The effects of temperature and light on ecosystem metabolism in a Japanese stream

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Abstract: Ecosystem metabolism is a fundamental process that governs biogeochemical C cycling through the fixation and mineralization of C by all the organisms in a system; however, the functional responses of ecosystem metabolism to light and temperature variability remain unknown in streams and rivers. In this study, we assessed the effects of temperature and light on ecosystem metabolism, namely gross primary production (GPP) and ecosystem respiration (ER), in a Japanese stream by monitoring the seasonal diel changes in dissolved oxygen. We found that the temperature dependence of metabolism, which is expressed as activation energy, was higher for ER (0.48 eV) than for GPP (0.39 eV), supporting the metabolic theory of ecology. Both daily GPP and ER increased with the daily integrated photosynthetically active radiation (PAR), peaking at moderate PAR values and decreasing at higher irradiance levels. This unimodal relationship between daily GPP and PAR was due to the rapid increase of instantaneous PAR during the early morning, suppressing the maximum rate of area-specific productivity, which was a main determinant of daily GPP. Moreover, daily GPP and ER were closely associated in this study stream, resulting in a unimodal pattern of daily ER with daily integrated PAR. Our results suggest that both temperature and light regulate stream ecosystem metabolism but that the sunlight regime (i.e., the rapid increase of solar irradiance in the early morning) rather than light intensity per se may be a critical factor for both GPP and ER in the study stream.

Key words: whole-stream metabolism, diel oxygen method, temperature dependence, photosynthesis–irradiance responses, organic matter supply, trophic state, flood disturbance

Over the past few decades, the C cycle in aquatic ecosystems and its changes due to anthropogenic impacts have been the focus of numerous studies (Wetzel 2001, Schlesinger and Bernhardt 2013). Ecosystem metabolism, comprising both gross primary production (GPP) and ecosystem respiration (ER), is a fundamental process that governs C fixation and mineralization by the organisms in a system. GPP and ER have been long-term foci of limnology and aquatic science studies (Odum 1956, Staehr et al. 2012, Bernhardt et al. 2018) in an attempt to understand the C cycle and budget in various environments. Indeed, the GPP and ER in streams and rivers contribute to global C cycling (Cole and Caraco 2001, Battin et al. 2008); however, previous estimates of GPP and ER have been based on limited data derived from streams and rivers in specific regions, such as Europe and North America. Thus, further research on GPP and ER is necessary to improve C flux estimates in lotic environments.

Ecosystem metabolism in streams and rivers is commonly measured using in-situ CO2 or O2 fluxes (Odum 1956). Even though incubation methods using bottles and chambers have been applied to measure GPP and ER in streams, these methods are challenging in terms of scaling up to the level of an ecosystem. In addition, it is difficult to conserve the original condition of the obtained biofilms and simulate lotic conditions in incubation chambers (Nozaki 2012). The open diel oxygen method, which measures the diel changes in dissolved oxygen (DO) in an open channel, has become a general approach for estimating the ecosystem metabolism in lotic environments (Iwata 2012, Hall and Hotchkiss 2017). Continuously recording data loggers have
facilitated DO monitoring, and as a result, many studies have used the open system, diel oxygen method to estimate GPP and ER in streams and rivers in North America (e.g., Beaulieu et al. 2013, Hall et al. 2016) and Europe (e.g., Izagirre et al. 2008, Demars et al. 2011).

Ecosystem metabolism is functionally dependent on temperature (e.g., Welker et al. 2015) and light (e.g., Savoy et al. 2019), as well as on nutrient availability (e.g., Manning et al. 2018). ER is generally considered to increase more substantially than GPP with increasing temperatures because of respiration’s greater dependence on temperature than photosynthesis. This general pattern of GPP and ER changes with temperature at the ecosystem level can be explained by the prediction of the metabolic theory of ecology (MTE; Allen et al. 2005), which describes the relationship between metabolic rate and temperature with the Arrhenius equation. Because of the growing interest in climate change and global warming, many studies have recently been conducted to verify the prediction of MTE in various ecosystems. For stream ecosystems, the rise in water temperature caused by climate warming may lead to the convergence of metabolic balance (i.e., the GPP:ER ratio), resulting in a continental-scale decrease in net primary productivity (Song et al. 2018). In contrast, a synthesis based on geothermal streams concluded that warming can increase GPP and ER to the same extent (Demars et al. 2016). Additionally, a field manipulation experiment in 1 stream also showed that GPP increased with warming by enhancing the efficiency of nutrient use but without increasing ER (Hood et al. 2017).

