Predicting Light Regime Controls on Primary Productivity Across CONUS River Networks

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Abstract Solar radiation is a fundamental driver of ecosystem productivity, but widespread estimates of light available for primary producers in rivers are lacking. We developed a model to predict light available for river primary producers and used it to estimate river primary production across the contiguous United States (CONUS). Successively accounting for riparian and water column processes improved predictions of primary production as a function of light. We calculated the ratio of river width to riparian tree height and used this metric to predict whether riparian zones or water column processes most limit productivity for over 2 million reaches. Water column processes limited productivity for 50% of the nation's river length and 80% of its surface area, with variations across ecoregions related to riparian forest cover. Our findings facilitate large-scale predictions of stream and river ecosystem productivity, as well as understanding the processes controlling productivity across networks.

Plain Language Summary The conversion of solar energy to organic matter through photosynthesis is an important component of global carbon cycling. While there are global estimates of solar radiation at the Earth’s surface, primary producers in rivers often only receive a small percentage of incoming light due to reductions from riparian shading, water depth, and water clarity. We developed a model to predict light available for river primary producers so that we could make estimates of productivity based solely on light. We predicted light and primary productivity for 173 rivers across the United States and also examined the degree to which riparian zones or water column processes limited productivity. Our model allowed us to make first approximations of productivity across many sites with varying conditions based solely on light availability. We also developed a metric to predict whether river productivity was most limited by riparian zones or water column processes and calculated this metric for over 2 million rivers in the United States. Our results suggested that riparian zones and water column process limit an equal percentage of river length nationally; however, these results varied across ecoregions and appear to be driven by changes in forest cover.

1. Introduction

The conversion of solar energy to organic matter through photosynthesis is the primary mechanism for new organic matter generation and affects global carbon cycling. Gross primary production (GPP) has been widely estimated in terrestrial and marine systems using models of light and photosynthesis (Farquhar et al., 1980; Jassby & Platt, 1976), along with global modeled or remotely sensed solar radiation (Pinker et al., 1995; Zhang et al., 2004). However, in streams and rivers maximum potential GPP may be constrained by incident light, but this potential is often not realized due to a combination of light attenuation and disturbance that decrease GPP (Bernhardt et al., 2018). Along river networks the dominant controls on light availability and GPP are expected to shift from shading by riparian zones in headwaters to the combined influence of depth and clarity in large rivers (Vannote et al., 1980). Longitudinal changes in light and GPP assessed from observations (Finlay, 2011; Finlay et al., 2011) or quantitatively through model simulations (Julian, Doyle, & Stanley, 2008; Julian, Stanley, & Doyle, 2008) represent considerable progress for understanding how light and GPP vary across river networks. However, we still lack quantitative predictions of stream light environments that specify the relative importance of riparian and water column controls on light availability, and ultimately on GPP at watershed to continental scales.

Riparian corridors influence light availability through a combination of shading by local topography (Yard et al., 2005), channel width, channel bank height, azimuth, and adjacent riparian vegetation on light attenuation (Julian, Doyle, & Stanley, 2008; Li et al., 2012). The strength of light attenuation through vegetation...
canopies depends on canopy structural properties (Campbell, 1986; Monsi & Saeki, 2005); therefore, the phenology of adjacent riparian canopies influences seasonal patterns in both light availability and GPP (Beaulieu et al., 2013; Roberts et al., 2007). Once light reaches the surface of the water it can be reflected (Kirk, 2011) before entering the water column where attenuation with depth and clarity further reduce light availability (Davies-Colley & Smith, 2001; Hall et al., 2015; Julian, Doyle, Powers, et al., 2008). While there are models that address several of these processes (Davies-Colley & Rutherford, 2005; DeWalle, 2008, 2010; Julian, Doyle, & Stanley, 2008; Li et al., 2012), none include the combined effects of the temporal dynamics of riparian canopies, water depth, and water clarity on light availability.

For this study, we developed a model that represents both riparian and water column controls on light availability as they vary both seasonally and spatially through stream networks. We expanded on a recent model (Savoy et al., 2021) which estimates light at the stream surface, by adding water column light attenuation as affected by dynamic changes in wetted stream widths, depths, and clarity. We used this model to estimate light available for stream primary producers and to examine controls on light availability and associated patterns of GPP at 173 sites with varying conditions across the contiguous United States (CONUS).

