associated differences in stream light availability.

As has been widely demonstrated in both natural and planned experiments, removing riparian vegetation and the shade that it provides leads to increased primary productivity and numerous changes to stream ecosystem processes, such as net ecosystem metabolism and food web dynamics (Noel et al. 1986; Bilby and Bisson 1992; Stone and Wallace 1998; Roberts et al. 2007). More subtle changes in stream light availability have also been shown to alter the availability of periphyton at the base of stream food webs (Kiffney et al. 2004; Wootton 2012; Matheson et al. 2012). Many of the studies evaluating or manipulating cover and light in streams assume a relatively uniform light environment when shading is present (Hill and Dimick 2002; Johnson et al. 2009; Matheson et al. 2012). This may indeed hold for streams with riparian forests in the early stages of stand development (Nislow and Lowe 2006) or in cases where stream width is the driver of changing light (Finlay et al. 2011; Julian et al. 2011). However, it is unlikely that light availability is uniform in systems with old-growth riparian forests where frequent canopy gaps can create “hotspots” of light on the stream benthos (Keeton et al. 2007; Stovall et al. 2009). In this study, we explicitly evaluate the issue of spatial variability in light along a stream reach. We hypothesized that stream reaches with old-growth riparian forests will have both higher mean light levels and greater variability in light than stream reaches with more uniform second-growth riparian forests.

Secondary forests recovering either from nineteenth century land-use in the eastern US, or twentieth century logging in the Pacific Northwest, are the predominant riparian cover along much of the stream network in these regions (Pan et al. 2011). Now in various stages of structural development (Franklin et al. 2002), these mostly young to mature riparian forests tend to have less

heterogenous canopy structure both vertically and horizontally (Van Pelt and Franklin 2000; Keeton et al. 2007). In the Pacific Northwest in particular, second-growth forests dominate much of the landscape with many of these regrowing forests comprised primarily of a single cohort of early-successional deciduous or coniferous trees. This is in contrast to the pre-European settlement condition in which landscapes were dominated by primary forests with complex, often old-growth structures, including variable tree density, frequent forest gaps, multiple canopy layers, and higher densities of large living and dead trees (Franklin et al. 2002; Keeton 2006; D’Amato et al. 2009; Curzon and Keeton 2010). These changes in age-class distribution and stand structure are likely to have profound consequences for light dynamics along low order streams, since canopy architecture strongly influences light attenuation. Light attenuation is often spatially and temporally transient in tall, complex canopies due to solar position (e.g. creating low-angle sunflecks originating from spatially offset canopy gaps. See Chen and Black 1992; Chen and Cihlar 1995; Van Pelt and Franklin 2000). Yet the vast majority of research on stream ecosystem function in forested streams has been conducted in young and early-mature second growth forests; systems where in-stream light is low and the influence of heterotrophic processes is large relative to autotrophy. Our understanding of forest-stream interactions and the influence of forests on stream ecosystems may be incomplete if the interactions between streams and the associated riparian forest do indeed differ in these younger simpler forests and older more complex forests.

Methods

Study site

This study was conducted in four headwater streams, each having a paired up and downstream sample location, in the HJ Andrews Experimental Forest (hereafter “HJAEF”) located in the Cascade Mountains of western Oregon. There were eight study reaches in total. Riparian forests investigated in our study were dominated by Douglas fir (*Pseudotsuga menziesii*, Franco) in two different age classes, early mature (dominant trees 40–60 years) and old-growth (dominant trees ~ 500 years). The juxtaposition of recently logged stands with adjacent stands of old-growth forest in the same watershed creates a unique opportunity to compare the influence of stand age and structure on light dynamics in upstream vs. downstream reaches of individual streams. Comparing riparian forest stand structure along a single stream eliminates the stream-to-stream variability that often complicates comparisons across streams.

The HJAEF encompasses the Lookout Creek basin on the eastern side of the Cascade Mountains in central Oregon (44.2 latitude and 122.2 longitude). This region has a maritime climate with wet, mild winters and dry, cool summers. The elevation of the four study streams ranges from about 500 m (Stream 3) to about 1100 m (Stream 4). The old-growth forests in this area are dominated by Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). Dominant canopy trees in the old-growth forests are about 500 years old. The second-growth forests are dominated by Douglas fir, but red alder (*Alnus rubra*, Bong.) also regenerates naturally in some areas creating a localized deciduous overstory. Understory trees were limited in the second-growth riparian forests adjacent to Streams 1–3. Stream 4 also had an understory of vine maple (*Acer circinatum*).

We selected four second-order fish-bearing headwater streams in the HJAEF that were representative of low-order streams in the study area (bankfull widths between 3.0 and 7.3 m, gradients between 3 and 10 % and basins that were unmodified apart from forest management over the past 20–60 years). Each stream had adjacent reaches with riparian zones that contained primary old-growth or mature second-growth forests and which were generally reflective of different canopy structures—homogeneous closed canopy (mature second-growth) versus frequent canopy gaps (primary old-growth). We deliberately focused on second-order fish-bearing headwater streams for two reasons. First, the presence of fish sets a biologically relevant size limit, which also has implications for riparian buffer delineation and management (Gregory 1997). Also, because small streams create little to no break in the canopy directly over channels, they represent systems where riparian forest influences on light availability if present are strongest (Finlay et al. 2011). Because influences of riparian forest structure have not been well explored, we focused first on the systems where hypothesized differences in stream light associated with the different stand ages are likely to manifest most clearly.

We first surveyed two south-facing streams in mid-July 2012. McRae tributary (Stream 1) had an 80 m long upstream section that was clearcut 59 years prior to our study and a contiguous 80 m long downstream section of old-growth forest (circ. 500 years). Study reaches were about 300 m apart with no tributaries entering between the reaches. The second-growth stand was not actively replanted in this site and was instead allowed to regenerate naturally following harvest. Regeneration of Douglas fir at this site was strong, with recruitment well established within a few years post-harvest (Table 1).

The second stream is a headwater section of McRae Creek (Stream 2). This site had a 100 m long upstream

reach of old-growth riparian forest and a 100 m long downstream reach in which the riparian forest had been cut in 1958 (Table 1). The managed forest at this site was replanted after harvest (Table 1). The study reach with old-growth riparian forest was about 200 m upstream of the reach with the second-growth riparian forest.