In addition to temperature, light, or solar irradiance, has also been identified as a fundamental variable affecting GPP through the regulation of photosynthetic reactions (Finlay 2011). The timing of incoming light influences GPP seasonal patterns in streams and rivers (Savoy et al. 2019). Moreover, the light environment may also affect ER by enhancing autotrophic respiration, as well as by stimulating heterotrophic respiration through the supply of algal exudates under high photosynthetic conditions (e.g., Huryn et al. 2014). However, the functional responses of GPP and ER to light and temperature variability in streams and rivers remain uncertain. More specifically, it is unclear whether increases in light and temperature induce monotonic or nonlinear responses in GPP and ER or whether the effects of light availability and temperature may confound stream ecosystem metabolism.

In Japan, several studies have used the open system, diel oxygen method to estimate GPP and ER for an artificial stream channel (Kayaba 2005), including those of 23 stream and river reaches in central Japan (Iwata et al. 2007) and 27 rivers across Japan (Gurung et al. 2019); however, the GPP and ER values obtained from these studies have been estimated for a short period of time (a few days) over a limited season (June and August). Moreover, these studies of Japanese streams (Kayaba 2005, Iwata et al. 2007, Gurung et al. 2019) did not evaluate the relationships between ecosystem metabolism and environmental factors, such as water temperature and light intensity. Clarifying the dependence of ecosystem metabolism on light and temperature in Japanese streams could be valuable for predicting the responses of stream ecosystem functioning to environmental change.

This study aimed to use the open system diel oxygen method to estimate GPP and ER, verify the prediction of the MTE by comparing the temperature dependence between GPP and ER, and examine the effect of light on GPP and ER in a stream in central Japan. There have been few empirical studies into the responses of stream metabolism to variation in light and temperature at the ecosystem level. Because of this limited knowledge, it is difficult to specify hypotheses on how temperature and light affect GPP and ER. In accordance with the MTE, we predicted that ER would be more temperature dependent than GPP; however, we expected that the effects of light on ecosystem metabolism would be more complex than those of temperature because of potential interactive effects of light and temperature on both GPP and ER. For example, light may directly increase GPP, but may also indirectly increase both GPP and ER via increasing water temperatures (Jones et al. 2017). Moreover, both GPP and ER may be suppressed under intense light conditions by light saturation, photoinhibition for photosynthesis, or a combination of both (Hill 1996). Therefore, in this study, we modeled the observed values of GPP and ER by considering the effects of both temperature and light to understand the precise responses of ecosystem metabolism to environmental change in lotic ecosystems. Furthermore, we assessed the metabolic variability across different seasons and the effects of temperature and light on ecosystem metabolism.

METHODS

To address our research objectives, we conducted field surveys to collect physicochemical data at 1 study reach during 7 monitoring periods with a duration of 1 wk each. We used the single-station diurnal DO change technique to determine whole-stream metabolism and maximum likelihood estimation inverse modeling to estimate daily GPP and ER. We also modified metabolic models of previous studies to describe the estimated daily GPP and ER as a function of the daily mean water temperature and the daily integrated solar irradiance to examine temperature dependences and light effects.

Study area

We conducted the field study from February 2016 to May 2017 at a reach (lat 36°00'40"N, long 139°00'50"E) of the Akabira River in the Chichibu region, Saitama Prefecture, Japan (Fig. 1A). This study’s reach is ~10 m wide and ~200 m long and is located 219 m a.s.l. in a 4th-order stream with a watershed area of ~120 km². Discharge measured at base flow condition on 29 March 2017 was 0.78 m³/s. The riparian forest in the study reach mainly consists of deciduous
broad-leaved trees and is surrounded by developed and agricultural land. There is no dam reservoir upstream of the study reach. The catchment around the reach receives annual precipitation of ∼1300 mm. In August 2016, a heavy rainfall event of 215 mm/d was recorded, which was the most significant rainfall in the past 10 y in the Chichibu region. A series of heavy rainfalls between August and September 2016 induced large floods, washing away the riparian vegetation in the Akabira River (Fig. 2A–C). After the storm, there were no major flood disturbances in the river during our study period. The study region was affected by heterogeneous atmospheric N deposition; thus, the NO₃-N concentrations were determined to be relatively high in the streams (Tabayashi and Koba 2011). However, seasonal variations in nutrient concentrations were small at 15 sites in the streams of the region (Yoh et al. 2001).

Figure 1. The study reach in the Akabira River watershed within the Chichibu region, Saitama Prefecture, Japan (star; A), and 2 data loggers with sensors for light and barometric pressure (○) and dissolved oxygen levels and water temperature (□; B). Arrow in panel B indicates the direction of flow.

