Reports

Ecology, 96(3), 2015, pp. 603–610

Does N_2 fixation amplify the temperature dependence of ecosystem metabolism?

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Abstract. Variation in resource supply can cause variation in temperature dependences of metabolic processes (e.g., photosynthesis and respiration). Understanding such divergence is particularly important when using metabolic theory to predict ecosystem responses to climate warming. Few studies, however, have assessed the effect of temperature–resource interactions on metabolic processes, particularly in cases where the supply of limiting resources exhibits temperature dependence. We investigated the responses of biomass accrual, gross primary production (GPP), community respiration (CR), and N_2 fixation to warming during biofilm development in a streamside channel experiment. Areal rates of GPP, CR, biomass accrual, and N_2 fixation scaled positively with temperature, showing a 32- to 71-fold range across the temperature gradient (~7°–24°C). Areal N_2-fixation rates exhibited apparent activation energies (1.5–2.0 eV; 1 eV = $\sim 1.6 \times 10^{-19}$ J) approximating the activation energy of the nitrogenase reaction. In contrast, mean apparent activation energies for areal rates of GPP (2.1–2.2 eV) and CR (1.6–1.9 eV) were 6.5- and 2.7-fold higher than estimates based on metabolic theory predictions (i.e., 0.32 and 0.65 eV, respectively) and did not significantly differ from the apparent activation energy observed for N_2 fixation. Mass-specific activation energies for N_2 fixation (1.4–1.6 eV), GPP (0.3–0.5 eV), and CR (no observed temperature relationship) were near or lower than theoretical predictions. We attribute the divergence of areal activation energies from those predicted by metabolic theory to increases in N_2 fixation with temperature, leading to amplified temperature dependences of biomass accrual and areal rates of GPP and R. Such interactions between temperature dependences must be incorporated into metabolic models to improve predictions of ecosystem responses to climate change.

Key words: activation energy; amplification; Arrhenius; biofilm; climate change; Hengladalsá River, Iceland; metabolic theory; nitrogen fixation; nutrient cycling; resource supply; temperature.

Introduction

Since 1880, global mean surface temperatures have risen by 0.85°C, and most models predict an increase of ~4°C by 2100 (IPCC 2013). Elevated temperatures have altered the species composition and biogeochemistry of Earth's ecosystems (Grimm et al. 2013), with largely unknown consequences. One of the greatest challenges for this century is to understand and predict how warming will affect the physical, chemical, and biological processes governing ecosystem fluxes of carbon and essential nutrients.

The metabolic theory of ecology (MTE; Brown et al. 2004, Sibly et al. 2012) offers one approach for developing predictions about how temperature influences ecosystem processes. The MTE argues that the relationship between ecosystem metabolism and temperature can be predicted from the temperature dependences of subcellular reactions, such as photosynthesis and cellular respiration. The rate of most subcellular reactions increases exponentially with temperature following the Van't Hoff-Arrhenius relationship $e^{-E/(kT)}$, where k is the Boltzmann constant (8.61×10^{-5} eV/K; 1 eV = $\sim 1.6 \times 10^{-19}$ J), T is temperature (K), and E is the activation

Manuscript received 30 August 2014; accepted 4 November 2014. Corresponding Editor: S. Findlay.
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energy (AE; in eV), which quantifies the change in reaction rate with temperature (Boltzmann 1872, Arrhenius 1889). Over a biologically relevant range of temperatures (e.g., 0–30°C), the AEs for respiration and gross primary production for both cells and ecosystems are predicted to be ~0.65 and ~0.32 eV, respectively (Gillooly et al. 2001, Allen et al. 2005). Research in a variety of ecosystems has generally supported this prediction, suggesting that the MTE may help forecast ecosystem responses to warming (Enquist et al. 2003, Demars et al. 2011, Perkins et al. 2012, Yvon-Durocher et al. 2012). However, broad application of the MTE is currently hindered by a lack of information about how its predictions are influenced by resource supply (Anderson-Teixeira and Vitousek 2012).

Since its conception, there has been considerable effort to incorporate the effects of resource supply into the MTE (Brown et al. 2004, Sterner 2004, Kaspari 2012). Such efforts have been motivated by a growing literature demonstrating both independent and interacting effects of temperature and resource availability on ecosystem processes (Pomeroy and Wiebe 2001, López-Urrutia and Morán 2007, Davidson et al. 2012). Indeed, recent models that explicitly incorporate these factors have refined predictions about how ecosystems respond to global change (e.g., Davidson et al. 2012). Nevertheless, few models incorporate the dynamics of temperature–resource availability relationships.

