

**Working Group Report – Post-ASM (2006)**  
**Metabolic Theory of Ecology and Stream Ecosystems**

**TITLE:** Metabolic Theory of Ecology and Stream Ecosystems

**FOLLOW-UP MEETING ORGANIZERS:** Jennifer Follstad Shah, Emily Bernhardt, Alex Huryn

**MEETING DATES:** May 2007 (meeting 1), summer 2008 (meeting 2)

**LOCATION:** Sevilleta LTER Biological Field Station, New Mexico

**PARTICIPANTS PRESENT AT MEETING 1 (LTER site, affiliation):** Faculty - Alex Huryn (ARC, Univ. of Alabama), Emily Bernhardt (CWT, Duke), James Brown (Univ. of New Mexico), Maury Valett (CWT, Virginia Tech), Pat Mulholland (CWT, Oak Ridge National Lab), Bob Sinsabaugh (SEV, Univ. of New Mexico), Bob Hall (Univ. of Wyoming), Bob Sterner (Univ. of Minnesota); Postdocs - Jennifer Follstad Shah (SEV, Duke), Brian Roberts (Oak Ridge National Lab<sup>1</sup>), Krista Anderson (SEV, Univ. of New Mexico), Jim Hood (Univ. of Minnesota); Graduate student - Jordan Okie (Univ. of New Mexico)

**BACKGROUND:** The recently formalized Metabolic Theory of Ecology (MTE) predicts how metabolic rate controls ecological processes at all scales (Brown et al. 2004). The MTE integrates first principles of thermodynamics, chemical kinetics, and physics to describe how metabolic processes are some function of body mass ( $M$ ), temperature ( $T$ ; in K), and the resource supply ( $R$ ) needed to fuel metabolism ( $Y$ ):

$$Y = Y_0 M^b e^{-E/kT} f(R) \quad (1)$$

where  $Y_0$  is a normalization constant,  $b$  is an allometric exponent,  $E$  is the average activation energy of metabolism, and  $k$  is Boltzmann's constant ( $8.62 \cdot 10^{-5}$  eV  $K^{-1}$ ). The MTE thus provides (1) a mechanistic model for understanding the complexity in nature and (2) testable predictions for a wide range of phenomena (including those related to core LTER research areas, such as population dynamics, primary production, and organic and inorganic matter processing). Though powerful, the MTE has limitations that constrain its application to ecological processes across ecosystems or landscapes. For example, the theory lacks a term that describes how resources (carbon, nitrogen, phosphorus, light) influence metabolic rate (Marquet et al. 2004). Also, most empirical tests of the MTE to date have used data from terrestrial ecosystems and often have mixed data from independent communities.

Analyses presented at the LTER 2006 ASM *Metabolic Theory of Ecology and Stream Ecosystems* working group were among the first to test MTE predictions using data from stream ecosystems. We found that scaling exponents describing the relationship between production:biomass ratios and body mass for macroinvertebrates within three temperate stream communities were consistent with predicted 1/4-power scaling relationships (Huryn and Benke 2007). However, residual variation of observed patterns was attributed to community-level differences in taxonomy and life history. We also found that the slope of the relationship between whole-stream respiration ( $g\ C\ m^{-2}\ d^{-1}$ ) and temperature ( $1/kT$ , where  $k$  is the Boltzmann constant and  $T$  is temperature in K) across 15 studies in North America, Europe, and New Zealand was indistinguishable from that predicted by the MTE (-0.6 to -0.7). However, the slope of this relationship was positive rather than negative for data collected seasonally over two years within a single heterotrophic stream, indicating that whole-stream metabolism was greatest in fall and winter likely due to carbon inputs associated with leaf fall from adjacent forests. This result highlighted the need to better understand how resources interact with body mass and temperature to influence rates of metabolism across ecological scales. The follow-up working group proposed to synthesize numerous datasets to (1) more fully test the MTE and (2) incorporate resource supply into the MTE.

**FOLLOW-UP MEETING GOALS & SCOPE OF WORK:** Primary goals of the follow-up working group included: (1) identification and synthesis of datasets from LTER and non-LTER sites; (2) tests of MTE predictions using these datasets; and (3) determination of how variation in resource supply may best be expressed as part of the MTE.

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Several questions were posed at the first working group meeting:

1. How do gradients or temporal fluctuations in resource supply alter scaling relationships between mass and metabolic rate or mass and population abundance? Are effects consistent across resource types?
2. Is resource supply temperature-dependent? If so, under which conditions?
3. How does taxonomic variation (e.g., trophic position, homeostatic regulation, up-regulation of N- or P- rich molecules, luxury consumption) alter mass- and temperature-dependent scaling relationships?
4. Does metabolic theory work in heterotrophic streams systems, in which carbon resources are donor-controlled (i.e., from adjacent forests) and occur in pulses during cooler temperatures?
5. Does metabolic theory work in non-equilibrium systems?