Figure 2. Temporal changes in the water level (m a.s.l.) of the Akabira River, Chichibu region, Saitama Prefecture, Japan, and photos of the impact of the flood upstream from the study reach (A–C). Photos of water level (inside the graph) show the riverbed of the study reach under normal conditions (D) and with a large amount of accumulated leaf litter and branches (E). Photo credit: Daisuke Nakano.
Data collection

We collected physicochemical data at the study reach during 7 monitoring periods from February 2016 to June 2017. Each monitoring period had a duration of 1 wk: 19 to 25 February 2016 (Feb 2016), 25 to 31 May 2016 (May 2016), 16 to 22 October 2016 (Oct 2016), 4 to 10 December 2016 (Dec 2016), 30 March to 5 April 2017 (Mar 2017), 22 to 28 April 2017 (Apr 2017), and 27 May to 2 June 2017 (May 2017) (Fig. 2A–E). We recorded DO levels and water temperatures instream using an optical sensor with a HOBO® data logger (U26-001; Onset®; Bourne, Massachusetts). We recorded barometric pressure and PAR on the riverbank about ~2 m away from the stream edge. We deployed both sensors (HOBO barometric pressure sensor S-BPB-CM50, HOBO PAR sensor S-LIA-M003) with a HOBO data logger H21-USB ~200 m upstream longitudinally from the location of the DO data logger in the study reach (Fig. 1B). The light received by the stream surface may change over both space and time because of differences in topography and channel characteristics (e.g., Savoy et al. 2021), so we carefully chose the location of the PAR sensor to be representative of the natural light conditions of the study reach. We set the recording interval for all of these measurement to 10 min. We measured mean stream depth at 5 equally spaced points along each of 10 lines transecting the stream at 20-m intervals upstream of the DO monitoring site before and after the large flood in August 2016. We estimated mean stream depth for each monitoring period by correcting the mean depth with water-level data from the gauging station (Kobansawa, Saitama Prefecture). We observed small changes in the water level associated with rain and low stream discharge during periods of water level fluctuation. Thus, we concluded that any turbidity changes were negligible for each monitoring period.

We measured nitrate (NO$_3$-N), phosphate (PO$_4$-P), and silicate (SiO$_2$-Si) concentrations during all monitoring periods, except for the 5th (Mar 2017) and 6th (Apr 2017) periods due to forgetting to collect samples. We collected water samples in a polypropylene bottle, which we transported to the laboratory on ice, filtered through a membrane filter with a 0.45-μm pore size, and froze (~20°C) within 1 wk until later analysis. The PO$_4$-P and SiO$_2$-Si concentrations were analyzed using an AutoAnalyzer (QuAAtro; BLTEC, Osaka, Japan). The NO$_3$-N concentration was analyzed using ion chromatography (IC-2010; Tosoh, Tokyo, Japan).

Estimation of ecosystem metabolism

We used the single-station diurnal DO change technique to determine the whole-stream rates for daily GPP (g O$_2$ m$^{-2}$ d$^{-1}$) and ER (g O$_2$ m$^{-2}$ d$^{-1}$). We used maximum likelihood estimation inverse modeling to estimate daily GPP and ER with the streamMetabolizer package (version 0.10.9; Appling et al. 2018) in R (version 3.5.1; R Project for Statistical Computing, Vienna, Austria). This modeling approach iteratively identifies the combination of GPP, ER, and air–water gas exchange of oxygen that provides the best match between the modeled and measured DO (Hall and Hotchkiss 2017):

$$O_i = O_{i-\Delta t} + \frac{GPP \times PAR \times \Delta t}{\sum PAR} + \frac{ER \times \Delta t}{\sum PAR} + k_o (O_{sat} - O_i) \Delta t.$$

(Eq. 1)

In this model, the DO concentration at time $i$ (O$_i$ g O$_2$/m$^3$) is equal to the DO concentration at the previous time ($O_{i-\Delta t}$) plus the step-specific rates of GPP, ER, and the air–water gas exchange by reaeration. We then incorporated the relative amount of light ($PAR_t$ / $\sum PAR$) to turn on and off GPP during the day and night, respectively (Hall and Hotchkiss 2017). The air–water gas exchange rate of oxygen is modeled as the reaeration coefficient ($k_o$) multiplied by the difference between dissolved O$_2$ (O) and dissolved O$_2$ at saturation ($O_{sat}$) for a given water temperature and barometric pressure (Garcia and Gordon 1992). We applied $k_{600}$ instead of $k_o$ in this study because $k_{600}$ has been commonly used in recent studies on ecosystem metabolism in streams and rivers (e.g. Appling et al. 2018, Munn et al. 2020). $k_{600}$ is the daily average value of the gas exchange rate coefficient after normalization for molecular properties and temperature to a Schmidt number of 600 (corresponding to O$_2$ at 17.5°C) and can be calculated from $k_o$ (Appling et al. 2018). We computed GPP, ER, and $k_{600}$ for each monitoring period (d) from 0400–0400 h the following day (d) using the model setting (type=’mle’, GPP_fun=’satlight’, ER_fun=’constant’) in streamMetabolizer. $z$ denotes mean stream depth (m) and $\Delta t$ denotes the measurement interval of 10 min. We used the coefficient of determination ($r^2$) from regression of observed vs estimated DO values to check the model fit. We visually inspected histograms and residual diagnostic plots to confirm data normality and homoscedasticity for both sets of DO values.