Rates of many physiological and geochemical processes that control resource supply (e.g., enzyme activity, weathering) increase with temperature (Rennie and Kemp 1986, Bland and Rolls 1998). Thus, warming can increase resource supply, leading to "apparent" AEs that diverge from canonical (i.e., intrinsic) predictions (Anderson-Teixeira and Vitousek 2012) that are based on temperature alone. Nitrogen (N_2) fixation is one process of particular interest, as it provides an additional source of N to ecosystems (Howarth 1988, Marcarelli et al. 2008, Scott et al. 2009) and has a strong biphasic temperature dependence at the enzymatic level (AE of nitrogenase = 2.18 eV below 22°C, 0.65 eV above 22°C; Ceuterick et al. 1978). As such, increases in N_2-fixation rates with temperature can increase the availability of a limiting resource (i.e., N), potentially leading to temperature dependences of whole-community primary production and respiration that are higher than those predicted by the MTE (Anderson-Teixeira et al. 2008). To test this prediction, we experimentally manipulated temperature under strongly N-limited conditions and quantified responses of N_2 fixation, primary production, and community respiration during stream biofilm development.

Methods

Temperature manipulation and experimental channels

We used experimental stream channels to examine the effect of temperature on biofilms. Our infrastructure was installed in a grassland watershed draining the Hengill volcanic area, 30 km east of Reykjavík, Iceland (64°03′23″ N, 21°17′01″ W). Hengill is an active geothermal landscape with streams and hot springs that vary in temperature (annual mean temperature range = ~6–100°C) due to localized warming (Árnason et al. 1969). Our experimental temperature gradient was achieved using three gravity-fed heat exchangers that were deployed in geothermal pools. These devices heated stream water from an unnamed tributary of Hengladalsá River (mean temperature = 7.5°C) to ~10°C and ~20°C above ambient (see Plate 1 and the Appendix: Figs. A1 and A2; O'Gorman et al. 2014). Water from the two heat exchangers was then mixed with unheated stream water to produce five water-temperature treatments that were supplied to 15 experimental stream channels (mean ± SD; 7.5° ± 1.8°, 11.2° ± 1.8°, 15.5° ± 1.9°, 19.0° ± 1.8°, 23.6° ± 2.0° C; $n = 3$ channels per temperature and divided into three blocks with the five temperatures randomized within each block; Appendix: Table A1 and Fig. A3). The bed of each channel was lined with ~110 25 × 25 mm basalt tiles (Deko Tile, Carson, California, USA) that were leached in tap water for 18 d and boiled for 5 min prior to deployment on 20 May 2013. Channels were colonized for 42 d before our first measurement period. We did not prevent macroinvertebrates from colonizing the channels, but very few invertebrates were observed on tiles during the study.

Metabolism and biofilm mass accrual

We measured biofilm metabolism in 0.3-L recirculating chambers constructed from clear Plexiglas (Arkema, Colombes, France; Appendix: Fig. A4). Biofilm metabolism, as change in dissolved oxygen (O_2) concentration, was measured simultaneously for all treatments within each randomly chosen block at days 42 and 58. Incubations were typically conducted between 10:00 and 16:00 during sunny conditions.

Each chamber measurement was based on four tiles randomly selected from a single channel. Tiles were sampled without replacement, placed in chambers filled with sieved (250-μm) water from the respective treatment, and incubated in a water bath at the appropriate temperature. We measured net ecosystem production (NEP) under ambient light conditions and community respiration (CR) in the dark. The same tiles were used for both measurements but chamber water was exchanged between measurements. O_2 and chamber temperatures were recorded at 1-min intervals (YSI Pro-ODO, Yellow Springs, Ohio, USA). Incubations were terminated after O_2 changed by >1 mg/L or at 1.5 h (mean = 1.1 h, range = 0.3–1.7 h). Net ecosystem production and community respiration (mg $O_2 \cdot m^{-2} \cdot h^{-1}$) were calculated as

$$(\text{NEP}) \text{ or } (\text{CR}) = \Delta O_2 \times V \times S^{-1}$$

where ΔO_2 is the slope of the relationship between O_2 concentration and time (mg $O_2 \cdot L^{-1} \cdot h^{-1}$), V is chamber