We surveyed our other two study streams in mid-September 2012. Gypsy Camp Creek (Stream 3) is a small tributary draining a northwest-facing watershed that runs directly into the Lookout Creek mainstem. The upstream section of this stream was harvested in 1952. The site was replanted with Douglas fir and had strong growth of Douglas fir seedlings (Table 1). The downstream section of this stream has not been harvested. We established 70 m study reaches in sections with the two age classes of riparian forest. Study reaches were about 400 m apart. The managed forest at this site underwent a pre-commercial thin of saplings in 1965 and a commercial thinning in 2000 (Mark Schultz, Director HJ Andrews Experimental Forest).

The fourth and final reach pair was established in Upper Lookout Creek (Stream 4). This reach pair had an upstream section with a second-growth riparian forest and a downstream section with an old-growth riparian forest. In contrast to the other three streams, it took 10 years after harvest before acceptable stocking and canopy cover were reached for Douglas fir and even then the stem density at this site was reported as being low relative to the second-growth forests along the other managed forest stream reaches (Mark Schultz, HJ Andrews Experimental Forest, personal communication). This relatively poor establishment of Douglas fir resulted in different composition and structure of the riparian forest relative to the other second-growth sites. The second-growth reach at Upper Lookout Creek had fewer conifers next to the stream but there was an understory cover of vine maple (*Acer circinatum*) that shaded the stream. Although second-growth forest stand structure differed here, we selected this site as a representative of this alternative recovery trajectory. Study reaches were about 50 m apart at this site.

Field measurements

We used two methods to estimate stream light availability across the eight study reaches. First, we used a spherical densiometer to quantify forest cover over the stream every five meters. Spherical densiometers use a convex reflective lens with a pre-defined grid on which one estimates canopy coverage. Densiometer measurements are not a direct measure of stream light; they are an estimate of canopy cover that is often used as a proxy for light availability. A number of studies have noted that densiometer measurements are prone to observer bias and sometimes less accurate than other measures of canopy (Vales and Bunnell

Table 1 Riparian forest and stream characteristics at each of the eight study reaches

Stand type	Year of cut	Year of stand origin	Management notes	Estimated age of dominant canopy trees	Reach length (m)	Mean (SE) bankfull width (m)	# LW per 100 m
Stream 1							
Old-growth	–	–	–	500	80	4.1 (0.43)	60
Second-growth	1953	na	Natural regeneration	59	80	3.6 (0.12)	53
Stream 2							
Old-growth	–	–	–	500	100	7.3 (0.12)	28
Second-growth	1958	1960	Planted; single thinning	52	100	6.6 (0.14)	14
Stream 3							
Old-growth	–	–	–	500	70	3.1 (0.11)	54
Second-growth	1952	1956	Planted; multiple thinnings	56	70	2.5 (0.7)	60
Stream 4							
Old-growth	–	–	–	500	90	4.6 (0.51)	39
Second-growth	1971	1981	Poor regeneration; no thinning	31	90	3.0 (0.08)	13

1988; Tinya et al. 2009). Yet densimeters do correlate with potential PAR in many cases (Comeau et al. 1998) and it remains the most commonly applied method to estimate or account for potential light availability in stream ecosystem studies (Nislow and Lowe 2006; Kreuzweiser et al. 2009; Moslemi et al. 2012; Riley and Dodds 2012). We were interested in quantifying the relationship between densimeter-based canopy cover estimates and specific quantified light measurements collected at a high frequency along each stream reach to assess potential error in this method as a proxy for benthic light exposure in stream studies. We avoided observer bias in our densimeter measurements by ensuring that the same individual conducted all of the estimates.

Point locations for densimeter readings were established systematically every five meters along the thalweg of each stream reach. At these points, a single densimeter operator estimated the percent overhead cover from each of four directions—upstream, downstream, left bank, and right bank (Kelley and Krueger 2005). It should be noted that the frequency of densimeter measurements here is high compared to other studies. We chose this close spacing in order to match densimeter values with specific in-stream light data collected at the same 5 m intervals. This high frequency in survey locations leads to overlap in the canopy included in adjacent survey locations, and can therefore result in counting a given gap (or tree crown) multiple times. Therefore, although our analysis comparing densimeter measurement to the dye photodegradation values used all data points, we used only the densimeter values collected every 15 m to estimate the overall mean percent cover along each study reach (see below).

The method that we used to estimate light reaching the bottom of the stream (the stream benthos) is a new technique which quantifies light exposure based on the photodegradation of a fluorescent dye (Bechtold et al. 2012). We deployed an array of three replicate dye vials every five meters at each of the same locations where densimeter measurements were conducted. Prior to deployment dye concentrations were measured in each vial on a Turner Designs Aquaflor fluorometer (Turner Designs, Sunnyvale, CA, USA). The vials were then attached to a wire flag that was secured to the stream benthos with rocks. Neither the flag nor the rocks securing the vial array shaded the vials. We used fluorescein dye in this study, which photodegrades rapidly (within a day in full sunlight; see Bechtold et al. 2012 for details), and we therefore implemented short deployments (2–3 days). After deployment, we collected vials from the stream and placed them directly into a darkened cooler. All samples were allowed to sit in the dark in the lab for 24 h so that they would return to the temperature at which concentrations were initially measured (the temperature of the sample can affect fluorometric reading—see Bechtold et al. 2012). The concentration of fluorescein in each vial was then measured on the same Aquaflor fluorometer. In addition to the open vials deployed in the field for light exposure, we also included a foil covered “field-dark” sample every 20 m. These field “blanks” were used to correct for non-light related changes in concentration (e.g. poor seals on the caps leading to dilution of the sample). We compared photodegradation responses only between reaches in the same stream. We did not compare photodegradation values across streams because deployment times (1–3 days) and dates of

deployment (mid-summer versus late-summer) differed between streams.

