PHOTOSYNTHESIS AND RESPIRATION IN AN ARCTIC TUNDRA RIVER: MODIFICATION AND APPLICATION OF THE WHOLE--STREAM METABOLISM METHOD AND THE INFLUENCE OF PHYSICAL, BIOLOGICAL, AND CHEMICAL VARIABLES

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Abstract

Global warming may significantly alter whole--stream metabolism (WSM) in Arctic rivers, which may change net CO_2 fluxes on an ecosystem scale. However, the whole--stream metabolism method has not been applied in high--latitude regions because it has been assumed that the 24--hour photoperiod during the summer would preclude accurate estimate of ecosystem respiration (ER) in the dark and subsequent calculation of gross ecosystem production (GEP) in the light. We found that --- with some modification --- the WSM method is applicable in Arctic streams near the Toolik Lake Field Station, Alaska (68^{o} N latitude).

Global warming will likely increase water temperatures, discharge, and SRP (soluble reactive phosphorous) in Arctic rivers and these physical and chemical drivers may influence WSM. By examining the influence of light, temperature, discharge, photosynthetic biomass, and nutrients on WSM, we can develop predictive models of photosynthesis and respiration based on which driving variables are important.

WSM was measured in three experimental reaches of the Kuparuk River, in Arctic Alaska, using the open--system, single--station method. Ambient SRP levels in the reference reach were ~ 0.05 μM. Phosphoric acid has been added to the fertilized reach of the Kuparuk River since 1983 to raise the SRP level to an average concentration of ~0.30 μM at the mean discharge of 2.3 m^3 sec^{-1}. In 2004, we created an ultra--fertilized reach below the historic fertilized reach in which we increased the SRP levels to 0.90 μM or 3 times the historic treatment level.

Gross ecosystem production (GEP) was significantly higher in the fertilized reaches where bryophytes (mosses) and associated epiphytic algae have established a large autotrophic biomass, than in the reference reach, which is dominated by epilithic diatoms only. Among all reaches, GEP was positively correlated with light, temperature, photosynthetic biomass, and SRP and negatively correlated with discharge. Two different modeling approaches (information theoretic and mechanistic) showed that submerged light, temperature, and photosynthetic biomass were the most important variables influencing GEP in all reaches.

Ecosystem respiration (ER) was not significantly different among any of the study reaches. In all reaches, ER was weakly correlated with temperature, discharge, and SRP. However, ER showed a positive response to temperature and a negative response to discharge in the fertilized reaches, most likely due to the extensive bryophyte and epiphyte biomass that have accumulated there. Analysis of multiple linear models using information theory suggests that ER in the fertilized reach was best described by temperature; ER in the reference reach was less well explained by temperature. SRP was of low to moderate importance among all reaches as a descriptor of ER.

The combined influence of increased water temperature, discharge, and SRP will decrease NEM, meaning that carbon sequestration in streams is expected to increase, although not substantially, in the future. This means that the net CO_2 flux out of these rivers and into the atmosphere will likely decrease.

Dedication

I dedicate this thesis to my mother, John West, brother, and Pop--Pop, for all their love and support, and to Nancey Kinlin, who inspired me to pursue my dreams.

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Introduction

Past studies show that Arctic Alaskan Rivers release substantial amounts of CO_2 into the atmosphere and influence the carbon budget on a landscape scale (Kling et al. 1991; Kling et al. 1992). Global warming may increase temperature, discharge, and phosphorous in Arctic rivers (Rouse et al. 1997, IPCC 2001, ACIA 2004). These physical and chemical changes may significantly alter whole--stream metabolism (WSM) in Arctic rivers, which may change net CO_2 fluxes on an ecosystem scale.

While open--system, WSM methods have been widely used to calculate gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) in temperate and tropical streams (Young and Huryn 1999, Mulholland et al. 2001, Uehlinger et al. 2003, Acuna et al. 2004), these method have not been used in Arctic streams. The Arctic ecosystem is unique because the summer photoperiod is 24 hours and so there is no "dark" period. The WSM method relies on a dark period to estimate ER, which is then used to calculate GEP from the net changes in oxygen measured in the stream. Thus, it had been assumed previously that the WSM method would not work in Arctic streams. However, we have found that with some modification the open--system WSM method works well in streams near the Toolik Lake Field Station in Arctic Alaska (68^{o}N latitude). The primary objective of the first chapter is to explain the methods we used to correct for the 24--hour photoperiod in these high--latitude streams.