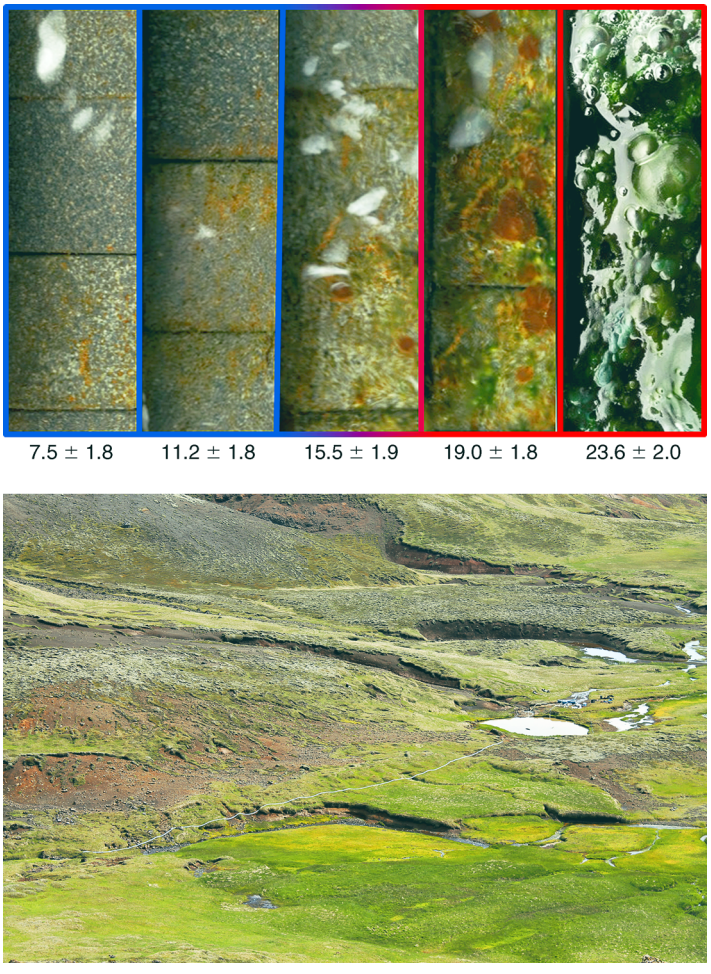

PLATE 1. (Top) Representative images of algal biomass in experimental stream channels 47 days post-deployment. The experimental temperature gradient was achieved by heating stream water from an unnamed tributary of the Hengladalsá River, Iceland (mean temperature = 7.5°C) using gravity-fed heat exchangers deployed in geothermal pools. Values represent mean temperature (±SD) in each treatment (n = 3 channels per temperature, divided into three blocks with the five temperatures randomized within each block) over the course of the experiment. (Bottom) Experimental stream channel study site in the Hengill region of Iceland. Photo credits: top, T. J. Williamson; bottom, Jackie Goldschmidt.

volume (L), and S is the active surface area of the tiles (m^2). Gross primary production (GPP) was calculated as GPP = NEP + CR (Bott 2006). We corrected for water-column metabolism by subtracting rates measured in blank chambers without tiles.

Tiles were scrubbed with a toothbrush following incubations and the resulting slurry was aggregated in 125 mL of water in amber bottles. A subsample was then filtered onto a pre-ashed, Whatman GF/F filter (Sigma-Aldrich, St. Louis, Missouri, USA), dried (55°C, ≥72 h), weighed and ashed at 500°C for 2 h and reweighed to determine biomass as ash-free dry mass (AFDM). Biomass accrual (mg AFDM·m^{-2}·d^{-1}) was calculated as the mean channel AFDM divided by the number of days incubated.

Nitrogen fixation

N_2-fixation rates were measured using acetylene reduction assays (Flett et al. 1976, Capone 1993) during 2-h midday incubations at 41 and 53 days post-deployment, using the sampling design and chambers described. Twenty mL of acetylene gas was injected directly into each chamber and mixed vigorously for 5 min prior to incubation. Gas samples were collected from each chamber at the beginning and end of the incubation. All gas samples, including field standards, were analyzed for ethylene concentration on an 8610 gas chromatograph (SRI Instruments, Torrance, California, USA) with a flame ionization detector (Hayesep T column, 80/100 mesh; Restek Corporation, Bellefonte, Pennsylvania, USA) within 48 h of collection. The rate of ethylene production in each chamber was calculated and a 3:1 N_2 : ethylene conversion ratio (Capone 1993) was used to estimate N_2-fixation rates.