Inverse modeling approaches can suffer from equifinality, where many possible combinations of GPP, ER, and $k_{600}$ yield indistinguishable diel DO curves (Appling et al. 2018). Therefore, we calculated $k_{600}$ using the nighttime regression method (Hall and Hotchkiss 2017) for each monitoring period (d) to confirm the validity of the modeled $k_{600}$ values. We also performed a linear regression analysis between ER and the modeled $k_{600}$ to verify the potential influence of equifinality.

Effects of temperature and light on ecosystem metabolism

Ecosystem metabolism in streams and rivers generally exhibits temperature dependence, as observed in other ecosystems (Yvon-Durocher et al. 2012). Gilllooly et al. (2001) demonstrated that the activation energy ($E_a$; eV) for rate-limiting, enzyme-catalyzed biochemical reactions is appropriate for describing the temperature dependence of metabolism, even
over a broad temperature range. Modifying the methodologies of Dell et al. (2011) and Iwata et al. (2016), we used the following equation to model the daily ecosystem metabolism (GPP and ER) rate \( R \) (obtained from the outputs of GPP and ER from streamMetabolizer) as a function of the daily mean water temperature \( T(K) \) and the daily-integrated solar irradiance \( (I; \text{mol quanta m}^{-2} \text{d}^{-1}) \):

\[
R = f(T, I) = b_0 \times \exp\left(\frac{E(T - T_0)}{kT T_{20}}\right) \times (\alpha I^2 + \beta I + \gamma),
\]

where \( b_0 \) is a normalization constant of GPP or ER, \( k \) is the Boltzmann’s constant \((8.62 \times 10^{-5} \text{eV/K})\), and \( \alpha, \beta, \) and \( \gamma \) are fitted constants for \( I \). We set \( \gamma = 0 \) in \( R_{GPP} \) and 1 in \( R_{ER} \) because there is no production \((GPP = 0)\) and no effect of light on ER when light is 0 \((I = 0)\). We estimated the unknown parameters \((E, b_0, \alpha, \) and \( \beta \) in Eq. 2) from \( R, T, \) and \( I \) using the maximum likelihood estimation method.

In this study, we applied the above model to estimate ER and GPP because solar irradiation may affect ER through the metabolic activity of autotrophic organisms and other mechanisms (Lambers and Oliveira 2019). In addition, because the relationships of \( I \) to GPP and ER were unknown, we constructed 2 candidate models with and without the quadratic term \((\alpha I^2)\) and used the lowest Akaike’s information criterion (AIC) to choose the best-fitting model describing the GPP and ER patterns. We used Python (version 3.7.7; Python Software Foundation, Wilmington, Delaware) to construct these models, and the code can be found at https://github.com/okadate/nakano2022_MLE.

**RESULTS**

**Riverine environments and ecosystem metabolism**

Water temperature in the study reach varied seasonally, but PAR did not. Temperatures were ~5°C in the winter (Feb 2016), ~20°C in the early summer (May 2016 and May 2017), and reached intermediate temperatures in the autumn and spring (Table 1). Daily integrated PAR ranged from 5.3 to 53.0 \( \text{mol m}^{-2} \text{d}^{-1} \), with no seasonal trend apparent. The correlation between mean water temperature and daily integrated PAR was low (Pearson’s \( r = 0.21 \)).

We successfully estimated ecosystem metabolism in the study reach for each monitoring day across the different seasons. The coefficient of determination between the observed and estimated DO values was high \((r^2 = 0.87–1.00)\) for each monitoring day (Fig. S1). GPP ranged from 1.8 to 36.4 and ER ranged from 2.1 to 31.2 g O₂ m\(^{-2}\) d\(^{-1}\) (Table 1, Fig. 3A). The highest daily GPP was observed in the Oct 2016 period after the large flooding events (Fig. 3A), whereas GPP was low in Feb 2016, when the mean water temperature was also low (<5.0°C). The intraperiod variation in daily GPP tended to be greater during warmer periods (May 2016, Oct 2016, and May 2017), with a mean water temperature >15.0°C. The highest daily ER value was observed in May 2016 before the large floods (Fig. 3B), whereas ER was very low in Feb 2016 with low water temperatures. As with GPP, the daily variation in ER was greater in periods with higher temperatures. In addition, daily GPP and ER values were correlated (Pearson’s \( r = 0.86 \)) across all monitoring periods.