Many of these questions were addressed at the first working group meeting through analyses conducted on four focus areas:

1. Bacterial production in the Ottawa, Maumee, and Hudson rivers
2. Stream macroinvertebrate secondary production and the Energy Equivalence Rule (EER)
3. Temperature-dependence of stream macroinvertebrate secondary production
4. Whole-stream rates of production and respiration

Results for each focus area are described below, in addition to research efforts being conducted between working group meetings. The objectives of the second working group meeting are to (1) review results of each focus area, (2) finalize manuscript drafts, and (3) draft an outline for a research proposal for future LTER cross-site aquatic studies focused on MTE-related research questions that cannot be addressed using existing datasets.

**RESULTS:**

*Focus area #1: Bacterial production in the Ottawa, Maumee, and Hudson rivers*

We re-examined data on annual cycles of bacterial production in the Ottawa, Maumee, and Hudson rivers. The data were originally reported in Sinsabaugh et al. (1997). We employed the MTE to isolate the effect of temperature on the activities of six extracellular enzymes (acetyl esterase, endopeptidase, leucyl aminopeptidase, alkaline phosphatase, alpha and beta glucosidase) used by riverine bacteria to obtain resources. We transformed enzyme activities measured in the lab at a standardized temperature (20 °C) to activity rates for ambient stream temperatures using the mean of enzyme activation energies (0.5 eV) that have been reported in scientific literature. We then applied a modified Michaelis-Menten function to the transformed data to calculate a turnover rate ( $h^{-1}$ ) for each enzymatic substrate pool as

$${}^{App}V_{max} / 2 \cdot {}^{App}K_m \quad (2)$$

where  ${}^{App}V_{max}$  is the maximum enzymatic activity rate, or catalytic capacity, and  ${}^{App}K_m$  is the half saturation constant.  ${}^{App}V_{max}$  is a measure of the rate of resource consumption by riverine bacteria, while  ${}^{App}K_m$  is a measure of resource supply in the environment. The superscript “App” stands for “apparent”, since true measures of  $V_{max}$  and  $K_m$  are possible only under controlled lab settings. Equation 2 represents the affinity of an organism for a resource substrate.

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We found that bacterial production was not correlated with resource supply ( $^{App}K_m$ ), but significant correlations existed between maximum enzymatic activity ( $^{App}V_{max}$ ) and bacterial production, especially for glucosidase activity (a measure of C use).  $^{App}V_{max}$  and  $^{App}K_m$  did not correlate within resources pools (i.e., for individual enzymes), but were well correlated ( $r^2 = 0.53$ ) across multiple resource pools over annual time scales (Fig.1). The slope of the regression was  $<1$ , indicating enzyme supply tends to trail increases in the size of substrate pools.

Organisms consume multiple resources simultaneously, which presents a challenge for integrating resource supply into the MTE. **A key finding of our research was the realization that utilization of multiple resources can be integrated using the turnover rate ( $^{App}V_{max}/2^{App}K_m$ ) as a common metric, which normalizes enzyme activities that vary over many orders of magnitude (Fig. 2).** Turnover rates summed across all six extracellular enzymes were significantly correlated with bacterial production ( $r^2 = 0.56$ ,  $n = 39$ ,  $F = 47$ ,  $p < 0.0001$ ), indicating a good relationship between total consumption of resources and bacterial production.

We are now using these relationships to explore seasonal patterns in bacterial resource use. **Our objectives are to determine (1) whether resource supply is dependent on temperature and (2) if there are critical temperature thresholds at which bacteria switch from predominantly using one resource over another.**

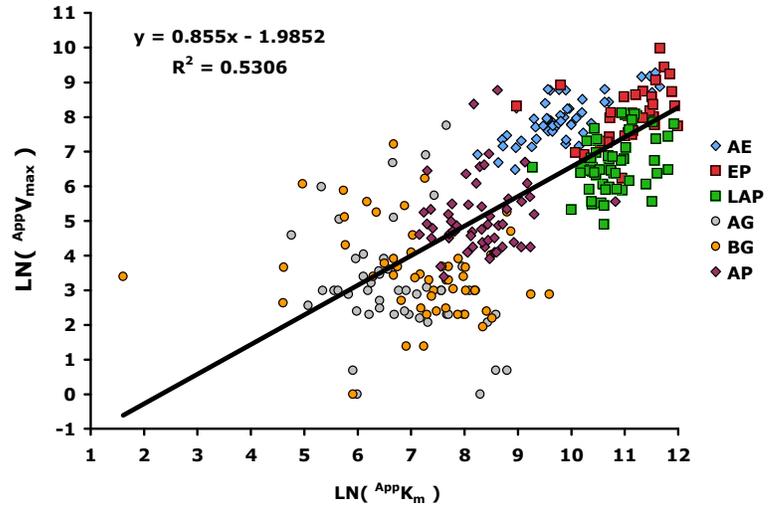


Figure 1. Across resource pools,  $^{App}V_{max}$  ( $\text{nmol h}^{-1} \text{L}^{-1}$ ), a measure of catalytic capacity, scales with  $^{App}K_m$  ( $\text{nM}$ ), a measure of substrate concentration. Enzyme abbreviations are as follows: AE = Acetyl-esterase, EP = Endoprotease “trypsin”, LAP = Leucyl-aminopeptidase, AG =  $\alpha$ -1,4-glucosidase, BG =  $\beta$ -1,4-glucosidase, AP = Alkaline phosphatase. Regression statistics:  $n = 317$ ,  $F = 338$ , slope  $SE = 0.047$ , slope 95% CI = 0.765 - 0.949.