Activation energies and statistical analysis

AEs were estimated for areal and mass-specific rates of GPP, CR, N_2 fixation, and biomass accrual using the Van't Hoff-Arrhenius relationship. We used linear least-squares regression to fit a relationship between ln-transformed process rates and $1/kT$ (R Core Team 2013). The AE is the absolute value of the slope; 95% confidence intervals were calculated with the confint function in the R package stats (R Core Team 2013). We tested for differences in AE among GPP, N_2 fixation, and CR, as well as between areal and mass-specific rates,

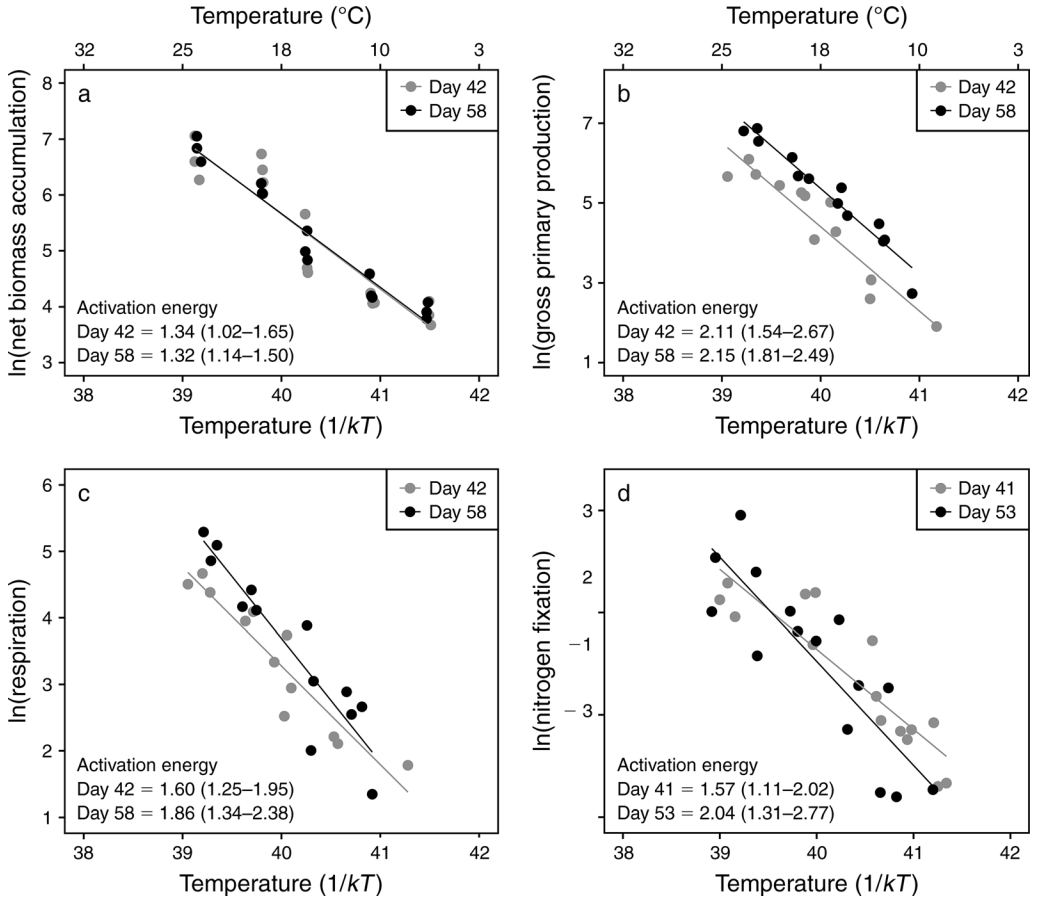

FIG. 1. Temperature dependence of (a) biomass (originally measured in mg ash-free dry mass (AFDM)·m^{-2}·d^{-1}), (b) gross primary production (originally measured in mg O_2·m^{-2}·h^{-1}), (c) community respiration (originally measured in mg O_2·m^{-2}·h^{-1}), and (d) N_2 fixation (originally measured in mg N·m^{-2}·h^{-1}) plotted as the relationship between ln-transformed biomass or areal rates and inverse temperature ($1/kT$), where k is the Boltzmann constant (8.61×10^{-5} eV/K; 1 eV = $\sim 1.6 \times 10^{-19}$ J) and T is temperature (K). The estimated activation energy (in eV) and 95% confidence intervals (in parentheses) are displayed for each measurement and sampling day when the slope differed significantly from zero ($\alpha = 0.10$). Lines were fit with least-squares regression.