Data analysis

We compared the direct measure of light availability (dye decay) and indirect measure of light potential (canopy cover) between the old-growth and second-growth riparian forest reaches separately in each of the four streams using a single-factor ANOVA. To avoid the inclusion of overlapping canopy images from adjacent densiometer sampling locations, we used the canopy cover data from sites every 15 m (rather than every 5 m) in the comparison of canopy cover between the two age classes along each reach. The distribution of the data from each reach were tested for normality (values every 15 m for densiometer and values every 5 m for dye photodegradation). In most cases, data were normally distributed, except for the densiometer data in the second growth section of Stream 1, dye photodegradation data the old-growth section of Stream 1, the second-growth of Stream 3, and the old-growth section of Stream 4. To make consistent comparisons within and among sites, all data were natural log-transformed for analysis. For the figures, however, we used the actual values to allow for easier interpretation and comparison to other studies. We used linear regression analysis to compare values from the mean densiometer readings with the mean dye photodegradation at each site location (every 5 m) in each reach. The linear regression was run on the natural log transformed data. To more clearly illustrate the spatial dynamics and correlation between dye photodegradation and cover, we plotted photodegradation values against the inverse of our cover values (i.e. open space) from each location. Finally, to evaluate the hypothesis that light in the old growth forest streams would be more variable than in the second-growth forest streams, we compared the standard deviations of the densiometer values (measurements every 15 m in each reach) and natural-log transformed dye photodegradation values (measurements every 5 m in each reach) from the four old-growth reaches ($n = 4$) versus the four second-growth reaches ($n = 4$) using an ANOVA.

Results

Both methods, measuring potential (densiometer) or actual (dye photodegradation) light exposure in the stream, indicated that headwater streams with old-growth riparian forests are likely to receive more light than streams with early-mature riparian forests in mid- and late-summer (Fig. 1). The differences in stream light availability and percent forest cover between old-growth and second-

growth reaches were significant in both of the south-facing watersheds (Streams 1 and 2) in mid-summer at an alpha of 0.01 for the dye results and 0.10 for the cover results (dye photodegradation analysis: $p < 0.001$, $F = 35.67$, and $p < 0.001$, $F = 19.09$ for Stream 1 and Stream 2, respectively; densiometer analysis: $p = 0.06$, $F = 4.41$, and $p = 0.03$, $F = 5.87$ for Stream 1 and Stream 2, respectively; Table 2; Fig. 1). Light availability results on the stream benthos, as measured by dye photodegradation, in the north-facing watersheds were broadly consistent with results from the south-facing watersheds, but the differences between old-growth and second growth riparian forest reaches were significant only at Stream 3 ($p = 0.013$, $F = 7.09$, and $p = 0.227$, $F = 1.51$ for Stream 3 and Stream 4, respectively; Table 2; Fig. 1). Similarly, differences in canopy cover over the old-growth reach was significantly lower in Stream 3 ($p = 0.027$, $F = 7.32$) but not in Stream 4 ($p = 0.262$, $F = 1.39$; Table 2; Fig. 1). In comparing the standard deviation of forest cover between age classes statistically and visually (Figs. 2, 3, 4, 5), streams with old-growth riparian forests had greater variability in cover ($p = 0.006$, $F = 17.7$). Average variability in streambed light exposure was also generally greater in streams with old-growth riparian forests than in those with mature second-growth forests, however the difference was not significant ($p = 0.275$, $F = 1.44$).

There was a significant negative relationship between the mean photodegradation loss and the cover estimate from densiometer readings in three of the four streams ($p < 0.001$, for Streams 1, 2, and 4; $p = 0.34$ for Stream 3; Fig. 6), but the correlations were poor as predictive relationships. Riparian forest cover directly over each sampling area explained about a third to a quarter of the variability in dye decay in the three streams where we found significant relationships between photodegradation and canopy cover ($r^2 = 0.35, 0.29, 0.24$ for Streams 1, 2, and 4, respectively; Fig. 6).

Discussion

Overall, we found support for the hypothesis that headwater streams with complex old-growth riparian forests receive more light in summer than streams with uniform riparian forests that are in the early-mature stage of stand development. Canopy closure along streams with old-growth riparian forests was also generally more spatially variable than in streams with second-growth riparian forests. This corresponded with greater variability in stream benthic light availability, although the canopy gaps did not necessarily correlate directly overhead with the areas of greater light on the streambed due to the effects of transient, spatially offset light (i.e., sunflecks) that can increase

Fig. 1 Mean percent cover and mean loss in fluorescein in each of four reach pairs with old-growth (*dark bars*) and second-growth (*light bars*) riparian forests. *Error bars* represent one standard deviation. *Asterisk* symbols represent significant differences at * $p < 0.1$ and ** $p < 0.05$

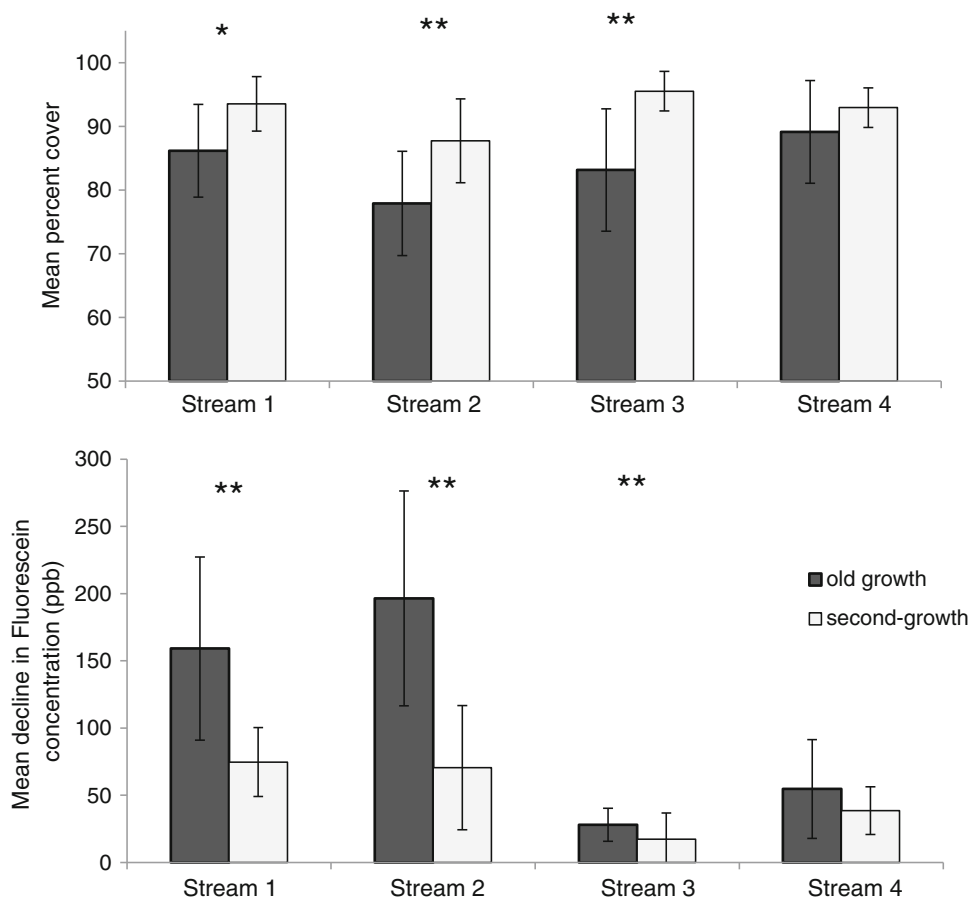


Table 2 Mean and standard deviation of the percent canopy cover and fluorescein photodegradation for each reach