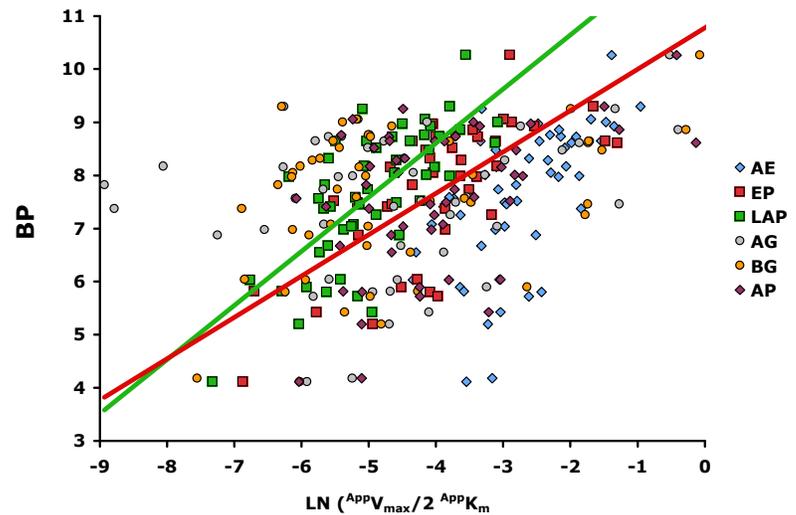


Figure 2. Bacterial production (BP,  $\text{nmol h}^{-1} \text{L}^{-1}$ ) in relation to resource supply ( $\text{h}^{-1}$ ), expressed as  $^{App}V_{max}/2^{App}K_m$ , for substrate pools linked to the activity of 6 extracellular enzymes. Enzyme abbreviations are given in Figure 1. Trend lines are shown for the two proteolytic enzymes, LAP (green) and EP (red), which have the strongest relationship with bacterial production (data not shown). There was a strong correlation across data points ( $r^2 = 0.56$ ,  $n = 39$ ,  $F = 47$ ,  $p < 0.0001$ ).

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*Focus area #2: Stream macroinvertebrate secondary production*

The flux, storage, and turnover of biologically controlled pools of resources in ecosystems are controlled by the sum of the metabolic processes of the constituent organisms (Enquist et al. 2003, Allen et al. 2005). The MTE purports that these processes scale predictably with body mass and temperature. Under steady state conditions, the metabolic rate of organisms has been shown to scale as a  $3/4$ -power of body size (Gillooly et al. 2001), while abundance ( $N$ ) has been shown to scale as a  $-3/4$ -power function of body size ( $N \propto M^{-3/4}$ ) (Damuth 1981, Enquist et al. 1998). Production across populations or assemblages is thus predicted to be mass-invariant, indicating that individuals of all size classes within an ecosystem share equally in resource supply (Damuth 1981, Enquist and Niklas 2001, Ernest et al. 2003). This phenomenon is known as the Energy Equivalence Rule (EER).

Data on secondary production of macroinvertebrates for three of the four streams presented in Huryn and Benke (2007) provided support for the EER. We have begun to test the EER for functional feeding groups within individual stream communities and across a multitude of stream ecosystems. We have chosen to focus on functional feeding groups within streams because they represent differences amongst macroinvertebrates in trophic position (and thus resource supply). We can better explore and understand the interaction of resource supply or resource use with body size and temperature should some functional feeding groups consistently deviate from MTE predictions.

**Across 7 streams (2 from LTER sites) and functional groups, we found a slope of 0.02, which supports the EER (Fig. 3a). However, the slope of this relationship varied across functional feeding groups.** We found support for the EER from data on filter feeders (slope = -0.04) and scrapers (slope = -0.02), while slopes ranged from -0.55 to 0.36 for collector-gatherers, shredders, and predators (Fig. 3a). Filter feeders consume periphyton or fine particulate organic matter (e.g., pieces of leaves) suspended in the water column, while scrapers feed on periphyton attached to submerged surfaces. Collector-gatherers also consume fine particulate organic matter, while shredders consume coarse particulate organic matter (e.g., leaves, twigs). Predators feed on other macroinvertebrates. We thus concluded that **support for the EER within the macroinvertebrate community is strongest for primary consumers vs. secondary consumers or detritivores.**

Carbon supply in streams is often dominated by allochthonous sources, rather than from in-stream primary production. Thus, highly heterotrophic streams are not at steady state, which is an assumption of the MTE. Deviation from steady state conditions may partially explain why the EER is not supported by data for detritivores, an effect that could cascade up the trophic ladder to predators. Alternatively, the lack of large variation in body size within a functional feeding group or the presence of only a few representatives in small or large body size categories for some feeding groups also may explain variation in slopes.