Furthermore, we developed metrics based on our findings that revealed patterns in how light availability limits GPP across over 2.2 million CONUS river reaches. Our continental-scale synthesis on patterns and controls of light availability and stream ecosystem GPP addressed the following key questions: (1) How does successively accounting for riparian and water column processes influence our ability to make first approximations of GPP based only on light availability? and (2) How does the relative importance of riparian and water column processes on light availability, and ultimately potential GPP, vary across river networks?

2. Methods

2.1. Modeling Framework

We modeled the processes which reduce available light in streams in series along the path traveled by light to the water column (Figure 1a). Specifically, we estimated photosynthetically active radiation (PAR) because this portion of the light spectrum is related to photosynthesis. Incoming PAR above terrestrial

Figure 1. Summary of the light model structure and the conversion to gross primary production (GPP). Simplified schematic diagram of our biophysically based light model (a). Incoming photosynthetically active radiation (PAR) \( I_{\text{inc}} \) can be intercepted and transmitted through vegetation canopies \( I_t \). The lengths of unshaded \( (U) \), canopy shaded \( (CS) \), and bank shaded \( (BS) \) water surface perpendicular to the banks are used to calculate a weighted mean PAR at the water surface \( I_{\text{sur}} \). The set of processes which reduce light between \( I_{\text{inc}} \) and \( I_{\text{sur}} \) are collectively referred to as riparian attenuation. Light may then be reflected by the water surface and attenuated by a combination of depth and water clarity as captured by the irradiance attenuation coefficient \( (K_d) \). The set of processes which reduce light between \( I_{\text{sur}} \) and light within the water column \( I_{\text{wat}} \) are collectively referred to as water attenuation. Each of the three light estimates are converted to GPP using a light use efficiency of 1.9% (Kirk et al., 2020). Observed and predicted GPP for each light source across all sites in this study are shown as time series of median values for a given day (b). Observed values also show the interquartile range (IQR) and the 90th percentile (P90) of values.
canopies \(I_{\text{inc}}\) can be reduced by several processes before reaching the stream surface including channel width, channel azimuth, bank height, and the height and structure of riparian vegetation. Collectively we refer to the processes influencing PAR reaching the stream surface \(I_{\text{sur}}\) as riparian attenuation. PAR within the water \(I_{\text{wat}}\) is further influenced by reflection from the water surface and attenuation as a function of depth and water clarity \((\text{Kirk, 2011})\) and we refer to the combined effect of those processes as water attenuation. PAR was modeled at hourly time steps and aggregated to total daily sums to coincide with the resolution of GPP. We incorporated the changes detailed in this paper into the StreamLight package \((\text{Savoy, 2021})\) through the addition of a new function, the aqua_light function. A full description of the model can be found in Supporting Information Text S1 and model inputs, outputs, and source code are freely available \((\text{Savoy & Harvey, 2021})\).

Ideally, direct measurements of irradiance attenuation coefficients \(K_d\) would be used to determine attenuation with depth. Because \(K_d\) is not frequently measured in streams, we instead used turbidity, which captures light scattering, to drive an empirical log-log relationship to predict \(K_d\) \((R^2 = 0.59)\) \((\text{Supporting Information Text S1})\). The slope of our relationship \((0.52)\) is consistent with the power law coefficient of 0.5 used to relate the combined effects of absorption and scattering on \(K_d\) \((\text{Kirk, 1984, 1994})\) and other reported relationships between turbidity and \(K_d\) \((\text{Davies-Colley & Nagels, 2008})\).

Each of the daily PAR estimates were converted to corresponding GPP estimates through multiplication by a light use efficiency (LUE) which resulted in predictions of GPP based on \(I_{\text{inc}}\) \((\text{GPP}_{\text{inc}})\), based on \(I_{\text{sur}}\) \((\text{GPP}_{\text{sur}})\), and based on \(I_{\text{wat}}\) \((\text{GPP}_{\text{wat}})\) \((\text{Figure 1, Supporting Information Text S1})\). Because we do not know whether GPP occurred at the benthic surface or within the water column, we calculated mean values of the ratio of photic depth to water depth for each site \((\text{PDR})\). For sites where on average the benthic surface was below the photic depth \((\text{i.e.}, \text{PDR} \less 1)\), daily light estimates were calculated as the integral of the vertical profile of light within the photic zone. Otherwise, all GPP was assumed to occur on the benthic surface. We compared our GPP estimates to measurements at a subset of 173 sites from \((\text{Appling et al., 2018})\). We acknowledge that the GPP data presented in Appling et al. \((2018)\) are modeled based on subdaily oxygen concentrations but for conciseness we refer to these estimates as observations throughout the text. Because each estimate of PAR \((I_{\text{inc}}, I_{\text{sur}}, I_{\text{wat}})\) used to estimate GPP \((\text{GPP}_{\text{inc}}, \text{GPP}_{\text{sur}}, \text{GPP}_{\text{wat}})\) required different amounts of data, we assessed the performance of our GPP estimates only for days where all data were available \((n = 179,799)\). We filtered GPP observations to remove unrealistically high values by calculating a maximum potential GPP based on \(I_{\text{inc}}\) and a 4% LUE \((\text{Odum, 1957})\), which is the highest reported value in aquatic systems. Filtering to remove unrealistically high values only removed 0.8% of days and did not substantially alter the size of our validation data set.