Stream	Riparian forest age class	Densimeter			Fluorescein dye		
		Mean	n	Standard deviation	Mean Δ in concentration	n	Standard deviation of Δ in concentration
Stream 1	Old-growth	86.2	6	7.28	159.2	17	68.1
	Second-growth	93.5	6	4.28	74.7	17	25.6
Stream 2	Old-growth	77.9	7	8.17	196.4	21	79.9
	Second-growth	87.7	7	6.59	70.5	21	46.2
Stream 3	Old-growth	83.2	5	9.60	28.1	15	12.2
	Second-growth	95.5	5	3.11	17.3	15	19.5
Stream 4	Old-growth	89.1	7	8.06	54.7	19	36.8
	Second-growth	92.9	7	3.10	38.6	19	17.8

light to a large degree some distance from a given gap. The irregular canopy gaps in old-growth forests studied here created a mosaic of light on the stream benthos, with a mix of high and low light availability patches. The young second-growth forest streams, in contrast, had consistently lower light availability. Overall, light in the streams studied here has the potential to be highly dynamic. Light varies spatially along a reach but it can also vary over the day and over seasons as sun angle changes, and it can vary on decadal and centennial time scales as riparian forests

develop structural complexity (Van Pelt et al. 1992; Chen and Black 1992). These results highlight the spatially complex nature of light in streams and suggest that transient or offset light attenuation through complex forest canopies affects both local and total light availability. The importance of sunflecks and light attenuation has been well documented in terrestrial ecosystems (Sims and Percy 1993; Chen and Cihlar 1995; Van Pelt and Franklin 2000; Percy and Way 2012) and warrants similar consideration in forested streams.

Fig. 2 Linear profile of fluorescein photodegradation and canopy cover estimate densiometer measurements along the stream profile for old growth (a) and second growth (b) reaches in Stream 1

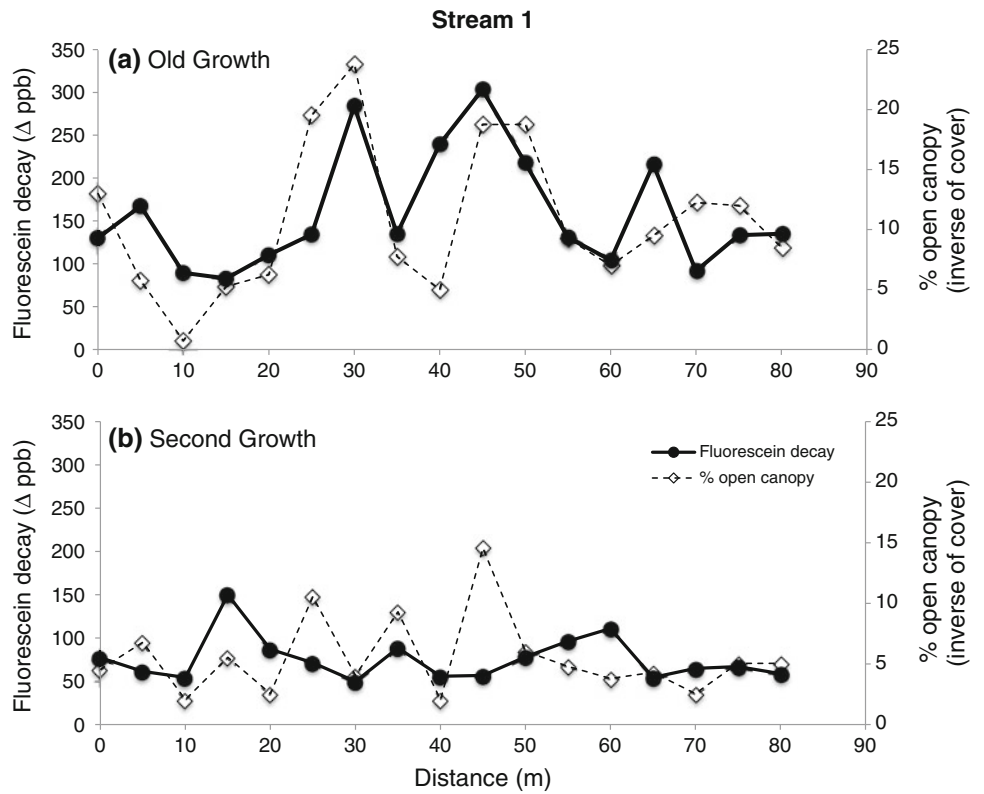


Fig. 3 Linear profile of fluorescein photodegradation and canopy cover estimate densiometer measurements along the stream profile for old growth (a) and second growth (b) reaches in Stream 2