We found interesting and opposing patterns when we compared data on secondary production for shredders and predators within two streams – Upper Ball Creek, NC (Coweeta LTER) and East Bear Brook, ME (Fig. 3b). Slopes for the log-log relationship between mass and production were positive in Ball Creek for predators, shredders, and across both groups. In contrast, slopes were negative within and across functional feeding groups in East Bear Brook. Thus, **we did not find support for the EER within individual stream ecosystems. We are currently exploring whether differences in hydrology, resource supply, or trophic structure can explain the observed patterns.**

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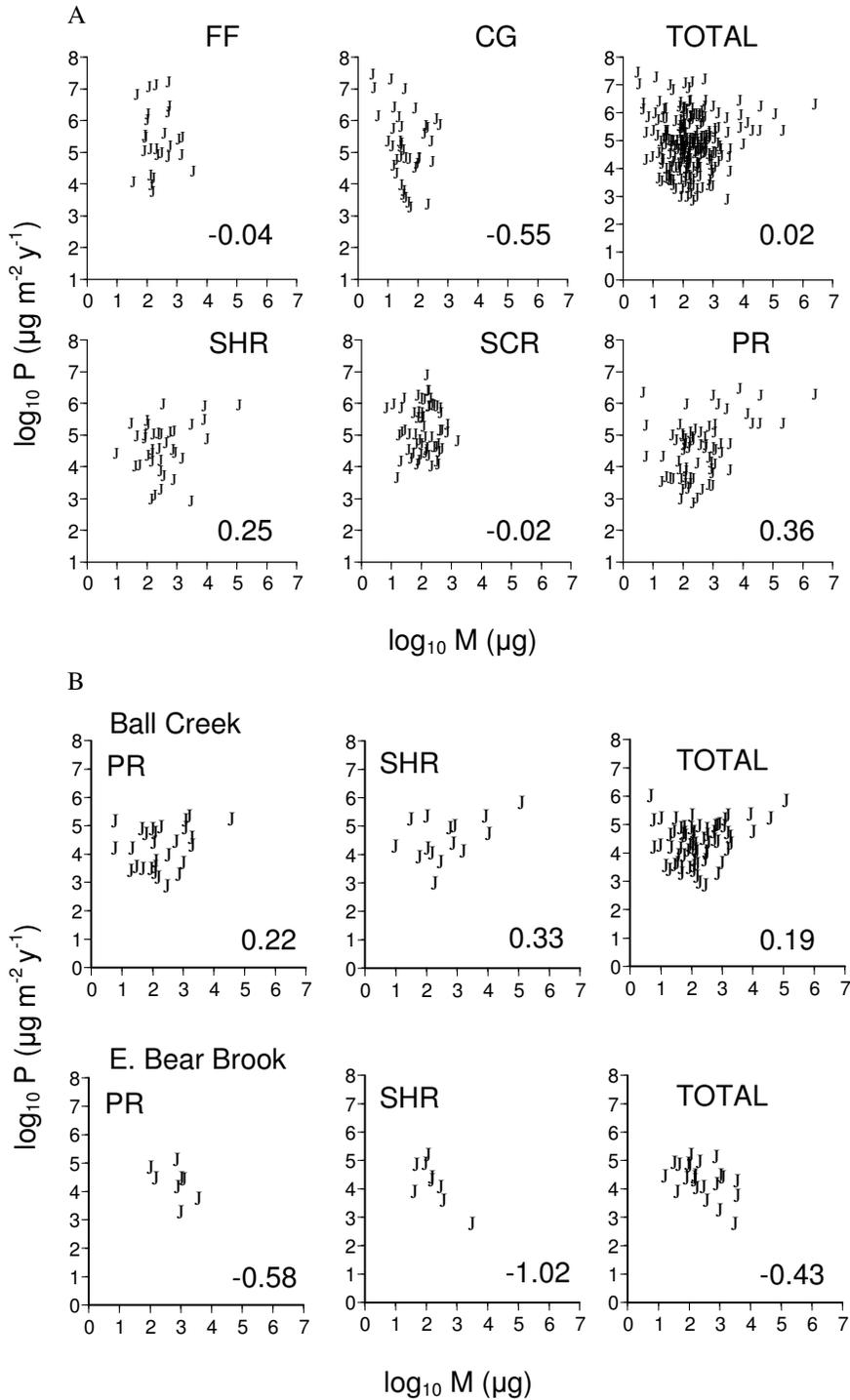


Figure 3. Scaling relationships between mass, denoted as  $M$  ( $\mu\text{g}$ ), and production, denoted as  $P$  ( $\mu\text{g m}^{-2}\text{y}^{-1}$ ) for functional feeding groups across 7 streams (USA: Ogeechee River, GA, Ball Creek, NC, East Bear Brook, ME; Venezuela: Rio Las Marias; New Zealand: Sutton Stream and Stony Creek) (a) and within 2 streams: Ball Creek, NC, USA and East Bear Brook, ME, USA (b). Functional feeding group acronyms: FF = filter feeder, CG = collector-gatherer, SHR = shredder, SCR = scraper, PR = predator. Values in the lower right corner of each graph represent the slope of each least squares regression, which was predicted to be 0.