using a linear model that predicted flux rate using $1/kT$ and the flux identity. A significant ($\alpha = 0.05$) interaction between $1/kT$ and the flux type indicated a significant difference among slopes. The mean channel temperature prior to the sampling day was used to calculate the AE of biomass accrual, while mean chamber incubation temperatures were used for the other flux measurements. Incubation temperatures during GPP, CR, and N_2-fixation measurements were strongly related to mean channel temperature prior to the sampling date ($°C_i = 4.04 + 0.81°C_c$; $R^2 = 0.92$, $P < 0.001$); however, incubation temperatures were slightly warmer because incubations generally occurred near maximum daily temperature (Appendix: Fig. A5).

To assess whether temperature or biomass best predicted ecosystem flux rates, we first compared the AEs of mass-specific and areal GPP and CR to canonical expectations. Second, we used repeated-measures mixed-effects models (lme function in the R package nlme [Pinheiro et al. 2014]; fixed effects of sampling day and either $1/kT$ or ln[biomass], the random intercept was channel ID, the random slope was sampling day) and compared the resulting AIC_c scores (Burnham and Anderson 2002) to identify whether temperature ($1/kT$) or biomass (ln-transformed AFDM) best predicted ln(areal GPP) and ln(CR). Tests for multicollinearity indicated a strong correlation between temperature and biomass (e.g., for areal GPP: $R^2 = 0.79$, $P < 0.001$); thus, we used a model selection approach to examine models containing only one of these terms.

RESULTS

Our temperature manipulations were effective and relatively consistent throughout the experiment (Appendix: Table A1 and Fig. A5). The daily ranges of temperature were similar both among treatments (Appendix: Table A1) and to those observed in nearby streams (W. F. Cross and J. P. Benstead, *unpublished data*). Biofilm mass accrual was strongly and positively related to temperature, varying on average ~18-fold over the 17°C range in mean temperature (Fig. 1a and Table 1; see Plate 1). Areal rates of GPP, CR, and N_2

TABLE 1. Estimates of the intercept, slope, P value, and R^2 from least-squares regression of the relationship between several ln-transformed measures (units) and $1/kT$.

Measure and day	Intercept	Slope	P	R^2
Areal rates				
Biofilm mass accrual (mg AFDM·m^{-2}·d^{-1})				
42	59.1 (5.91)	−1.34 (0.15)	<0.001	0.86
58	58.28 (3.36)	−1.32 (0.08)	<0.001	0.95
Gross primary production (mg O_2·m^{-2}·h^{-1})				
42	88.68 (10.09)	−2.11 (0.25)	<0.001	0.87
58	91.26 (6.15)	−2.15 (0.15)	<0.001	0.95
Respiration (mg O_2·m^{-2}·h^{-1})				
42	67.24 (6.39)	−1.60 (0.16)	<0.001	0.90
58	78.17 (9.44)	−1.86 (0.24)	<0.001	0.85
N_2 fixation (mg N·m^{-2}·h^{-1})				
41	62.89 (8.52)	−1.57 (0.21)	<0.001	0.81
53	81.57 (13.55)	−2.04 (0.34)	<0.001	0.74
Mass-specific rates				
Gross primary production (mg O_2·[mg AFDM]$^{-1}$·h^{-1})				
42	14.00 (9.05)	−0.47 (0.23)	0.065	0.30
58	6.70 (7.12)	−0.27 (0.18)	0.065	0.18
Respiration (mg O_2·[mg AFDM]$^{-1}$·h^{-1})				
42	−3.3 (7.06)	−0.07 (0.18)	0.712	0.01
58	−0.88 (8.33)	−0.13 (0.21)	0.555	0.03
N_2-fixation (mg N·[mg AFDM]$^{-1}$·h^{-1})				
41	46.81 (16.3)	−1.39 (0.4)	0.004	0.48
53	56.47 (22.04)	−1.64 (0.55)	0.011	0.41