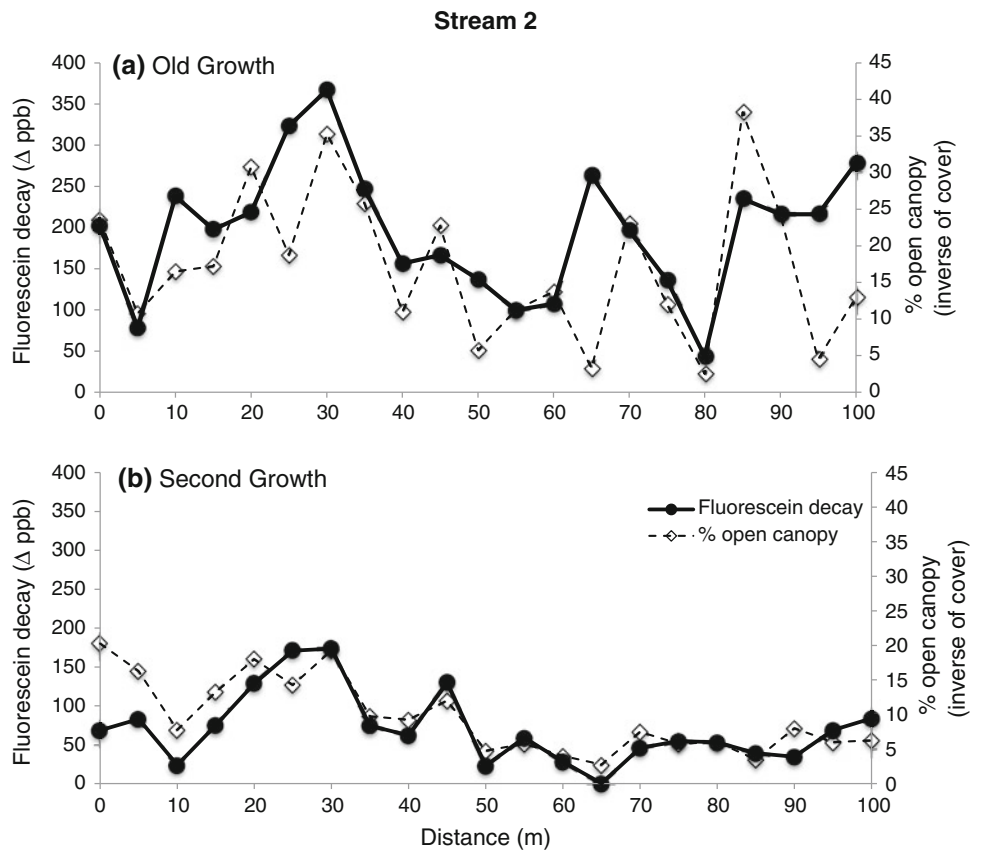


Fig. 4 Linear profile of fluorescein photodegradation and canopy cover estimate densiometer measurements along the stream profile for old growth (a) and second growth (b) reaches in Stream 3

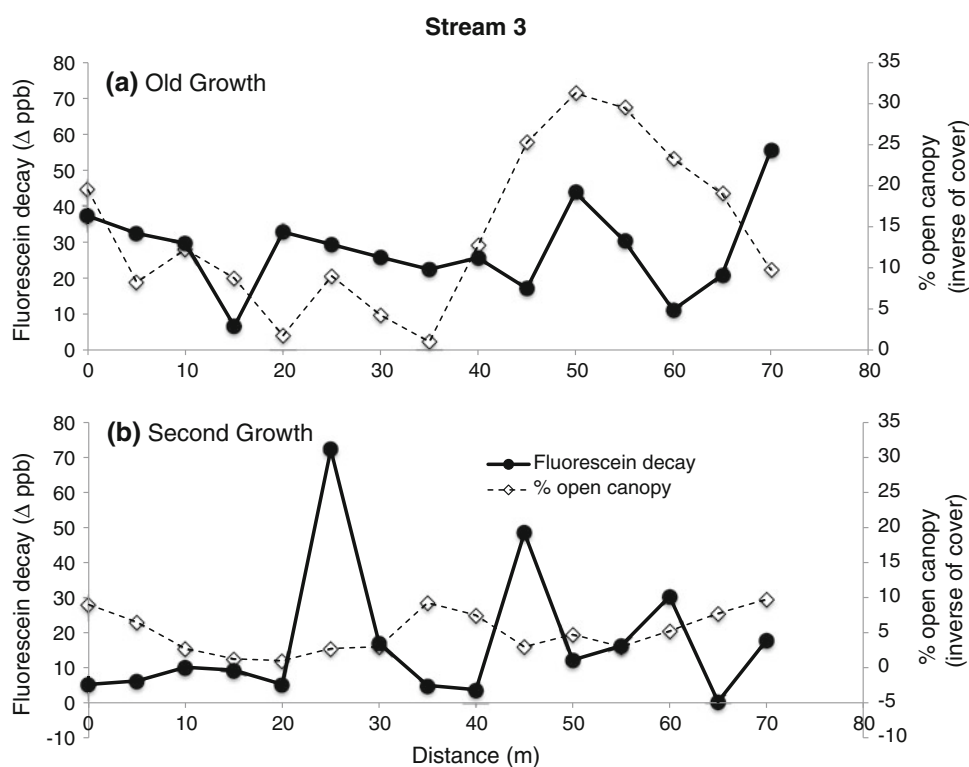
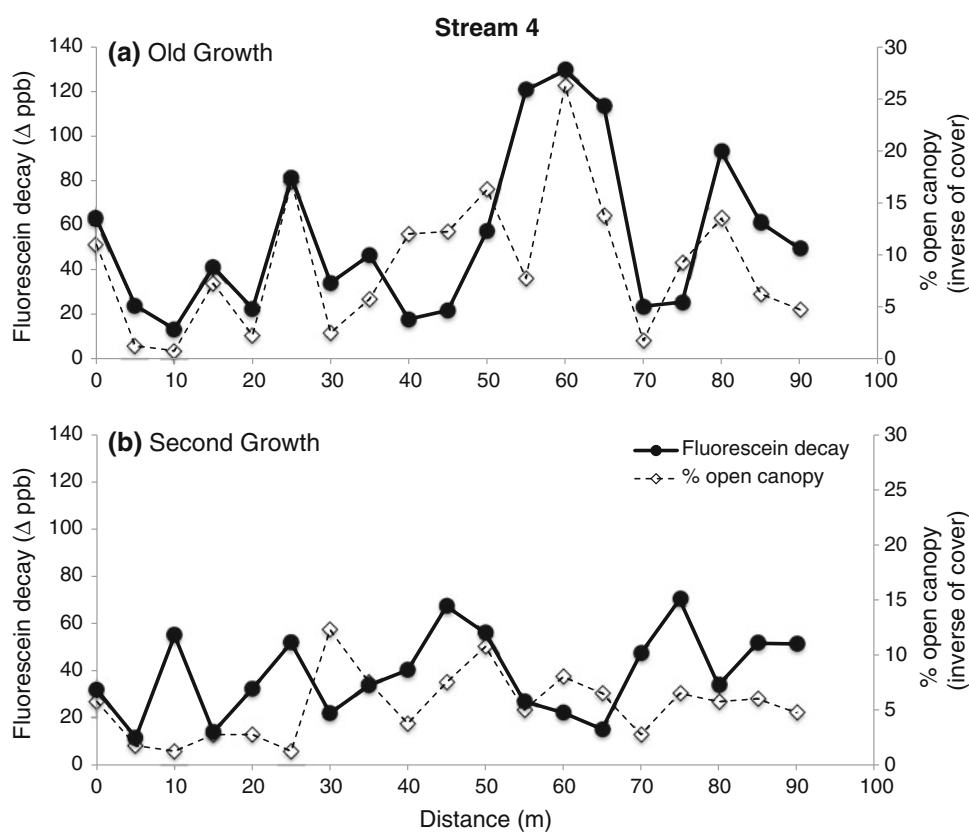