Our light model has two sets of inputs: (1) model parameters which typically represent site characteristics and (2) model drivers which are time series inputs \((\text{Figure S2 and Table S2})\). A full description of the data sources and relevant processing steps can be found in Supporting Information Text S1.

### 2.2. Validation and Assessment

Three measures were calculated to assess the performance of model estimates vs. observations: (1) Pearson’s correlation coefficient \((r)\), (2) the normalized root mean squared error \((\text{NRMSE})\), and (3) the mean bias. These metrics provide complimentary information about the correlation of estimates to observations, the magnitude of errors, and whether there is a tendency toward over-estimation or under-estimation. The interpretation of the strength of correlations was done following the convention suggested by Evans \((1996)\). These fitting statistics were calculated at the study-wide level, where observations were pooled across all sites.

We also sought to quantify the relative importance of riparian attenuation and water attenuation on light environments and ultimately on GPP. We quantified the relative importance of each process based on the percent reduction in GPP. For each day, we calculated the percent reduction of \(\text{GPP}_{\text{sur}}\) and \(\text{GPP}_{\text{wat}}\) with respect to \(\text{GPP}_{\text{inc}}\). Because estimates accounted for processes in series, that is, \(\text{GPP}_{\text{wat}}\) includes the influence of riparian attenuation plus water attenuation, the percent reduction of water attenuation in isolation could be calculated by subtracting the percent reduction due to riparian attenuation. Therefore, for each day we
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assigned the percent reduction in GPP associated with each process and we refer to this as the percent limitation.

One of our objectives was to examine network patterns of GPP limitation but within a stream order, channel widths can be highly variable (Downing, 2012). We interpreted these changes using the ratio of channel width to the height of riparian vegetation (WHR) because it has proven useful for characterizing the importance of riparian control on light reaching the stream surface (Rutherford, Davies-Colley & Meleason, 2018; Rutherford, Meleason, & Davies-Colley, 2018). Sites were binned into 10 equally sized groups based on WHR and median values of the percent limitation were calculated for sites within each bin. Based on this analysis, the point where water attenuation becomes the dominant control could be identified.

We also calculated WHR for 2,236,010 stream and river reaches from the National Hydrography Data Set (NHDPlusV2.1, https://nhdplus.com/NHDPlus/NHDPlusV2_home.php). This was done using empirically derived channel widths for each reach (McManamay & DeRolph, 2019) and global estimates of canopy heights at 30-m resolution (Potapov et al., 2021). To capture the upper bounds of tree height, the 90th percentile of tree height was extracted for each reach based on the reach midpoint and a buffer that extended 60 m into the riparian zone after accounting for channel width. Canopy height data were also used to determine whether a reach was forested (height ≥ 3 m) following Potapov et al. (2021). We also explored these results across the aggregated level III Omernik ecoregions that were used by the Wadeable Streams Assessment (WSA) (US Environmental Protection Agency, 2006) to capture patterns in WHR across regions with variable physiographic, hydroclimatic, and ecological settings.

3. Results

3.1. Predicted GPP

Study-wide median seasonal trajectories of observed GPP and estimated GPP were calculated to examine how well each estimate captured seasonal dynamics across the data set (Figure 1b). Both GPP_{inc} and GPP_{sur} overestimated GPP throughout the year, particularly during the middle of the year. Accounting for water attenuation (GPP_{wat}) produced considerably lower estimates of GPP that more closely matched median daily rates of observations. Study-wide NRMSE (GPP_{inc} = 6.15, GPP_{sur} = 3.45, GPP_{wat} = 1.73) and bias (GPP_{inc} = 12.72, GPP_{sur} = 5.81, GPP_{wat} = 0.07) decreased as additional processes were accounted for in each model of light availability. The largest change in NRMSE was between GPP_{inc} and GPP_{wat}, which coincides with the inclusion of riparian attenuation within the model structure. Correlations between observed and estimated GPP at the study-wide level increased from GPP_{inc} (r = 0.25) to GPP_{sur} (r = 0.43) but the inclusion of additional processes reduced the correlation for GPP_{wat} (r = 0.19).