Global warming will likely increase water temperatures, discharge, and SRP (soluble reactive phosphorous) in Arctic rivers and these physical and chemical drivers

may influence WSM. By examining the influence of light, temperature, discharge, photosynthetic biomass, and nutrients on WSM, we can develop predictive models of photosynthesis and respiration based on which driving variables are important. The long--term (20+ years) phosphorous fertilization experiment in the Kuparuk River near Toolik Lake, Alaska, provides a unique opportunity to examine the key environmental variables that affect whole system photosynthesis and respiration (Peterson et al. 1993, Slavik et al. 2004). This phosphorous fertilization simulates the phosphorous increase due to global warming for rivers in the foothills of the North Slope of Arctic Alaska. Phosphorus --- which is typically the limiting nutrient in these rivers (Peterson et al. 1993) --- has been added to Kuparuk River at low, but ecologically notable levels, during summer open--flow season of every year since 1983. Several key changes in the biology have occurred in the fertilized reach: *Hygrohypnum spp.* (mosses) have overtaken *Schistidium agassizii* (a moss) and epilithic diatoms as the dominant primary producers (Arscott et al. 1998); photosynthetic biomass has increased (Arscott et al. 1998); insect abundance has increased and species composition has changed (Lee and Hershey 2000); and fish growth rates have increased (Deegan and Peterson 1992).

We have previously used closed--system methods to examine metabolic processes in the Kuparuk River (Peterson et al. 1985, Bowden et al. 1992, Arscott et al. 1998, Arscott et al. 2000). Closed--system stream metabolism experiments measure changes in dissolved oxygen (DO) in closed chambers that recirculate water around a sample of benthos (McIntire et al. 1964). The closed--system method is well suited to studies of isolated taxa or communities (Bott et al. 1978, Bott et al. 1997). For example, Arscott et

al. (1998) isolated *S. agassizii*, *Hygrohypnum spp.*, and micro--epilithon (Diatoms) from the Kuparuk River and examined the metabolism of these key autotrophs in the reference and fertilized reaches. Arscott et al. (2000) also examined the influence of light, temperature, and desiccation on metabolism of *S. agassizii* and *Hygrohypnum spp.*. While closed--system metabolism experiments provide good experimental control; they are subject to nutrient depletion and other unnatural changes (Bott et al. 1978, Bott et al. 1997). Furthermore, closed--system methods usually underestimate whole--system respiration because they do not normally include hyporheic sediments (Grimm and Fisher 1984, Mulholland et al. 1997, Naegeli and Uehlinger 1997, Fellows et al. 2001) although new chamber methods have included hyporheic sediments (Uzarski et al. 2001, Uzarski et al. 2004).

Open--system experiments of stream metabolism are based on measurements of DO in open stream channels (Odum 1956). Changes in DO are the result of photosynthesis and respiration but also include corrections for oxygen exchange with the atmosphere (or reaeration, Kilpatrick et al. 1989) and in some cases, oxygen dilution caused by groundwater (e.g., McCutchan et al. 2002, Hall and Tank 2005). The open--system method offers the opportunity to measure stream metabolism with natural conditions. In addition, the open--system approach can be used to measure metabolism continuously for long periods and integrates metabolism in the water column, benthos, and hyporheos.