Fig. 5 Linear profile of fluorescein photodegradation and canopy cover estimate densiometer measurements along the stream profile for old growth (a) and second growth (b) reaches in Stream 4



The method comparison here indicated that a mean densiometer value from multiple points along a stream provide an accurate general picture of potential stream light

exposure at the reach scale and therefore potential light penetration to the stream benthos, but this method may be inappropriate for quantifying light availability at specific

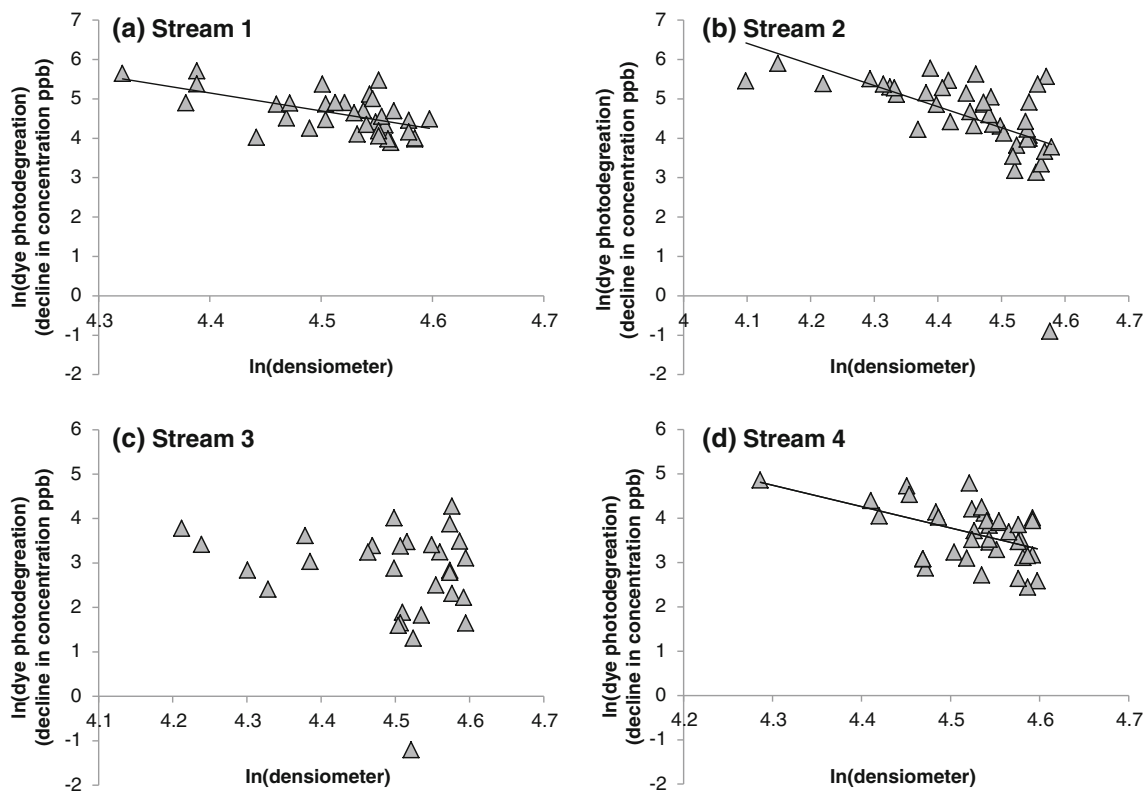


Fig. 6 Regressions of the natural log of percent cover estimates versus natural log of fluorescein dye photodegradation (reflecting actual stream benthic light exposure). Greater photodegradation indicates greater light exposure over the duration of deployment.

Lines indicate significant relationships between canopy cover and benthic light exposure in Stream 1 ($p < 0.001$, $r^2 = 0.35$), Stream 2 ($p < 0.001$, $r^2 = 0.29$) and Stream 4 ($p < 0.001$, $r^2 = 0.24$). The relationship was not significant in Stream 3 ($p = 0.34$, $r^2 = 0.03$)

locations in the stream. Although there were significant correlations between the densiometer value and the dye photodegradation across locations in three of the four streams, the relationship strengths were surprisingly poor. At the sites where the correlation was significant, canopy cover over a given point in the stream never explained more than 35 % of the variability in benthic light exposure (as measured by dye photodegradation). Despite poor correlation on a point-by-point basis, when considered on a whole-reach basis, the two methods yielded similar overall results in regard to stream light. This suggests that for small headwater streams, estimating canopy cover regularly along a reach may capture influences of forest gaps even if the location of the light associated with a specific gap was not necessarily directly related to the densiometer measurement location.

The poor correlation between these two methods highlights the need to consider the whole of the riparian forest, not just a single point. Our results indicate that canopy gaps can increase light in areas adjacent to the gap more than to the areas directly below the gap, depending upon the angle of the sun (varying daily and seasonal time scales) (Canham 1988; Van Pelt et al. 1992; Van Pelt and Franklin 2000). The process of transient, spatially offset light

(sunflecks) has been shown to be an important feature in upland forests with implications for understory plant community dynamics (e.g. see Van Pelt and Franklin 2000; Percy and Way 2012). Similarly, in streams where riparian canopy gaps create sunflecks, light intensity will vary along the streambed and throughout the day and year. Spatially and temporally transient sunflecks may be an important, but to date, understudied consideration in forested headwater streams.