3.2. Factors Limiting Light and GPP

Study-wide, 56% of days were most limited by riparian attenuation and 44% of days were most limited by water attenuation. At the site-level, the number of sites most limited by riparian attenuation (n = 88) and by water attenuation (n = 85) was approximately equal. Limitation by riparian attenuation declined nonlinearly with increasing WHR and changed from being the dominant control when the ratio of channel width to tree height was 1.7 (Figure 2a). In other words, where WHR is < 1.7 we predict that GPP will be primarily limited by riparian attenuation, and where WHR is greater than or equal to 1.7 GPP will be primarily

![Figure 2. Changes in the percent limitation of gross primary production (GPP) and the percent of potential GPP. Median values were calculated by placing sites into bins based on their ratio of channel width to tree height (WHR), resulting in 10 bins of approximately the same number of sites. The percent limitation by riparian attenuation and water attenuation is shown along with total combined limitation (a). The percent of potential GPP for observations and predictions (b). Potential GPP was determined based on GPP estimated from incoming photosynthetically active radiation (GPP_{inc}). Predicted values are based on GPP estimated from PAR in the water (GPP_{wat}).](image)
limited by water attenuation. For sites where WHR was <1.7, a total of 85 out of 87 sites were most limited by riparian attenuation. Conversely, for sites where WHR was greater than or equal to 1.7, 83 out of 86 sites were most limited by water attenuation. Using GPP_{inc} as an indicator of potential GPP, we also found that observed GPP was consistently a small fraction of potential GPP and was especially constrained for smaller values of WHR (Figure 2b). For our 173 sites, the coefficient of variation for channel widths was 1.8 but only 0.6 for tree height, which suggests channel width was the primary driver of WHR across our sites.

Based on our national estimates of WHR, and our identified WHR threshold of 1.7, an equal percentage (50%) of total river length was predicted to be most limited by riparian attenuation and water attenuation. In our national predictions, small streams (first third order) constituted 91% of total river length, and if channel size was the only determinant of riparian attenuation, we would expect a higher proportion of river length to be limited by riparian zones. To account for differences in riparian cover we also examined our predictions for only forested rivers. In this subset of forested reaches small streams comprised a similar percentage of total river length (90%) but 86% of total river length was predicted to be most limited by riparian attenuation. The fractal nature of river networks means that although small streams represent a majority of stream length, they represent a smaller percentage of surface area (41%). Nationally we found 20% of river surface area was most limited by riparian attenuation. Again, if this is considered only for forested streams then 33% of surface area is riparian limited, which is much closer to their contributed percentage of total stream surface area in forested reaches (39%). Across WSA ecoregions the percentage of river length predicted to be most limited by riparian attenuation ranged from 7% in the Northern Plains (NPL) to 88% in the Northern Appalachians (NAP) and appears to be positively related to the percentage of forested reaches (Figure 3b).

We examined mean daily GPP for each site with respect to WHR and PDR to capture changes in factors regulating light reaching the stream surface and within the water column (Figure 4a). The predicted transition from riparian attenuation to water attenuation of GPP (WHR = 1.7) and the point where depth to the benthic surface is greater than the photic depth (PDR = 1) divide this plot into four quadrants. These quadrants could be interpreted to represent riparian attenuation limited streams with benthic GPP (I), water attenuation limited streams with benthic GPP (II), riparian attenuation limited streams with water column GPP (III), and water attenuation limited rivers with water column GPP (IV). We also calculated median seasonal trajectories of GPP for all sites in each quadrant. Moving from riparian attenuation and benthic GPP (Figure 4b) to water attenuation and water column GPP, the timing of peak GPP moved from earlier in spring toward the middle of the year and there was an increase in both the magnitude and variability of GPP.
Figure 4. Mean daily gross primary production (GPP) for each site plotted against the ratio of channel width to the height of riparian vegetation (WHR) and the mean values of the ratio of photic depth to water depth (PDR) for each site (a). The predicted transition points where water attenuation becomes the primary limitation to light and GPP (dashed line) and where depth to the benthic surface equals the photic depth (solid line) are used to divide the plot into four quadrants. For all sites in each quadrant, time series of the median and interquartile range (IQR) of observed GPP were calculated (b–d).
4. Discussion