Note: The apparent activation energy for each measure is the product of −1 and the slope. AFDM stands for ash-free dry mass. Standard error is given in parentheses for intercept and slope. In $1/kT$, k is the Boltzmann constant (8.61×10^{-5} eV/K; 1 eV = ~1.6×10^{-19} J) and T is temperature (K).

fixation were also strongly and positively related to temperature. Areal rates of GPP varied on average 53-fold across the treatments on both measurement dates, while areal rates of CR and N_2 fixation varied on average 32- and 71-fold, respectively. On both measurement dates, apparent AEs for the different flux rates (i.e., areal GPP, CR, and N_2 fixation) were statistically indistinguishable ($P > 0.2$). Mean apparent AEs for areal GPP and CR were 6.5- and 2.7-fold higher than values predicted by the MTE on both measurement days (Fig. 1 and Table 1). In contrast, the AE of areal N_2-fixation rates, although more variable across measurements, was similar to expectations (Fig. 1d and Table 1), based on the AE of nitrogenase when isolated in the laboratory (2.18 eV below 22°C; Ceuterick et al. 1978).

In contrast to areal rates, the AEs of mass-specific rates differed among flux types ($P < 0.05$). Mass-specific GPP varied 3.8-fold across the thermal gradient and showed a relatively weak positive relationship ($P = 0.065$) with temperature (Fig. 2a and Table 1). The apparent AE of mass-specific GPP approached canonical expectations (i.e., 0.32 eV; Fig. 1a, Table 1) and was much lower than that of areal GPP (both dates: $P < 0.001$). Mass-specific CR rates were not related to temperature (Fig. 2b) and strongly differed from those of areal CR (both dates: $P < 0.001$). Mass-specific N_2-fixation rates increased ~36-fold over the 17°C range and showed mean apparent AEs (i.e., 1.39 eV at day 41 and 1.64 eV at day 53) that were similar to AEs for areal N_2-fixation rates (both dates: $P > 0.05$). Models that contained temperature, rather than biomass, best predicted both areal GPP (temperature model $AIC_c = 38.9$, biomass model $AIC_c = 41.8$), and areal CR (temperature model $AIC_c = 38.7$, biomass model $AIC_c = 47.1$); however, models predicting ecosystem flux rates using only biomass still performed exceptionally well (Appendix: Table A2).

DISCUSSION

Our experiment revealed several patterns in the relationships between temperature and the development and metabolic activity of stream biofilms. Chief among these was the frequent divergence of apparent areal AEs from their expected canonical values. In our study, amplification of the apparent AEs for biomass accrual, and areal GPP and CR, was associated with the dominance of N_2 fixers, a key functional group, which developed across the temperature gradient (>90% of total biomass in all treatments was comprised of N_2 fixers; Williamson 2014). This can be explained by the high canonical AE of N_2 fixation compared with GPP and CR, which results in substantive increases in N supply and, therefore, metabolic activity associated with reduced N limitation of GPP and biomass accrual along the temperature gradient. Although such amplification has been described in terrestrial systems, typically in the context of soil carbon decomposition (Davidson and Janssens 2006, Yvon-Durocher et al. 2012) or forest