Until recently, we thought that the open--system method could not be used in the Arctic, where there is 24--hour sunlight, because the open--system method relies on a

'dark' period to estimate ecosystem respiration. Recently, we showed that with some minor modification, the open system method could be used successfully at high--latitude sties such as the Kuparuk River (Chapter 1, Cappelletti and Bowden in review). We initiated this study to determine how important driving variables --- light, temperature, discharge, photosynthetic biomass, and nutrients --- influence whole--system photosynthesis and respiration in Arctic streams. This information is necessary to understand the potential influences of climate warming in the Arctic and to calibrate stream process models. The specific objectives of this study were:

- to measure whole--stream metabolism in the reference, fertilized and ultra--fertilized reaches of the Kuparuk River continuously over the 2004 field season,
- to measure and model key environmental driving variables (surface light, submerged light, temperature, discharge, photosynthetic biomass, and nutrients) for whole--stream metabolism in this environment, and
- to apply a combination of information theoretic and mechanistic models to identify the statistical significance of the key driving variables on stream metabolism in the Kuparuk River.

Comprehensive Literature Review

Measuring Metabolism

Basics

Primary productivity is the formation of organic matter from inorganic carbon by photosynthesizing organisms. Autotrophic organisms utilize light energy and convert it to reduced chemical energy. The general equation for photosynthesis is:

$$6CO_2 + 12\ H_2O + \text{light} \Rightarrow 6O_2 + C_6H_{12}O_6 + 6H_2O \qquad \text{(eq. 1)}$$

Some of the fixed energy is lost through autotrophic respiration (R_a). The portion of fixed energy that is converted to biomass is net primary productivity (NPP). The total amount of fixed energy is gross primary production (GPP), which is the sum of NPP and R_a.

$$GPP = NPP + R_a \qquad \text{(eq. 2)}$$

Primary productivity can be determined by measuring the changes in dissolved oxygen (DO) concentration ns in water (Odum 1956, Owens 1974). Aquatic photosynthesis creates DO while aquatic respiration uses DO. Changes in DO concentrations during daylight are the result of photosynthesis and respiration. No photosynthesis occurs at night, therefore, changes in the DO concentrations at night are due to respiration alone.

Respiration includes metabolism by heterotrophs (R_h) and autotrophs (R_a); together, they are termed ecosystem respiration (ER).

$$R_h + R_a = ER \quad \text{(eq. 3)}$$

Average nighttime respiration is extrapolated through the daylight hours. Net ecosystem metabolism (NEM) is equal to GEP plus ER.

$$NEM = GEP + ER \quad \text{(eq. 4)}$$

Thus, GEP is calculated by subtracting ER from NEM. The stream is termed autotrophic when GEP/ER is greater than 1; likewise, the stream is termed heterotrophic when GEP/ER is less than 1.

Stream metabolism can be measured in closed--system chamber experiments or in open--system stream experiments. Closed--system experiments measure DO changes in chambers that recirculate water around a sample of benthos and are similar to the light and dark bottle method used by limnologists (Wetzel 2001). Open--system stream experiments require accurate reaeration measurements because, unlike the closed--system approach, exchange with atmospheric oxygen occurs in the open--system approach and could easily mask changes in dissolved oxygen caused directly by photosynthesis and respiration. Thus, corrections for this effect are essential.

Reaeration

The oxygen flux between the atmosphere and a stream is called reaeration. To calculate whole--stream (open--system) metabolism it is necessary to account for this oxygen flux. Numerous simple reaeration equations exist (Tsivoglou and Neal 1976, Wilcock 1982, Genereaux and Hemond 1992). The predictor variables in these equations include stream velocity, depth, and slope. However, these equations are frequently inaccurate for small streams (Genereux and Hemond 1992; Young and Huryn 1999; Mulholland et al. 2001).

Stream reaeration is most accurately determined by adding a conservative and a non--conservative volatile solute (e.g., propane or SF_6) into the river and measuring the relative concentrations of both solutes downstream (Kilpatrick et al. 1989, Aumen 1990, Edwardson et al. 2003, Gooseff et al. 2003). Conservative solutes do not react with biotic or abiotic processes in the stream; conversely, non--conservative solutes react with biotic or abiotic processes in the stream. In the case of reaeration experiments, the conservative tracer is usually a salt (NaBr or NaCl) or a dye (Rhodamine WT) and the non--conservative tracer is a gas (propane or sulfur hexafluoride [SF_6]). The conservative solute is used to account for lateral water inputs and transient storage that will dilute or delay the non--conservative solute. Lateral inputs into the stream include groundwater and tributary inputs. Transient storage refers to the temporary storage of solutes in pools, eddies, and the hyporheic zone. The non--conservative tracer gas degasses (volatilizes) from the stream water and enters the atmosphere at the air--water interface. The reaeration rate of oxygen is calculated based on the premise that the volatilization rate of