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*Focus area#3: Temperature-dependence of stream macroinvertebrate secondary production*

Individual-level metabolic rate has been shown to have a temperature dependence that reflects the activation energy of ATP synthesis, 0.65 eV (Gillooly et al. 2001). Broad geographic patterns in abundance have been predicted to have a temperature dependence that is the inverse of the temperature dependence of metabolism, -0.65 eV (Savage et al. 2004). Thus, production across populations or assemblages ought to be temperature-invariant (i.e., 0 eV), as well as mass-invariant.

Dr. Robert Hall of the University of Wyoming has found support for temperature invariance of secondary production across macroinvertebrate assemblages from 32 streams (3 from LTER sites; *personal communication*). His study is the first to test the prediction that production is temperature-invariant. **We are now testing whether the pattern of temperature-invariance for secondary production holds within individual stream macroinvertebrate communities and across functional feeding groups both within and across streams.**

*Focus area #4: Whole-stream rates of production and respiration*

Whole-stream metabolism is the measure of the diel changes in oxygen concentrations within a stream ecosystem. Oxygen produced during daylight hours is a measure of net primary production, while oxygen consumed at night is a measure of autotrophic plus heterotrophic respiration. The activation energy of primary production differs from that of autotrophic or heterotrophic respiration. Respiration has a temperature dependence that reflects the activation energy of ATP synthesis, 0.65 eV (Gillooly et al. 2001). In contrast, individual-level photosynthetic rate has an activation energy that reflects the activation energy of Rubisco carboxylation in C<sub>3</sub> photosynthesis, 0.32 eV (Allen et al. 2005). Autotrophs also differ from heterotrophs because the abundance of autotrophs (e.g., trees) does not vary across latitudes (a proxy for temperature) (Enquist and Niklas 2001). The lack of temperature dependence for autotroph abundance has been attributed to light as a limiting factor for photosynthesis. As a result, scaling relationships for night-time carbon flux from forest canopies are not temperature-invariant, but rather reflect the activation energy of autotrophic respiration, 0.65 eV (Enquist et al. 2003). This pattern has been found within and across forests spanning several biomes. Similarly, net primary production of forests as a function of temperature has been shown to reflect the activation energy of photosynthesis, 0.32 eV (Allen et al. 2005).

These studies suggest rates of production within stream ecosystems should have an activation energy of 0.32 eV. This pattern also should hold across stream ecosystems, if the abundance of stream autotrophs does not vary across streams that do vary with respect to temperature.

Whole-stream respiration within individual streams is predicted to have an activation energy of 0.65 eV, which is the activation energy for both autotrophic and heterotrophic respiration. Predicting the temperature-dependence of whole-stream respiration across stream ecosystems is complicated by the fact that scaling relationships between temperature and abundance, which are evident only across geographic gradients, potentially differ for autotrophs and heterotrophs. If the temperature-dependence of abundance is the inverse of the temperature-dependence of respiration for both autotrophs and heterotrophs, then whole-stream respiration should be temperature-invariant across stream ecosystems. As mentioned, temperature-invariance of abundance has been found across macroinvertebrate assemblages for 32 streams. However, further research is needed to determine the relationship between abundance and temperature for stream primary producers. If the scaling relationships between abundance and temperature do indeed vary for stream autotrophs and heterotrophs, tests of whole-stream respiration ought to be conducted separately for streams characterized as either highly autotrophic or heterotrophic. Whole-stream respiration within autotrophic streams should then have an activation energy of 0.65 eV. In contrast, whole-stream respiration within heterotrophic streams should depict temperature-invariance.

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We are using three datasets on whole-stream metabolism to test these predictions: (1) Lotic Intersite Nitrogen eXperiment (LINX) II, (2) Nitrogen Partitioning and Retention in Streams (NPARS), and (3) West Fork of Walker Branch, Oak Ridge National Lab, TN, USA. The LINX dataset includes data for 27 streams (all within or near LTER sites) in which whole-stream metabolism was measured on a single occasion. The NPARS dataset includes seasonal measures of whole-stream metabolism for six streams (2 from LTER sites) in three regions of the US. The Walker Branch dataset includes continuous measures of whole-stream metabolism over two years for a single site. We converted all measures of production and respiration from units of oxygen to units of carbon, using published conversion factors (Bott 2007). Conversions were conducted to reflect the energetic basis of metabolism.

Before we tested MTE predictions, we explored whether whole-stream primary production, a process limited by light availability, was correlated with photosynthetically active radiation (PAR). Primary production and PAR were not well correlated for the LINX II and NPARS datasets, but there was a strong linear fit between the two variables for the Walker Branch dataset. Thus, we normalized production data in Walker Branch by PAR before regressing it against temperature. (For brevity, the results reported below omit analyses conducted with LINX II data, which were similar to NPARS data.) Recently, a modified Michaelis-Menten model has been used to incorporate the effects of light on primary production within the context of MTE (Lopez-Urrutia et al. 2006). We found that Michaelis-Menten kinetics were not an appropriate fit for modeling the effects of light on production for any of our datasets.