Trophic status in the study reach seemed to shift from heterotrophs to autotrophs after the large flood events. Before the large floods that occurred between August and September 2016, the GPP:ER ratio was <1 (i.e., mean 0.60 ± 0.05 SD and 0.81 ± 0.14 in Feb and May 2016, respectively), indicating the overall predominance of heterotrophic metabolism (Fig. 3C). After the large floods, the GPP:ER ratio was often >1, reaching 1.28 ± 0.22 in Oct 2016, 1.96 ± 0.84 in Mar 2017, 1.53 ± 0.21 in Apr 2016, and 1.04 ± 0.11 in May 2017, with the exception of 0.88 ± 0.08 in Dec 2016.

The standardized rate coefficient for the gas exchange rate \( k_{600} \) ranged from 24.1 to 83.1 d\(^{-1}\) (Fig. 3D). This range was similar to the range of \( k_{600} \) calculated via the nighttime

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**Table 1.** The physicochemical environment and ecosystem metabolism during each sampling period in the Akabira River, Chichibu region, Saitama Prefecture, Japan. – indicates no data, WT = water temperature, PAR = photosynthetically active radiation, GPP = gross primary production, ER = ecosystem respiration, NO\(_3\)-N = nitrate, PO\(_4\)-P = phosphate, SiO\(_2\)-Si = silicate.

| Period | Physical environment (mean ± SD) | Chemical environment | Ecosystem metabolism (mean ± SD) |
|--------|---------------------------------|----------------------|----------------------------------|
|        | Mean daily WT (°C) | Daily-integrated PAR (mol m\(^{-2}\) d\(^{-1}\)) | NO\(_3\)-N (mg/L) | PO\(_4\)-P (µg/L) | SiO\(_2\)-Si (mg/L) | GPP (g O₂ m\(^{-2}\) d\(^{-1}\)) | ER (g O₂ m\(^{-2}\) d\(^{-1}\)) |
| Feb 2016 | 4.8 ± 0.45 | 23.6 ± 9.5 | 1.9 | – | – | 2.0 ± 0.3 | 3.4 ± 0.6 |
| May 2016 | 19.0 ± 0.74 | 23.8 ± 11.0 | 0.6 | 17.5 | 4.8 | 16.1 ± 5.3 | 20.2 ± 7.5 |
| Oct 2016 | 16.0 ± 0.84 | 19.3 ± 8.5 | 0.7 | 16.6 | 4.8 | 25.5 ± 9.7 | 19.7 ± 6.7 |
| Dec 2016 | 7.4 ± 0.97 | 12.3 ± 5.9 | 0.9 | 23.7 | 4.4 | 14.3 ± 1.8 | 16.4 ± 2.4 |
| Mar 2017 | 9.3 ± 1.51 | 15.7 ± 2.5 | – | – | – | 10.9 ± 3.0 | 6.2 ± 2.8 |
| Apr 2017 | 13.3 ± 0.62 | 33.5 ± 16.1 | – | – | – | 9.2 ± 4.6 | 5.9 ± 2.7 |
| May 2017 | 19.2 ± 1.22 | 37.8 ± 13.7 | 1.0 | 27.0 | 5.0 | 13.0 ± 6.4 | 12.5 ± 6.2 |
regression method (23.0–91.5/d). Moreover, the correlation between ER and modeled \( k_{600} \) \( (r = 0.57) \) was not strong (see Appling et al. 2018). Therefore, we deemed the equifinality of the inverse model to be of minor importance in this study.

Increases and decreases in DO were closely related to changes in light and also appeared to follow photosynthesis–irradiation (P–I) responses. Photosynthetic light saturation was observed for all monitoring days, except for rainy or cloudy days with low irradiation (maximum PAR < 500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)). However, no apparent photoinhibition was observed throughout the study period (Fig. S2). DO changes were closely related with PAR values (Figs S1, S2), which suggests that the location of the PAR sensor was representative of the natural light condition of the study reach. However, there were time lags between decreasing DO and PAR values in the afternoon in winter (December 2016), when the sun’s elevation was low, which seemed to be a result of the effects of bank shading due to topographic characteristics in the study stream. The fit of the inverse model was high on monitoring days in December 2016 \( (r^2 = 0.87–0.99) \), indicating that the effects of bank shading were likely minimal in this study.