the tracer gas is directly related to the exchange rate of oxygen in inverse proportion of the molecular weight of the tracer and oxygen molecules, as follows:

$$R_p = \frac{K_2}{K_p} = 1.39 \qquad \text{(eq. 5)}$$

thus,

$$K_2 = K_p * 1.39 \qquad \text{(eq. 6)}$$

where K_p is the propane gas desorption rate coefficient, K_2 is the reaeration rate for oxygen and R_p is the ratio of the propane gas desorption rate coefficient and the reaeration rate of oxygen (Rathbun et al. 1978). Gas solubility decreases with temperature thus, the reaeration rate is dependent on temperature. The reaeration coefficient is usually standardized at 20°C using the equation:

$$K_{2_{20}} = 1.39 K_{p_\gamma} (1.0241)^{(20-\gamma)} \qquad \text{(eq. 7)}$$

where K_{p_γ} is the propane gas desorption rate coefficient at stream temperature γ (Elmore and West 1961).

Closed--system versus Open--System Methods

McIntire (1964) developed the first closed--system stream metabolism experiment. Closed--system experiments measure DO changes in chambers that recirculate water around a sample of benthos. The water in the chambers has no contact with the atmosphere so reaeration calculations are unnecessary.

Odum (1956) developed the first open--system stream metabolism experiment. Open--system experiments measure diurnal oxygen changes in an open stream channel. The open system method is based on the premise that photosynthesis produces oxygen, respiration consumes oxygen, and reaeration exchanges oxygen at the air--water interface (Fig. 1).

Bott et al. (1978) compared open--system and closed--system results. They found open--system primary production estimates were lower than those of the closed--system. They also reported difficulty in accurately calculating reaeration for the open--system method. Closed--system chamber methods exhibited significant variation in photosynthesis and respiration because of temporal and spatial heterogeneity of the samples (i.e. when the sample was taken and where the sample was taken). However, photosynthesis normalized for chlorophyll a (chl *a*) was significantly less variable. Their results underscored a weakness in both methods: open--system methods require an accurate reaeration calculation while closed--system methods require replication because the benthic samples may not be representative of the temporal and spatial heterogeneity of a reach over time.

Marzolf et al. (1994) improved the open system method by measuring reach travel time, using high frequency, high--precision DO instruments, and directly measuring reaeration with solute tracers, as described above. They compared open--system results with closed--system chambers experiments and found that closed--system CR was one--third of the open--system ER. In addition, GEP was 20% higher in the open--system at midday than GPP in the closed--system.

Young and Huryn (1998) corrected the reaeration flux equation in the Marzolf et al. (1994) paper:

$$Reaeration\ Flux = DO_{deficit} \times e^{-k_{oxygen} \times T} \quad \text{(eq. 8)}$$

because under constant conditions, short reaches will have larger fluxes of DO than larger reaches. This calculation may result in negative GEP during the day and positive NEM at night in stream with high reaeration coefficients and overestimation of metabolism in streams with low reaeration coefficients. Young and Huryn (1998) state that the correct equation is:

$$Reaeration\ Flux = DO_{deficit} \times k_{oxygen} \times T \quad \text{(eq. 9)}$$

Fellows et al. (2001) measured the contribution of respiration from the hyporheic zone. They calculated the difference between open--system ER and closed--system CR to estimate hyporheic zone respiration. Of the four reaches studied, the hyporheic zone

contributed from 40% to 93% of the total ER. Naegeli and Uehlinger (1997) performed a similar experiment in which the hyporheic zone contributed from 76 -- 96% of the total ER. Thus, closed--system methods may grossly underestimate ER because it does not include the hyporheic zone respiration.