The activation energy of primary production was steeper than predicted (0.32 eV) for both the NPARS and Walker Branch datasets. However, the activation energies for both datasets were similar (0.51 and 0.55 eV, respectively; Fig 4a and 4b). The 95% CI included the predicted slope for NPARS data, but not for Walker Branch data. However, the regression for NPARS data explained little variation and was not significant. Thus, **we found little support for MTE predicted scaling relationships between temperature and primary production within stream ecosystems.**

We found that the activation energy of whole-stream respiration was steeper than predicted (0 eV) for NPARS data (0.25 eV; Fig. 5a). Although the 95% CI comes close to including the predicted slope, the regression explained little variation and was not significant.

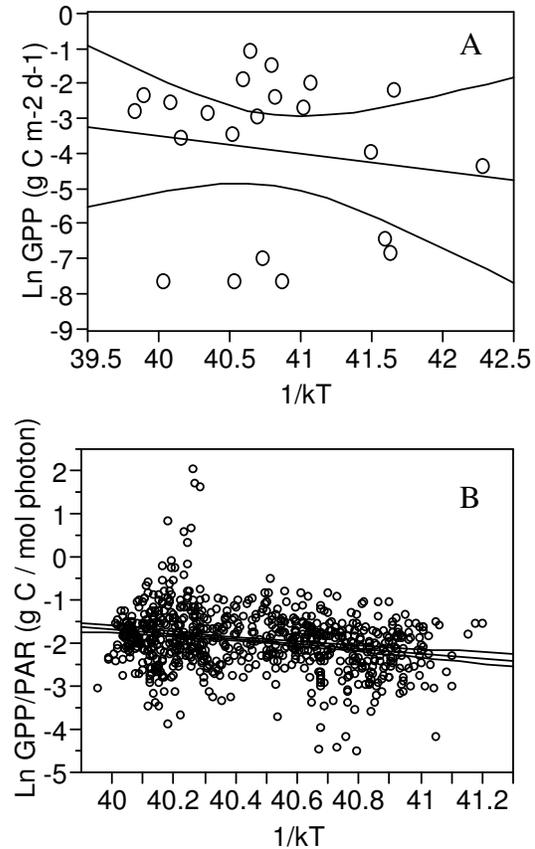


Figure 4. Temperature-dependence of whole-stream production (GPP) for (a) NPARS data ( $GPP = 16.91 e^{-0.51/kT}$ , 95% CI: -1.63 to 0.22,  $n = 22$ ,  $r^2 = 0.02$ ,  $p = 0.52$ ); and (b) Walker Branch data in 2004-2005 ( $GPP/PAR = 20.36 e^{-0.55/kT}$ , 95% CI: -0.63 to -0.47,  $n = 730$ ,  $r^2 = 0.06$ ,  $p < 0.001$ ). The predicted slopes for NPARS and Walker Branch data were -0.32. Dashed lines around the regression represent the 95% CI. Walker Branch data were normalized by photosynthetically active radiation (PAR; mol photon m<sup>-2</sup> d<sup>-1</sup>) prior to analysis. The x-axis represents warm to cool temperatures going from left to right.

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We also predicted that the slope of the relationship between temperature and the whole-stream respiration within streams would have a slope of -0.65, reflecting the activation energy of ATP synthesis. **The direction of the relationship between whole-stream respiration and temperature for Walker Branch data was positive rather than negative, indicating that respiration was greater at cooler vs. warmer temperatures** (Fig. 5b). However, the activation energy of respiration in spring 2004-2005 at Walker Branch was 0.54 eV, and had a 95% CI that included the predicted activation energy of 0.65 eV (Fig. 5c). The regression explained little variation, but was significant (likely due to the large sample size). In contrast, the activation energy of respiration in fall/winter 2004-2005 was shallower (0.27 eV) than predicted (Fig. 5d).