GPP and ER models

We developed metabolic models with maximum likelihood estimation to describe the daily GPP and ER observed throughout the study period by estimating each of the parameters \( E, b, \alpha, \gamma, \beta \) (Table S1). The models with quadratic terms were selected for both GPP (with AIC values of 331.2 and 375.2 for models with and without the quadratic term, respectively) and ER (with AIC values of 318.3 and 323.4 for models with and without the quadratic term, respectively). The selected models for \( R_{GPP} \) and \( R_{ER} \) were the following:

\[
R_{GPP} = 2.44 \times \exp \left( \frac{0.39(T - T_{20})}{kTT_{20}} \right) 
\times \left( -0.014I^2 + 0.74I \right), \quad \text{(Eq. 3)}
\]
\[
R_{ER} = 12.13 \times \exp \left( \frac{0.48(T - T_{20})}{kTT_{20}} \right) 
\times \left( -0.002I^2 + 0.08I + 1.00 \right).
\]

The estimated activation energy \( (E) \) for GPP (mean ± SE = 0.39 ± 0.06 eV) and ER (0.48 ± 0.07 eV) showed that both GPP and ER increased exponentially as mean daily water temperature increased (Fig. 4A, B). ER values in Dec 2016 were higher than that predicted by water temperature (dashed circle in Fig. 4B). The metabolism–irradiance curve showed that both GPP and ER varied with the variation in PAR (Fig. 5A, B). They both increased with the daily integrated PAR, peaked between 20 and 30 \( \text{mol m}^{-2} \text{d}^{-1} \), and decreased with further increases in PAR.

Relationship between GPP and light

We found a light-saturated relationship in the P–I curves between productivity rate and irradiation at 10-min intervals almost every day. There was little photoinhibition in the curves (Fig. S1). The maximum rate of area-specific productivity \( (p_{\text{max}}) \) had a high daily difference, ranging from 0.021
Daily GPP was positively correlated with \( p_{\text{max}} \) (\( r = 0.92; \text{Fig. 6A} \)), and \( p_{\text{max}} \) values were low on the days when the integrated PAR was high for several hours after dawn as irradiation steeply increased (Fig. 6B, C). We also found positive correlations among the daily integrated PAR and the integrated PAR values for 3 (\( r = 0.71 \)) and 4 h (\( r = 0.70 \)) after dawn. To better understand the difference in \( p_{\text{max}} \) among patterns of light increase after dawn, we looked at 3 d in the May 2017 monitoring period that varied in the rate of irradiation increase after dawn (Fig. 7A–C). The differences in P–I curves among the 3 d indicate that \( p_{\text{max}} \) could reach higher levels on days when irradiation gradually increases (e.g., 1 June 2017) and remain lower on days when irradiation increases more steeply (e.g., 29 May 2017).

**DISCUSSION**

This study examined the effects of temperature and light on GPP and ER in a stream. As we expected, temperature dependence of ER was higher than that of GPP. Both daily GPP and ER increased with daily integrated PAR, peaking at moderate light levels and decreasing at higher light levels. Low GPP at higher light level was related to rapid increase of light intensity during the early morning. In this section, we discuss these results in relation to light regime, as well as effects of organic matter input on ecosystem metabolism. Our findings suggest that not only light intensity but also light variation patterns may influence GPP and ER, which has implications for understanding the responses of stream ecosystem function to environmental changes.

**Seasonal patterns of GPP and ER in the Akabira River**

The ranges of GPP and ER in the study reach largely varied across the study period (GPP = 1.8–36.4, ER = 2.1–31.2 g O\(_2\) m\(^{-2}\) d\(^{-1}\)), which reflects the results of previous studies in various geographic locations. We observed distinct seasonal patterns that both rates of daily GPP and ER were higher during the warmer months of sampling (May and October) and lower during the colder months of sampling (February, March, April, and December). These values were similar to...
Figure 6. The relationship of daily gross primary productivity (GPP) in the Akabira River, Chichibu region, Saitama Prefecture, Japan, with the maximum rate of area-specific productivity ($p_{\text{max}}$) (A) and the relationships of integrated photosynthetically active radiation (PAR) 3 (B) and 4 h (C) after dawn with $p_{\text{max}}$.