In summary, the advantages of the closed--system stream metabolism experiments are that this approach is reproducible and requires no measurement of reaeration. In addition, metabolism rates can be measured for a particular taxa or community. The disadvantages of the closed--system method are the potential for non--representative sampling (temporal and spatial), benthic disturbance, and hyporheic zone exclusion. Further, chamber experiments may exhibit unnatural environmental conditions such as nutrient limitation, flow regime alteration, and surface area to volume ratio alteration. Open--system metabolism experiments have the advantage of being whole--system experiments including all components of the stream community: benthic, water column, and hyporheic. Furthermore, communities are undisturbed by the experiment and environmental conditions are natural. However, the open system method has some disadvantages. Experimental replication is not possible because natural stream conditions will always be different. Tributary inputs into the experimental reach must be negligible. Lastly, accurate reaeration measurements are crucial.

Dual Station versus Single Station Techniques

The open--system method includes two different measurement techniques: dual station and single station. For the dual station method, DO is measured at an upstream and downstream station (Owens 1974). In contrast, DO is measured at only the

downstream station for single station method (Bott et al. 1978). In the single station method it is assumed that an unmeasured upstream location behaves is exactly the same way as the measured downstream location, with a time lag equivalent to the average time of travel between the two locations. The dual station method is acceptable for all stream reaches. However, when the metabolic rates (DO curves) are similar for both upstream and downstream stations then the single station method is acceptable. The single station method is preferable because less equipment is needed.

The single station method requires a calculation of reach length. Bott et al. (1978) derived the following equation to calculate reach length:

$$L = \frac{Q\Delta C}{(wfM) - R} \qquad \text{(eq. 10)}$$

where L is reach length (m), Q is discharge ($m^3\ h^{-1}$), ΔC is the measured gas change between stations ($gO_2\ m^{-3}$), w is mean width (m), f is the reaeration coefficient ($m\ h^{-1}$), M is the mean saturation deficit between stations ($gO_2\ m^{-3}$), and R is nighttime respiration ($gO_2\ m^{-2}\ h^{-1}$).

Reach length can also be calculated based on the premise that the oxygen signal will decrease with time (reach length) because proportionally, more of dissolved oxygen changes can be attributed to the earlier part of the stream reach than the latter part. Oxygen fluxes can be attributed to GEP, ER, and reaeration. Thus, reach length can be

determined with an exponential decay by calculating the time it takes for a set portion (say 90%) of the DO in the stream to turnover:

$$[O_{2(t)}] = [O_{2(0)}] * e^{-kt} \quad \text{(eq. 11)}$$

where t is time, $[O_{2(t)}]$ is 10% of the original upstream DO that flowed downstream with respect to time, $[O_{2(0)}]$ is the original upstream DO at t = 0, and k is the mean oxygen turnover rate. Reach length is then calculated with the following equation:

$$L = v * t \quad \text{(eq. 12)}$$

where L is the calculated reach length (m), v is the stream velocity (m s^{-1}), and t is time (s).

Metabolism Calculations

The following series of equations calculate NEM. The first step in calculating NEM is to calculate the change in DO for the same parcel of water upstream and downstream with respect to time:

$$\Delta DO(t) = [DO_{DOWN}(t) - DO_{UP}(t - t_T)] \quad \text{(eq. 13)}$$

where t is time, t_T is transit time between the upstream station and the downstream station, $\Delta DO(t)$ is the change in DO (mg O_2 L^{-1}) at time t, $DO_{DOWN}(t)$ is the downstream

DO concentration (mg O_2 L^{-1}) at time t, and DO_{UP} $(t - t_T)$ is the upstream DO concentration (mg O_2 L^{-1}) at time t minus transit time. Thus, the $\Delta DO(t)$ is result of GEP, ER, and reaeration. The next steps involve calculating the net flux of oxygen into and out of the river due to reaeration and correcting for this net oxygen flux. The net oxygen flux into and out of the river depends on whether the stream water is supersaturated or unsaturated with DO. If the river is supersaturated with DO then the net oxygen flux is going out of the river while a river that is unsaturated with DO then the net oxygen flux is going into the river. Thus, equation 14 calculates the expected DO saturation at mean temperature with respect to time:

$$DO_{SAT}(t) = (-0.00005 * T_m(t)^3) + (0.0067 * T_m(t)^2) - (0.3883 * T_m(t)) + 14.548 \quad \text{(eq. 14)}$$

where $DO_{SAT}(t)$ is DO saturation (mg O_2 L^{-1}) at mean temperature at time t, and T_m is mean reach temperature (°C). The next equation calculates the mean DO deficit/surplus with respect to time by subtracting the difference between expected DO saturation and actual DO saturation:

$$DO_{DEF}(t) = ([(DO_{SAT}(t - t_T) - DO_{UP}(t - t_T)] + [(DO_{SAT}(t) - DO_{DOWN}(t)])/2 \quad \text{(eq. 15)}$$

where $DO_{DEF}(t)$ is the DO deficit/surplus (mg O_2 L^{-1}) at time t. The following equation calculates the mean reaeration flux of oxygen into and out of the water with respect to time:

$$F_R(t) = (DO_{DEF}(t) * k(t) * t_T) \quad \text{(eq. 16)}$$

where $F_R(t)$ is the mean reaeration flux at time t (mg O_2 L^{-1}), and k(t) is the reaeration coefficient at mean temperature at time t. Now that the oxygen flux into and out of the water is accounted for, NEM can be calculated. The next equation calculates volumetric NEM:

$$NEM_{VOL}(t) = [\Delta DO(t) - F_R(t)] / (t_T/60) \quad \text{(eq. 17)}$$

where $NEM_{VOL}(t)$ (mg O_2 L^{-1} h^{-1}) is the volumetric NEM. Most of the NEM occurs on the stream bottom and not the water column. Thus, the subsequent equation calculates NEM with respect to reach length and wetted perimeter:

$$NEM_{BOX}(t) = [NEM_{VOL}(t) * 1000] * [(Width * Depth)/(Width + 2*Depth)] \quad \text{(eq. 18)}$$

where $NEM_{BOX}(t)$ (mg O_2 m^{-2} h^{-1}) is the NEM.

Changes in DO concentrations during daylight are the result of GEP and ER. No photosynthesis is assumed to occur at solar midnight, therefore, changes in the DO concentrations at night are due to ER alone. Nighttime ER is equal to NEM at solar midnight because GEP is supposed to be 0.

$$ER = NEM - GEP, \text{ if } GEP = 0 \text{ at solar midnight then, } ER = NEM \quad \text{(eq. 19)}$$

The ER value calculated at solar midnight is extrapolated through the daylight hours to the next ER value at the following solar midnight. Finally, GEP is calculated by subtracting ER from NEM.

$$GEP = NEM - ER \quad \text{(eq. 20)}$$

However, GEP may not be 0 at midnight because the Arctic summer has 24 hours of sunlight. This complication will be explained later.

Physical Factors Affecting Metabolism

Light

The sun emits radiation over a wide range of wavelengths. Light utilized for photosynthesis is termed photosynthetic active radiation (PAR); PAR has a wavelength range of 400nm - 700nm.

However, only a portion of the light incident on the surface of a stream actually makes it to the bottom of the stream to support benthic photosynthesis. Portions of the incident light may be reflected, scattered or absorbed. Reflection occurs when light frequency is identical to the surface--atom dipole frequency. Light reflection ensues

because it cannot penetrate the substance. Reflection increases with the incident light angle.

Aquatic light scatter is dependent on the concentration and size of suspended material. An increased concentration of suspended particles will increase light scatter and decrease light penetration. Small particles scatter light at greater angles than large particles; hence, small particles have greater scattering ability. Thus, an increased concentration of small--suspended particles will increase light scatter and decrease light penetration.

Light absorption occurs when the energy difference among ground state and excited states of the absorbing substance are equal to the photon energy. A variety of different substances (e.g., dissolved organic carbon or DOC) can absorb light in stream water.

Photosynthesis by benthic algae is dependent on light absorption by chl *a* and accessory pigments. Light absorption by chl *a* is not equal throughout the PAR spectra. The maximum light absorbance of chl *a* occurs at 665nm but plants utilize wavelengths from 400nm – 700nm with accessory pigments. Accessory pigments: chlorophyll b and c, carotenoids, and phycobilipigments absorb light at characteristically different wavelengths and transfer absorbed excitation energy to chl *a*.