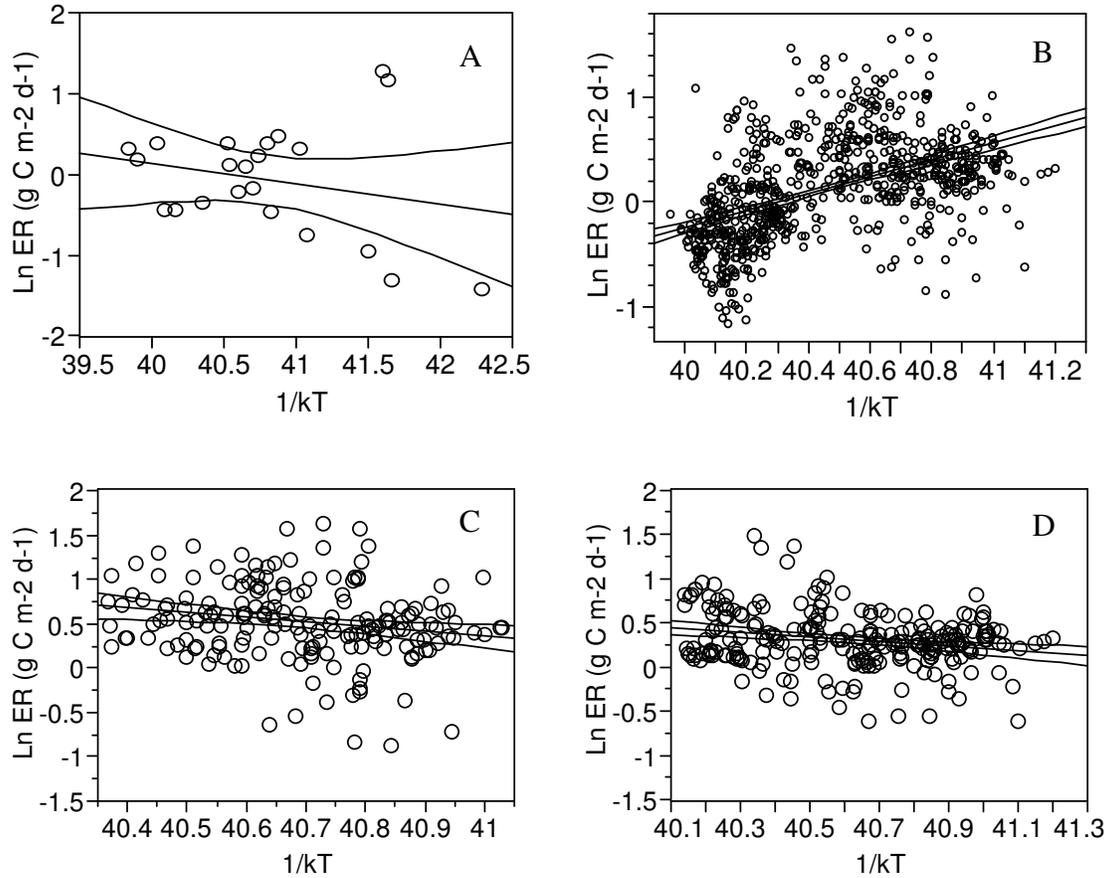


Figure 5. Temperature-dependence of whole-stream respiration (ER) for (a) NPARS data ( $ER = 10.26 e^{0.25/kT}$ , 95% CI: -0.49 to -0.01,  $n = 22$ ,  $r^2 = 0.06$ ,  $p = 0.29$ ); (b) Walker Branch in 2004-2005 ( $ER = -32.66 e^{0.81/kT}$ , 95% CI: 0.76 to 0.86,  $n = 730$ ,  $r^2 = 0.25$ ,  $p < 0.001$ ), (c) Walker Branch in spring (February-April) 2004 and 2005 ( $ER = 22.31 e^{0.54/kT}$ , 95% CI: -0.74 to -0.34,  $n = 179$ ,  $r^2 = 0.04$ ,  $p = 0.01$ ), (d) Walker Branch in fall/winter (October-January) 2004 and 2005 ( $ER = 11.07 e^{0.27/kT}$ , 95% CI: -0.33 to -0.19,  $n = 245$ ,  $r^2 = 0.05$ ,  $p < 0.001$ ). The predicted slopes for NPARS and Walker Branch data were 0 and -0.65, respectively. Dashed lines around the regression represent the 95% CI. The x-axis represents warm to cool temperatures going from left to right.

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The difference in activation energies in spring vs. fall/winter at Walker Branch 2004-2005 highlight that **the MTE is better supported under more autotrophic conditions** (mean P:R of 0.66 in spring and 0.20 in fall/winter within Walker Branch). This trend was further supported by patterns observed for whole-stream respiration when assessed for conditions of low vs. high PAR across the NPARS dataset (Fig. 6a). We predicted that if the relationship between temperature and abundance scales differently for autotrophs and heterotrophs, then whole-stream respiration within autotrophic and heterotrophic streams should have activation energies of 0.65 eV and 0 eV, respectively. Under low PAR (heterotrophic) conditions, there was a positive relationship between respiration and temperature, with an activation energy of -0.65 eV. Under high PAR (autotrophic) conditions, the activation energy was in the predicted direction, but steeper than expected (1.01 vs. 0.65 eV). Thus, our results did not support our predictions. However, temperature still explained 57% ( $p = 0.005$ ) and 78% ( $p = 0.001$ ) of the variation in whole-stream respiration under low and high PAR conditions, respectively.

**C supply in the form of leaf litter was another driver of whole-stream respiration for heterotrophic streams** within the NPARS dataset (Fig. 6b), explaining 40% of the variation ( $p = 0.02$ ). The majority of leaf litter inputs to streams occur in fall and winter, when temperatures are cool. These inputs stimulate microbial and fungal respiration in streams. Thus, the timing of leaf litter inputs to heterotrophic streams causes the slope of the relationship between temperature and whole-stream respiration to be positive rather than negative.