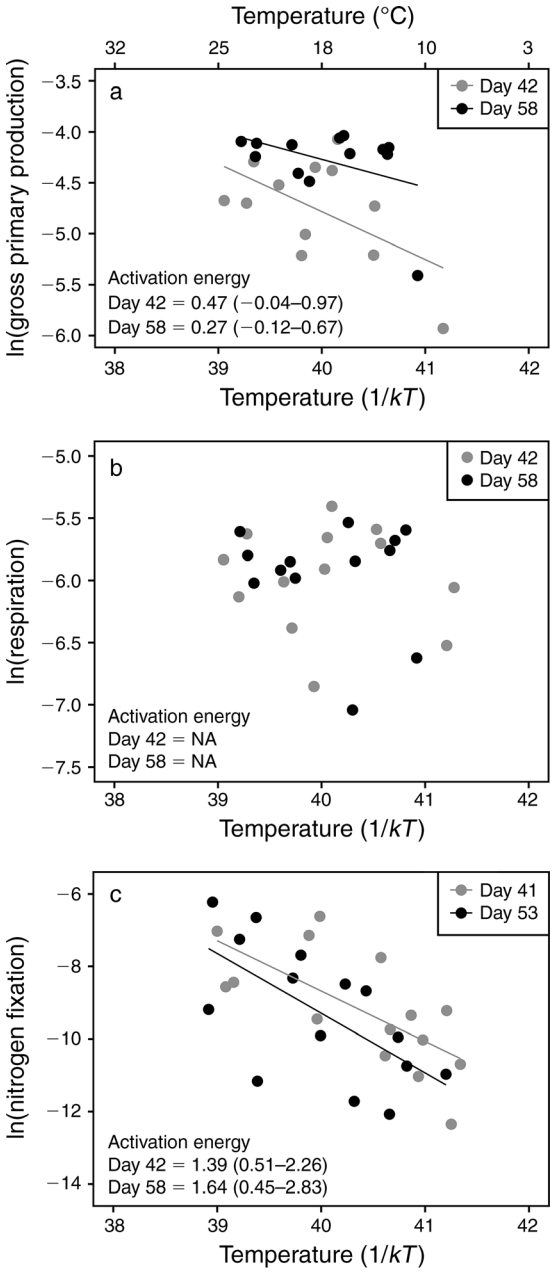

FIG. 2. The temperature dependence of mass-specific rates of (a) gross primary production (originally measured in mg O_2·[mg AFDM]$^{-1}$·h^{-1}), (b) community respiration (originally measured in mg O_2·[mg AFDM]$^{-1}$·h^{-1}), and (c) N_2 fixation (originally measured in mg N·[mg AFDM]$^{-1}$·h^{-1}) plotted as the relationship between ln-transformed rates and inverse temperature ($1/kT$). The estimated activation energy and 95% confidence intervals (in parentheses) are displayed for each measurement and sampling day when the slope differed significantly from zero ($\alpha = 0.10$). Lines were fit with least-squares regression. Mass-specific respiration rates were not related to temperature.

primary succession (Anderson-Teixeira et al. 2008), our study highlights the potential for N_2 fixation to also amplify the temperature dependence of ecosystem processes.

Our hypothesis that amplified AEs of areal GPP and CR are driven by increased N supply is supported by the patterns in N_2 fixation measured in our experiment. Areal N_2 fixation rates exhibited an AE that was close to expectations for the nitrogenase enzyme (i.e., 2.18 eV below 22°C, 0.65 eV above 22°C; Ceuterick et al. 1978), while the temperature dependences of GPP and CR were much higher than canonical values (i.e., AE for areal GPP = 2.11–2.15 eV vs. canonical value of 0.32 eV; AE for CR = 1.60–1.86 eV vs. canonical value of 0.60–0.70 eV; Allen et al. 2005). Importantly, the apparent AEs of areal GPP and CR paralleled the AE of N_2 fixation, suggesting the observed amplification of GPP and CR was driven by a new source of N supplied by elevated rates of N_2 fixation at warm temperatures. This interpretation is consistent with a growing body of literature demonstrating that temperature dependences of resource supply rates can influence the response of ecosystem processes to warming (Anderson-Teixeira et al. 2008, Yvon-Durocher et al. 2012). In essence, the AE of the supply rate of the limiting resource should dictate the apparent AEs of GPP and CR. Thus, in N-poor environments, we might expect significant amplification of ecosystem metabolism in response to warming when N_2 fixers dominate.

The amplified temperature dependences observed in our study could result from two different, non-mutually exclusive mechanisms. First, temperature could directly influence subcellular rates of N_2 fixation, resulting in higher N supply and subsequent increases in rates of photosynthesis and cellular respiration on a per-cell basis (e.g., Rhee and Gotham 1981, Robarts and Zohary 1987). Such a response should be reflected in amplified AEs of mass-specific rates of GPP and CR. Second, increased temperature and N supply (via N_2 fixation) could amplify rates of biomass accrual, based simply on the addition of more metabolically active cells per area. While the strong correlation between temperature and biomass observed in our study ($R^2 = 0.79$, $P < 0.001$) precludes us from clearly distinguishing these direct (subcellular reactions) and indirect (biomass accrual) effects, the strongly amplified AEs of areal GPP and CR vs. the AEs of mass-specific rates, which encompassed canonical expectations (e.g., AE for mass-specific GPP: 0.27–0.47 eV), suggest that biomass accrual was a key driver of the amplified response. Such indirect effects of temperature have been largely underappreciated but may help explain why temperature per se may not directly predict large-scale patterns of primary production (e.g., Michaletz et al. 2014).