Unlike the relatively uniform increases in light associated with increasing stream size or manipulations using shade cloth, the differences in light between streams with complex old-growth riparian forests and those with young even-aged riparian forests are due to the presence of high light patches. This can translate to local and patchy increases in primary production. DeNicola et al. (1992), for example, compared both hemispheric-photos and PAR meter measurements at four locations along a single stream with 4 different canopy structures and found greater periphyton standing stocks in the sites with less canopy cover (and therefore more light). Stovall et al. (2009) working across streams with a range of riparian forest stand structures in the northeastern US also found greater periphyton standing stocks in systems with more gaps in

the canopy. Patch size and frequency are clearly important in projecting how these local responses scale up to whole-ecosystem processes, but the question of how these potential localized hotspots of productivity translate to whole-stream ecosystem processes has not been widely evaluated.

The riparian forest age classes in this study were representative of two different stand development conditions with associated variation in stand structural complexity. We compared light associated with the complex structure of an old growth riparian forest, having variable canopy heights and multiple canopy gaps based on field observations, to what we initially assumed would be fairly uniform closed-canopy riparian forest in the second-growth sites. This was broadly true in regard to canopy gaps. The densiometer assessments documented more and larger gaps in reaches with the old-growth riparian forests compared to those with the second-growth riparian forests. However, observational assessments of the second-growth riparian forests suggested greater variability among these sites than initially anticipated and highlighted the importance of considering thinning history, regeneration history, and degree of vertical layering when using age class as a proxy for structure.

Light availability in the two north-facing streams broadly supported results from the two south-facing streams, but the magnitude of the differences in light exposure were not as large. We attribute this more moderate difference in benthic light exposure and canopy cover to three primary factors. First, as noted above, forest regrowth was poor along the previously logged section of Stream 4. While there was understory cover above the stream, we observed less canopy cover from larger trees than in any of the other sites with regenerating Douglas fir forests. There was more diffuse light reaching the stream in this Upper Lookout Creek reach (Stream 4). At Stream 3, the managed site is part of an active stand thinning experiment and was thinned within the past 10 years. In addition to aspect and management history, Streams 3 and 4 surveys were conducted later in the summer when the sun angle was lower. These factors likely contributed to the more moderate differences in benthic stream light availability as measured with the dye photodegradation in streams 3 and 4. This highlights the importance of considering not only aspect but cloud cover and total daylight hours when using this new method.

Conclusions

The results from this study and related work in other regions demonstrate that stand development conditions and the structural complexity of riparian forests are important

in controlling stream light (Nislow and Lowe 2006; Keeton et al. 2007; Stovall et al. 2009). Riparian forests are changing across North America as ecosystems recover from historic landuse, undergo species invasions, change in response to altered climate, and experience new management pressures (Foster et al. 1998; Snyder et al. 2002). Understanding how riparian forest structure—not just the presence or absence of a riparian forest—relates to fundamental drivers of stream ecosystem processes such as light and temperature will improve our understanding of how these landscape scale changes in the forests will influence headwater streams.

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References

- Bechtold HA, Rosi-Marshall EJ, Warren DR, Cole JJ (2012) A practical method for measuring integrated solar radiation reaching streambeds using photodegrading dyes. *Freshw Sci* 31(4):1070–1077. doi:[10.1899/12-003.1](https://doi.org/10.1899/12-003.1)
- Bilby RE, Bisson PA (1992) Allochthonous versus autochthonous organic-matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Can J Fish Aquat Sci* 49(3):540–551
- Boston HL, Hill WR (1991) Photosynthesis light relations of stream periphyton communities. *Limnol Oceanogr* 36(4):644–656
- Bott TL, Newbold JD, Arscott DB (2006) Ecosystem metabolism in piedmont streams: reach geomorphology modulates the influence of riparian vegetation. *Ecosystems* 9(3):398–421
- Brooks RT, Nislow KH, Lowe WH, Wilson MK, King DI (2012) Forest succession and terrestrial-aquatic biodiversity in small forested watersheds: a review of principles, relationships and implications for management. *Forestry* 85(3):315–327. doi:[10.1093/Forestry/Cps031](https://doi.org/10.1093/Forestry/Cps031)
- Canham CD (1988) An index for understory light levels in and around canopy gaps. *Ecology* 69(5):1634–1638
- Chen JM, Black TA (1992) Foliage area and architecture of plant canopies from sunfleck size distributions. *Agric Forest Meteorol* 60(3–4):249–266. doi:[10.1016/0168-1923\(92\)90040-B](https://doi.org/10.1016/0168-1923(92)90040-B)
- Chen JM, Cihlar J (1995) Quantifying the effect of canopy architecture on optical measurements of leaf-area index using 2 gap size analysis-methods. *IEEE Trans Geosci Remote* 33(3):777–787. doi:[10.1109/36.387593](https://doi.org/10.1109/36.387593)
- Comeau PG, Gendron F, Letchford T (1998) A comparison of several methods for estimating light under a paper birch mixedwood stand. *Can J Forest Res* 28(12):1843–1850. doi:[10.1139/Cjfr-28-12-1843](https://doi.org/10.1139/Cjfr-28-12-1843)
- Curzon MT, Keeton WS (2010) Spatial characteristics of canopy disturbances in riparian old-growth hemlock—northern hardwood forests, Adirondack Mountains, New York, USA. *Can J Forest Res* 40(1):13–25. doi:[10.1139/X09-157](https://doi.org/10.1139/X09-157)