*Implications of working group results*

The MTE is based on the premise of steady state conditions (i.e., when production = respiration). **Our results indicated that MTE predictions are better supported when stream conditions most closely approximate steady conditions.** Examples include: (1) findings of mass-invariance of secondary production for macroinvertebrate primary consumers, whose growth and reproduction is closely tied to in-stream algal production and (2) a confidence interval that includes the predicted activation energy for whole-stream respiration from data collected in spring 2004-2005 at Walker Branch, a season during which C supply is provided largely by in-stream primary production.

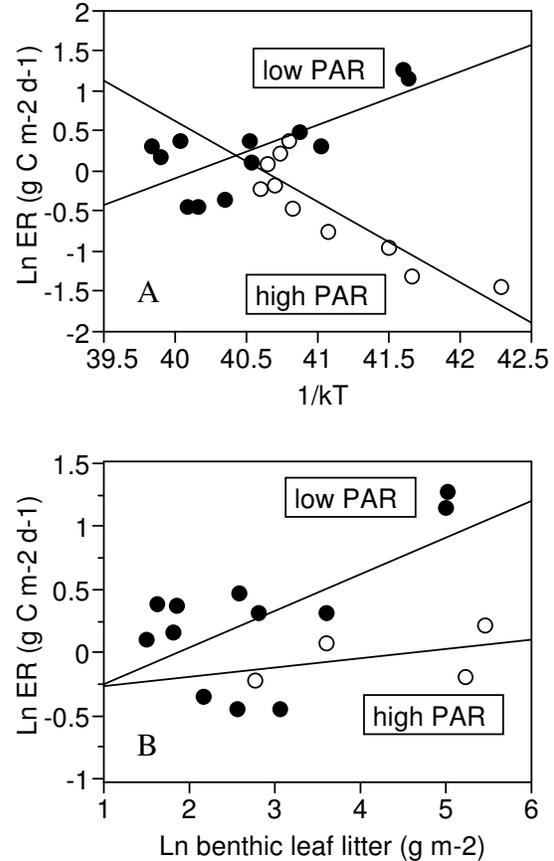


Figure 3. Temperature (a) and carbon supply (b) dependence of whole-stream respiration (ER) under low and high photosynthetically active radiation (PAR) conditions. The median value of PAR was 3.85 mol photons m<sup>-2</sup> d<sup>-1</sup> across data points. We thus defined low and high PAR conditions as  $\leq 3.85$  and  $> 3.85$  mol photons m<sup>-2</sup> d<sup>-1</sup>, respectively. (a) Low PAR:  $ER = -26.81 e^{0.67/kT}$ , 95% CI: 0.48 to 0.84,  $n = 12$ ,  $r^2 = 0.57$ ,  $p = 0.005$ ; High PAR:  $ER = 40.86 e^{-1.01/kT}$ , 95% CI: -1.20 to -0.82,  $n = 10$ ,  $r^2 = 0.78$ ,  $p = 0.001$ . (b) Low PAR:  $y = -0.54 + 0.29 x$ ,  $n = 12$ ,  $r^2 = 0.40$ ,  $p = 0.02$ ; High PAR:  $y = -0.34 + 0.07 x$ ,  $n = 4$ ,  $r^2 = 0.19$ ,  $p = 0.56$ .

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Streams, and many other ecosystems, are not typically found at steady state. The majority of streams are heterotrophic, in which respiration far exceeds primary production because C supply is dominated by sources other than in-stream primary production. Streams are thus considered “donor-controlled” systems. The dynamic flux (both in terms of quantity and timing) of C to streams is a likely mechanism causing deviations from predicted scaling relationships between (1) mass and macroinvertebrate secondary production of detritivores and predators and (2) temperature and rates of whole-stream respiration. Thus, **our results indicated that both the quantity and time lags associated with resource supply (i.e., C) need to be incorporated into MTE, particularly for systems that are not at steady state.**

A simplified Michaelis-Menten function has been successful for modeling, within a MTE context, resource-dependent (light or chl  $\alpha$ ) rates of primary production and respiration for individual phytoplankton (Lopez-Urrutia et al. 2006) and cell-specific rates of oceanic bacterial production (Lopez-Urrutia and Moran 2007). Similarly, we found that a rearrangement of the Michaelis-Menten function provides a framework for describing how the turnover rates for a multitude of resources (as measured via extracellular enzyme activity) control riverine bacterial production. These results show **Michaelis-Menten kinetics can be incorporated within the MTE to model interacting effects of mass, temperature, and resource supply for individual organisms or populations.** However, the ability to do so may depend on the system in question. Furthermore, **application of the Michaelis-Menten model may not be appropriate at the ecosystem level because resource saturation often is not achieved in nature.** For example, we found the Michaelis-Menten model does not accurately describe the relationship between light availability and primary production in streams. Therefore, we will continue to examine alternative models for incorporating resource supply and turnover within the MTE, under both steady state and dynamic conditions.

**DELIVERABLES:** Results for each focus area will be the subject of separate manuscripts we are preparing for publication. Draft manuscripts have already been created for focus areas 1 and 4. We also will draft a proposal for future LTER cross-site aquatic studies focused on MTE-related research questions that cannot be addressed using existing datasets.

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