The excitation energy absorbed and transferred to chl *a* modifies the electronic structure of chl *a*. This modification results in a series of oxidation--reduction reactions that transfer excited electrons down an electron transport chain. These series of

oxidation--reduction reactions produce the energy needed to synthesize carbohydrates. The initial electron donor is water and the final electron acceptor is oxygen.

Photosynthesis--irradiance (PI) curves model photosynthesis (P) as a function of light intensity. At low light levels, P typically increases linearly with light. The linear slope of this PI curve is denoted α. At some light level, P reaches a plateau because light has saturated the photosynthetic reaction. The light--saturated portion of the PI curve is denoted P_{max}. Table 1 displays several different PI curve equations: where P is the photosynthetic rate, α is the initial curve slope, I is light intensity, and P_{max} is the maximum photosynthetic rate, K_m is the light intensity at one--half the maximum photosynthetic rate. Presently, the most widely used PI curve is equation 28 (Uehlinger 2000; Arscott et al. 1998; Arscott et al. 2000).

PI curves were developed primarily for lentic or laboratory environments (Pfeifer and McDiffett 1975, Jassby and Platt 1976, McBride 1992). Natural lotic environments are characterized by rapid physical changes in other key variables, including temperature, discharge, depth, turbidity, shear forces, and surface abrasion. Each of these variables may have a strong influence on photosynthesis, and so PI curves may not accurately estimate GEP in natural lotic systems.

Benthic diatoms usually dominate photosynthesis in the Kuparuk River and similar tundra rivers. However, in some locations (natural springs and the experimentally fertilized reach of the Kuparuk River, bryophytes are important and even dominant autotrophs (Miller 1992, Peterson 1993, Slavik 2004). Arscott et al. (1998) used PI curves to compare algal and bryophyte metabolism in the Kuparuk River. Arscott et al.

(2000) used PI curves to compare temperature and light effects on metabolism of the two bryophytes most commonly found in the experimental reaches of the Kuparuk River. In both cases, closed--system metabolism was measured for each community. These two articles will be discussed in more detail, later.

Temperature

As a general rule of thumb, a 10°C rise in temperature doubles the reaction rate of most biochemical reactions (Smith 1988). Physically, increases in temperature result in greater molecular collision frequency and energy with the latter being most important.

The Arrhenius equation is used by physical chemists to calculate the precise effect of temperature on reaction rates:

$$k = A * e^{\left(\frac{-E_a}{R*T}\right)} \qquad \text{(eq. 30)}$$

where k is reaction rate, A is a constant, E_a is the activation energy, R is the universal gas constant, and T is temperature. Goldman and Carpenter (1974) used the Arrhenius equation to model the effect of temperature and nutrients on algal growth.

In ecological systems, the correct values for A and E_a in the Arrhenius equation are typically not known. The van't Hoff equation provides a simpler way to describe the effect of temperature on reaction rates:

$$Q_{10} = \left(\frac{k_2}{k_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)} \qquad \text{(eq. 31)}$$

where Q_{10} is the reaction rate, k_1 is the reaction rate at temperature T_1, and k_2 is the reaction rate at temperature T_2. The van't Hoff equation predicted reaction rates in many aquatic ecosystems (Williams 1971, Chen and Orlob 1972, Thomann et al. 1975).

Thornton and Lessem (1978) stated two weaknesses with the van't Hoff equation. First, many researchers calibrated Q_{10} curves with a small variation in temperature. Thus, at extreme temperatures, the Q_{10} curve may incorrectly model reaction rate. Further, most biological reactions increase with temperature to a maximum value then decrease with any further increase in temperature because proteins begin to denature; which the van't Hoff equation does not account for.