- D'Amato AW, Orwig DA, Foster DR (2009) Understory vegetation in old-growth and second-growth *Tsuga canadensis* forests in western Massachusetts. *Forest Ecol Manag* 257(3):1043–1052
- DeNicola DM, Hoagland KD, Roemer SC (1992) Influences of canopy cover on spectral irradiance and periphyton assemblages in a prairie stream. *J N Am Benthol Soc* 11(4):391–404
- Finlay JC, Hood JM, Limm MP, Power ME, Schade JD, Welter JR (2011) Light-mediated thresholds in stream-water nutrient composition in a river network. *Ecology* 92(1):140–150
- Fisher SG, Likens GE (1973) Energy flow in bear brook, New Hampshire—integrative approach to stream ecosystem metabolism. *Ecol Monogr* 43(4):421–439
- Foster DR, Motzkin G, Slater B (1998) Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* 1(1):96–119
- Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen JQ (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecol Manag* 155(1–3):399–423
- Gregory SV (1997) Riparian management in the 21st century. In: Kohm KA, Franklin JF (eds) *Creating forestry for the 21st century: the science of ecosystem management*. Island Press, Washington D.C., pp 69–86
- Hill WR, Dimick SM (2002) Effects of riparian leaf dynamics on periphyton photosynthesis and light utilisation efficiency. *Freshw Biol* 47(7):1245–1256
- Hill WR, Ryon MG, Schilling EM (1995) Light limitation in a stream ecosystem—responses by primary producers and consumers. *Ecology* 76(4):1297–1309
- Johnson SL (2004) Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. *Can J Fish Aquat Sci* 61(6):913–923. doi:10.1139/F04-040
- Johnson LT, Tank JL, Dodds WK (2009) The influence of land use on stream biofilm nutrient limitation across eight North American ecoregions. *Can J Fish Aquat Sci* 66(7):1081–1094
- Julian JP, Doyle MW, Stanley EH (2008) Empirical modeling of light availability in rivers. *J Geophys Res Biogeosci* 113:G03022
- Julian JP, Seegert SZ, Powers SM, Stanley EH, Doyle MW (2011) Light as a first-order control on ecosystem structure in a temperate stream. *Ecohydrology* 4(3):422–432. doi:10.1002/Eco.144
- Keeton WS (2006) Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *Forest Ecol Manag* 235(1–3):129–142
- Keeton WS, Kraft CE, Warren DR (2007) Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. *Ecol Appl* 17(3):852–868
- Kelley CE, Krueger WC (2005) Canopy cover and shade determinations in Riparian zones. *J Am Water Resour Assoc* 41(1):37–46. doi:10.1111/J.1752-1688.2005.Tb03715.X
- Kiffney PM, Richardson JS, Bull JP (2004) Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. *J N Am Benthol Soc* 23(3):542–555
- Kreutzweiser DP, Capell SS, Holmes SB (2009) Stream temperature responses to partial-harvest logging in riparian buffers of boreal mixedwood forest watersheds. *Can J Forest Res* 39(3):497–506. doi:10.1139/X08-191
- Matheson FE, Quinn JM, Martin ML (2012) Effects of irradiance on diel and seasonal patterns of nutrient uptake by stream periphyton. *Freshw Biol* 57(8):1617–1630. doi:10.1111/J.1365-2427.2012.02822.X
- Moslemi JM, Snider SB, MacNeill K, Gilliam JF, Flecker AS (2012) Impacts of an invasive snail (*Tarebia granifera*) on nutrient cycling in tropical streams: the role of riparian deforestation in Trinidad, West Indies. *Plos One* 7(6). doi:10.1371/journal.pone.0038806
- Nislow KH, Lowe WH (2006) Influences of logging history and riparian forest characteristics on macroinvertebrates and brook trout (*Salvelinus fontinalis*) in headwater streams (New Hampshire, USA). *Freshw Biol* 51(2):388–397
- Noel DS, Martin CW, Federer CA (1986) Effects of forest clearcutting in New England, USA on stream macroinvertebrates and periphyton. *Environ Manage* 10(5):661–670
- Pan Y, Chen JM, Birdsey R, McCullough K, He L, Deng F (2011) Age structure and disturbance legacy of North American forests. *Biogeosciences* 8(3):715–732. doi:10.5194/Bg-8-715-2011
- Pearcy RW, Way DA (2012) Two decades of sunfleck research: looking back to move forward. *Tree Physiol* 32(9):1059–1061. doi:10.1093/Treephys/Tps084
- Riley AJ, Dodds WK (2012) The expansion of woody riparian vegetation, and subsequent stream restoration, influences the metabolism of prairie streams. *Freshw Biol* 57(6):1138–1150. doi:10.1111/J.1365-2427.2012.02778.X
- Roberts BJ, Mulholland PJ, Hill WR (2007) Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* 10:588–606
- Sabater F, Butturini A, Marti E, Munoz I, Romani A, Wray J, Sabater S (2000) Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *J N Am Benthol Soc* 19(4):609–620
- Sims DA, Pearcy RW (1993) Sunfleck frequency and duration affects growth-rate of the understory plant, *Alocasia-Macrorrhiza*. *Funct Ecol* 7(6):683–689. doi:10.2307/2390189
- Snyder CD, Young JA, Lemarie DP, Smith DR (2002) Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Can J Fish Aquat Sci* 59(2):262–275. doi:10.1139/F02-003
- Stone MK, Wallace JB (1998) Long-term recovery of a mountain stream from clearcut logging: the effects of forest succession on benthic invertebrate community structure. *Freshw Biol* 39(1):151–169
- Stovall JP, Keeton WS, Kraft CE (2009) Late-successional riparian forest structure results in heterogeneous periphyton distributions in low-order streams. *Can J Forest Res* 39(12):2343–2354. doi:10.1139/X09-137
- Tinya F, Mihok B, Marialigeti S, Mag Z, Odor P (2009) A comparison of three indirect methods for estimating understory light at different spatial scales in temperate mixed forests. *Commun Ecol* 10(1):81–90. doi:10.1556/Com.ec.10.2009.1.10
- Vales DJ, Bunnell FL (1988) Comparison of methods for estimating forest overstory cover I. Observer effects. *Can J Forest Res* 18(5):606–609. doi:10.1139/X88-088
- Valett HM, Crenshaw CL, Wagner PF (2002) Stream nutrient uptake, forest succession, and biogeochemical theory. *Ecology* 83(10):2888–2901
- Van Pelt R, Franklin JF (2000) Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Can J Forest Res* 30(8):1231–1245
- Van Pelt R, Spies TA, Franklin JF (1992) Disturbance succession and species interactions around canopy gaps in old-growth Douglas-fir forests. *Northwest Environ J* 8(1):210–211
- Von Schiller D, Marti E, Riera JL, Sabater F (2007) Effects of nutrients and light on periphyton biomass and nitrogen uptake in Mediterranean streams with contrasting land uses. *Freshw Biol* 52(5):891–906
- Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest streams linked to terrestrial litter inputs. *Science* 277:102–104

Warren DR, Bernhardt ES, Hall ROJ, Likens GE (2007) Forest age, wood, and nutrient dynamics in headwater streams of the Hubbard Brook Experimental Forest, NH. *Earth Surf Proc Land* 32:1154–1163

Wootton JT (2012) River food web response to large-scale riparian zone manipulations. *Plos One* 7(12). doi:[10.1371/journal.pone.0051839](https://doi.org/10.1371/journal.pone.0051839)