Figure 7. Temporal changes in integrated photosynthetically active radiation (PAR) (A), its enlarged portion for several h after dawn (B), and photosynthesis–irradiation ($P$–$I$) curves (black lines) (C) for 3 d (28 May, 29 May, and 1 June) in 2017 in the Akabira River, Chichibu region, Saitama Prefecture, Japan. Solid icons in panel B represent the time to reach the maximum rate of area-specific productivity ($p_{\text{max}}$) each day.
the results of previous studies on ecosystem metabolism estimated for >1 y. For example, GPP and ER range from <0.05 to 20.2 and 0.8 to 14.6 g O₂ m⁻² d⁻¹, respectively, in the alpine rivers of Switzerland where metabolism was affected by extreme flows and recovery rates varied seasonally (Uehlinger 2000); from 0.05 to 1.9 and 0.4 to 32 g O₂ m⁻² d⁻¹, respectively, in a Mediterranean stream with seasonal changes related to variation in both light and temperature (Acuña et al. 2004); and from 0.01 to 10.8 and 0.99 to 16.0 g O₂ m⁻² d⁻¹, respectively, in a United States forest stream with variation driven by decreased GPP with canopy closure and increased growing-season ER (Roberts et al. 2007). Moreover, Demars et al. (2011) reported that GPP and ER ranged from 2 to 28 and 3 to 67 g O₂ m⁻² d⁻¹, respectively, in naturally geothermal Icelandic streams with different temperature conditions. In this study, we ascribe the seasonal patterns of GPP and ER to seasonal changes in water temperature, consistent with previous studies (e.g., Savoy et al. 2019). Temperature is a primary factor for determining GPP and ER in streams and rivers. In addition, we noted substantial daily changes in GPP and ER (Fig. 3A, B) that were at least partially related to daily differences in light conditions.

**Temperature dependence and the MTE**

This study indicates that the temperature dependence of ER was higher than that of GPP in the study stream, in support of the MTE. This difference in temperature dependence has been the subject of much interest because climate warming may have a positive or negative impact on lotic ecosystems, depending on the functional response of GPP and ER to warming through CO₂ flux from river networks (Yvon-Durocher et al. 2012, Demars et al. 2016, Manning et al. 2018, Song et al. 2018). According to the MTE, the predicted activation energy of GPP (E<sub>GPP</sub>), based on the temperature dependence of the Rubisco enzyme, is 0.57 eV (Galmés et al. 2015) and that of ER (E<sub>ER</sub>), based on the temperature dependence of the respiratory complex, is 0.62 eV (Gillooly et al. 2001). Another previous empirical study supported the MTE, with average E<sub>GPP</sub> and E<sub>ER</sub> of 13 arctic streams of 0.54 ± 0.24 and 0.67 ± 0.23 eV, respectively (Demars et al. 2011). In our study, the E<sub>ER</sub> (0.48 eV) was also higher than the E<sub>GPP</sub> (0.39 eV), although these values were somewhat lower compared with those reported in previous theoretical and empirical studies. Our results imply that the stream ecosystem in this study site may change into a predominantly heterotrophic system because of future increases in water temperature.

**Ecosystem metabolism relationship with light**

Interestingly, this study showed that daily GPP declined at a higher range of the daily integrated PAR (Fig. 5A), even though there was little photoinhibition between the productivity rate and irradiation (Fig. S1). Previous studies have also found linear or light-saturated P–I relationships with the open system technique in stream and river ecosystems (Uehlinger et al. 2000, Iwata 2012), but there have been few reports of photoinhibition. Photoinhibition is usually found in phytoplankton assemblages (Platt et al. 1980), which often decrease the GPP in lakes (Staehr et al. 2016) and oceans (Long and Humphries 1994, Alderkamp et al. 2010). In contrast, although photoinhibition may occur for immature assemblages of stream periphyton (Laviale et al. 2009), it is considered a rare phenomenon in lotic ecosystems where periphyton assemblages with layer structures are the primary producers (Dodds et al. 1999). Therefore, because of the lack of photoinhibition in the instantaneous P–I curve, our observed pattern of the negative effect of PAR on daily GPP seems paradoxical.

There may be plausible physiological mechanisms that explain the unimodal shape of GPP with daily integrated PAR. We also observed that daily GPP was determined mainly via the maximum possible GPP (P<sub>max</sub> Fig. 6A). Therefore, strong solar irradiance is likely to influence P<sub>max</sub> thereby corresponding with lower daily GPP. In fact, P<sub>max</sub> values decreased with an increase in integrated PAR values for 3 and 4 h after dawn, indicating that the maximum potential GPP was suppressed in the days when irradiance increased sharply (Fig. 7A–C). Several possibilities may explain this interesting phenomenon. Damage to the photosynthetic system from a rapid increase in solar irradiation after dawn may suppress P<sub>max</sub> in benthic algal communities of stream ecosystems. Also, rapid increases in photosynthetic activities may induce limitations of resources other than light, such as inorganic C and nutrients, that are required for photosynthesis. Thus, more research is required to elucidate the mechanisms behind the responses of ecosystem metabolism to irradiation changes.