We estimated GPP using only modeled PAR and light use efficiencies and were able to capture important seasonal patterns of GPP and provide first-order approximations of the upper limits of stream ecosystem productivity. Our light model accounted for several important processes including reduction of light to the stream surface as influenced by channel geometry, riparian phenology, water surface reflection, and light attenuation in the water column as influenced by depth and clarity. Accounting for riparian attenuation had the greatest reduction in the magnitude of errors for estimated GPP across all sites but accounting for all components (riparian attenuation and water attenuation) yielded the lowest overall errors. Nationally, we estimated an equal percentage of river length was most limited by riparian attenuation and water attenuation but that 80% of river surface area was limited by water attenuation. However, there was substantial variation in these proportions across ecoregions which appear to be driven by the amount of riparian forest.

Existing conceptual models predict that the relative importance of riparian elements on light availability and GPP decreases from small headwaters to large rivers as the importance of water column processes increases (Vannote et al., 1980). A number of studies have documented the importance of terrestrial control on stream GPP through the effects of land use or riparian canopies (Hill & Dimick, 2002; Hoellein et al., 2013; Roberts et al., 2007). Similarly, reduction in water clarity in higher order rivers (Julian, Doyle, Powers, et al., 2008) combined with channel widening and deepening indicate the importance of water column processes on light availability in larger rivers (Julian, Stanley, & Doyle, 2008). Our results generally support these conclusions and also lend further support to the role of turbidity in mediating GPP (Hall et al., 2015; Izagirre et al., 2008). Nationally we predicted that 50% of river length was most limited by riparian attenuation. This estimate is lower than expected considering that small (first–third order) streams constitute the majority of stream length. However, when we only considered forested reaches the percentage of total reach length most limited by riparian attenuation (86%) and total percentage of length in small streams (90%) are in close agreement. These results support the expectation that riparian shading greatly limits GPP in forested headwater streams (Vannote et al., 1980). While nationally riparian attenuation only limited half of river length, this varied greatly across ecoregions and appears to covary with the percentage of forested reaches. Our model of light availability used turbidity as a measure of water clarity, but gradients of coloration also influence light availability and GPP (Kirk et al., 2020). We assumed that light was a first-order control on GPP and sets the upper boundary of ecosystem productivity, but GPP is not solely determined by light. The arrangement of biomass can influence photosynthesis-irradiance relationships due to self-shading (Boston & Hill, 1991; Dodds et al., 1999) and disturbances can impact GPP through the scouring and burial of autotrophic biomass (Biggs et al., 1999; O’Connor et al., 2012; Uehlinger, 2006; Uehlinger & Naegeli, 1998). Frequent disturbance events may even limit productivity through much of the year (Blaszczak et al., 2018; Qasem et al., 2019). While nutrient limitation on GPP has been shown (Grimm & Fisher, 1986), it is often a secondary factor compared to land use or light availability (Bernot et al., 2010; Hoellein et al., 2013) and nutrients may become limiting to GPP only when light is not limiting (Greenwood & Rosemond, 2005). Water temperature can also influence GPP, though likely indirectly through increased responses of GPP to light at warmer temperatures (Beaulieu et al., 2013) consistent with the temperature dependence of photosynthesis at a cellular level (DeNicola, 1996). While representing stream light environments is an important step for predictive models of stream GPP, including these other factors is necessary to truly move toward mechanistic models of stream productivity.

Light availability influences the ecology of flowing waters in many ways. Alterations to riparian zones or water clarity impact light transmission into rivers and have far-reaching implications on light-mediated processes including thermal regimes (Sinokrot & Stefan, 1993; Webb & Zhang, 1999), photodegradation of organic materials (Larson et al., 2007), benthic community structure and function (Bengtsson et al., 2018; Grubisic et al., 2017), or indirectly through GPP-mediated patterns in nutrient dynamics (Finlay et al., 2011; Hall & Tank, 2003; Quinn et al., 1997). Because our modeling framework incorporates the influence of riparian zones and water column processes on light penetration into rivers, it has the potential to be applied to assess changes in multiple important river ecosystem processes. Our approach allowed us to quantify the relative importance of controls on light availability and primary production as they vary across river networks. The ability to make spatially extensive and temporally variable estimates of light penetration in rivers should provide new insights into the influence of light on stream ecosystem structure and function.
Data Availability Statement
The model inputs, outputs, and validation are available at https://doi.org/10.5066/P9LREC3P

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