It is possible that amplified temperature dependence of biomass accrual alone can lead to higher ecosystem-level AEs for metabolism, but results from previous studies are mixed. For instance, Anderson-Teixeira et al. (2008) showed that amplified temperature dependence of forest primary succession resulted, in part, from positive effects of warming on accrual and storage of soil and leaf biomass. In contrast, Yvon-Durocher et al. (2010, 2011) demonstrated that warming actually reduced storage of photosynthetic biomass in experimental ponds, while

biomass accrual (as net primary production) roughly followed MTE predictions (AE = 0.41 eV). Such discrepancies may be explained by how temperature influences the supply rate of limiting nutrients or reactants, as well as how nutrients are utilized and stored (e.g., assimilation and cell stoichiometry), or transformed (e.g., dissimilatory processes) as they become available. Our study indicates that warming may elevate N_2 fixation in aquatic systems and alleviate N limitation of biomass accrual, leading to amplified temperature dependence of metabolism in stream biofilms. However, whether or not this amplification also occurs at the whole-stream scale depends on the total flux and fate of N introduced to the ecosystem from N_2 fixation. Interestingly, previous measurements of whole-stream metabolism across a natural thermal gradient in the Hengill area (Demars et al. 2011) showed that AEs of GPP and ER were not amplified, but relatively close to MTE predictions, suggesting that the temperature-dependent N supplement to the biofilm is either not sufficient to amplify metabolism at the ecosystem scale or is unaccounted for in whole-stream metabolism as a result of increases in N loss via denitrification, downstream export, or transfer to the terrestrial environment.

In contrast to patterns in areal fluxes, the AEs of mass-specific flux rates were often near or lower than predictions based on MTE. We attribute these results to the differential rate of biofilm accrual across the experimental temperature gradient and its effect on biofilm thickness and associated shifts in cell physiology. The negative effect of biofilm thickness on mass-specific process rates is well documented, with potential mechanisms including self-shading and limitation by nutrients or inorganic carbon supply (Lamberti and Resh 1983). Such limitation would have become progressively more severe with warming in our experiment, as cells deep in the biofilm experienced reduced access to resources, including light. The suppression of temperature dependence due to resource limitation of cell activity in the higher temperature treatments, where biofilm biomass was high, is consistent with our hypothesis of amplified temperature dependences of areal rates being driven by increased N supply.

Although anthropogenic N inputs have significantly altered N cycling on a global scale (Galloway et al. 2008), the supply of N, in addition to phosphorus, can still limit productivity in terrestrial, marine, and freshwater ecosystems worldwide (Smith et al. 1999, Elser et al. 2007, LeBauer and Treseder 2008). Thus, amplified responses of ecosystem metabolism to warming, in response to increased N_2 fixation, could conceivably be widespread. The ability to scale up or otherwise extrapolate the results of our experiment to different systems is difficult, however, because despite the high AE of nitrogenase activity (Ceuterick et al. 1978), empirical estimates of the AE of N_2 fixation are quite variable (e.g., Brouzes and Knowles 1973, Kashyap et al. 1991), potentially due to intrinsic factors such as temperature-dependent resource limitation of N_2 fixation itself (e.g., by phosphorus, iron, or molybdenum). Nevertheless, amplified responses of ecosystem metabolism to warming may be significant worldwide, but particularly within the acutely nutrient-limited ecosystems of the Arctic and sub-Arctic, where warming is expected to be most severe (e.g., Slavik et al. 2004, Weintraub and Schimel 2005).

Acknowledgments

This study was funded by the National Science Foundation (DEB-0949774 and DEB-0949726) and additional support from St. Catherine University to J. R. Welter. We thank Chau Tran for assisting in the construction of the heat exchangers, and undergraduate students Aimee Ahles, Jackie Goldschmidt, and Ellie Zignego for their collaboration in the development of methods and assistance with all field and laboratory work associated with this project. We also thank Jón Ólafsson, Gísli Már Gíslason, and the scientists and staff at the Institute of Freshwater Fisheries in Iceland for their knowledge, support, and laboratory facilities that made this work possible.

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Supplemental Material

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-1667.1.sm

Reports