Similarly, ER increased with the daily integrated PAR, peaking at moderate PAR values and decreasing at higher irradiance levels (Fig. 5B). These results contradict those of a previous study that demonstrated that terrestrial plant species cultured in higher irradiation showed higher respiration rates under both light and dark conditions after irradiation (Dahal et al. 2017). One possible explanation for the decreased ER under strong light conditions is that ER was highly correlated with GPP in this study stream and, thus, closely associated with GPP fluctuations. It is plausible that autotrophic respiration constituted a large portion of ER and more labile C provided from autotroph photosynthesis stimulated heterotrophic respiration at moderate PAR levels. Another possibility is that high ultraviolet radiation (Nunez et al. 1994, Kelly et al. 2003) can cause microbial communities, including autotrophs, to collapse, resulting in a decrease in ER. Decrease in respiration caused by ultraviolet radiation has been observed for both benthic algal biomass in freshwater ecosystems (Bothwell et al. 1993, Vinebrooke and Leavitt 1996) and bacterial respiration (Kelner 1953).

**Leaf-litter input effects on ER**

In addition to the effects of temperature and light, organic matter input may be important for ecosystem metabolism. In
the study stream, the ER value in December 2016 was higher than that predicted by water temperature (Fig. 4B), which may have been caused by considerable accumulation of organic matter on the riverbed from fallen autumn leaves in November and December (Fig. 2E). Many studies have investigated the role of organic C from terrestrial ecosystems in the structure and ecosystem functioning of streams (Gulis and Sukkerkopp 2003, Acuña et al. 2007). ER has been found to be high in the period when organic matter accumulations on the streambed are extremely high (Acuña et al. 2004). In addition, the temperature dependence of ER has been found to be affected by the quantity and quality of available organic matter (Jankowski et al. 2014), which could help to explain the deviation of ER from the regression line in December 2016. Further studies are needed to examine the effects of organic matter on the temperature dependence of ER.

**Shift in trophic status**

Trophic status in streams may sometimes shift because of flood events and the presence of grazers, but stream ecosystem metabolism is usually heterotrophic (Hoellein et al. 2013). After the large floods, the study stream often showed net autotrophy (i.e., GPP:ER > 1; Fig. 3C). Differences in the resistance (magnitude of change) and resilience (speed of recovery) of GPP and ER to flooding may have produced net autotrophy. Beaulieu et al. (2013) found short-term suppression of GPP following storm pulses but noted that GPP quickly recovered. In contrast, several studies have shown that ER often exhibits greater resistance than GPP against flood disturbances, causing shifts in the ecosystem metabolism toward net heterotrophy after flooding (Uehlinger and Naegeli 1998, Uehlinger 2000, Qasem et al. 2019). These findings appear to contradict our results of the predominance of autotrophy after flooding disturbance, likely because of differences between the resistance and resilience of the respiratory activities of the microbial communities in the stream. Once severe floods cause catastrophic damage to the microbial community, these communities may require a relatively long time for functional recovery. Frequent and intense flooding caused by precipitation patterns associated with climate change (Ohba and Sugimoto 2019) may act as a buffer in preventing CO₂ degassing by shifting to net autotrophy; however, further studies are necessary to understand the mechanism behind the shift from net heterotrophy to net autotrophy associated with large flood disturbances in streams and rivers.

GPP:ER ratio was particularly high in the spring season (March and April) of 2017 (Fig. 3C), which could have been related to intensive grazing of periphyton. Grazing decreases attached algal biomass (and respiration) but enhances primary productivity because competition for light and nutrients is less severe in the grazed than in the ungrazed periphyton (Liess and Hillebrand 2004, Vadeboncoeur and Power 2017). As a result, the GPP:ER ratio may become high in a sea-son with warm, grazer-active conditions. Further studies are needed to understand effects of grazing on the balance of ecosystem metabolism.

**Broader implications**

This study showed that both temperature and light strongly influence ecosystem metabolism (GPP and ER) in a stream in Japan, where there is a geographical gap in research on ecosystem metabolism in streams and rivers. Our results supported the MTE in that ER showed higher temperature dependence than GPP. Although there was no apparent photoinhibition in the P–I curve, the unimodal relationship between daily GPP and integrated PAR was caused by $p_{\text{max}}$, a main determinant factor of daily GPP, which was suppressed because of the rapid increase of instantaneous PAR during early mornings. The mechanism for the effect of light on both GPP and ER remains uncertain. Nevertheless, our results suggest that both temperature and light regulate stream ecosystem metabolism. More specifically, the sunlight regime (i.e., a rapid increase of solar irradiance in the early morning), rather than strictly light intensity, may be a critical factor for both GPP and ER, as well as for C cycling in the study stream. Further studies are required to understand the effects of light on ecosystem metabolism in streams and rivers.

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