Thornton and Lessem (1978) developed a temperature algorithm to modify respiration rates. The respiration rate at any environmental temperature is the product of the maximum respiration rate with a multiplier. The multiplier varies from 1 (optimum) to 0 (worst) and is a function of temperature. The algorithm uses the form of a logistic equation:

$$KA(\theta) = \frac{K_1 * e^{\gamma_1(\theta-\theta_1)}}{K_1 * (e^{\gamma_1(\theta-\theta_1)} - 1)} \qquad \text{(eq. 32)}$$

where KA = reaction rate multiplier, θ = environmental temperature, K_1 = reaction rate multiplier near lower threshold temperature, γ_1 = specific rate coefficient, and θ_1 = lower threshold temperature. The value for γ_1 can be determined with the following equation:

$$\gamma_1 = \frac{1}{\theta_2 - \theta_1} \ln \frac{K_2(1 - K_1)}{K_1(1 - K_2)} \quad \text{(eq. 33)}$$

where θ_2 = temperature at maximum reaction rate, and $K_2 = 0.98$.

Chapra and DiToro (1991) modeled GEP with a 2--part equation including light and temperature variables:

$$P_{\max,T} = P_{\max,20^o} * \theta^{(T-20)} \quad \text{(eq. 34)}$$

$$GPP = P_{\max,T} * \tanh\left(\frac{I}{I_k}\right) \quad \text{(eq. 35)}$$

where $P_{max,T}$ is the maximum photosynthetic rate at temperature T, $P_{max,20°C}$ is the maximum photosynthetic rate at 20°C, θ is the exponential value of the Q_{10} multiplier, T is temperature, I is light intensity, and I_k is light intensity at half--saturation.

Temperature optimums vary among and within photosynthetic species both seasonally and geographically (Madsen and Adams 1989). According to Dilks and Proctor (1975), most aquatic bryophytes have optimum growth rates at relatively low temperatures and can resist freezing to at least ¯5 -- ¯10°C. Glime and Acton (1979) revealed that temperature affected metabolism of the stream moss ***Fontinalis duriaei*** with

peak C assimilation at 10°C. Glime and Raeymaekers (1987) studied 6 *Fontinalis* species and determined maximum growth at temperatures less than 20°C.

Arscott et al. (2000) tested the effects of temperature on photosynthesis/irradiance curves for *S. agassizii*, and *Hygrohypnum spp*.. They determined that P_{max} increased from 5° -- 20°C but decreased at 30°C for *S. agassizii* in the reference reach of the Kuparuk River. However, both *S. agassizii* and *Hygrohypnum* from the fertilized reach displayed increased P_{max} from 5 -- 30°C. The authors explain that the additional phosphorous from the fertilized reach increased *S. agassizii's* tolerance for high temperatures. Meanwhile, the P_{max} for the *Hygrohypnum* was greater than that for *S. agassizii*.

Fornwall and Glime (1982) tested temperature acclimation of mosses; mosses acclimated to warm temperatures grew faster in warm water (35°C) than cool water (10°C). However, *Fontinalis spp*. began deteriorating for long periods at 15°C (Glime 1982, 1987a, 1987c, 1987b). Sanford (1979) reported that optimum growth of *Hygrohypnum ochraceum* was at 18 -- 21°C while growth ceased at 26°C. Thus, the P_{max} of *Hygrohypnum ochraceum* may temporarily increase at 30°C but will be detrimental in the long--term. However, the Kuparuk River rarely exceeds 20°C.

Eppley (1972) measured algal growth rate with different temperature treatments in the laboratory. The empirically calculated Q_{10} was 1.88 and algal growth increased with temperature and algal growth continued to increase with temperatures greater than 35°C. Goldman and Carpenter (1974) gathered data from 14 studies testing algal growth rate at different temperature in the laboratory. The Q_{10} was 2.08 and the R^2 of the

regression analysis was 0.90. Again, algal growth was not inhibited by temperatures greater than 35°C.

The data suggest that algae grow better in warmer water while mosses grow better in cooler water. These differences may be attributed to different life strategies. Algae have less investment in structure and more investment in maximizing photosynthetic rates. Thus, algae can met the energy demands of increased respiration due to higher temperatures while moss cannot.

Nutrients

Light energy absorbed by pigments is transferred down an electron transport chain through a series of oxidation--reduction reactions. Photosynthetic proteins are catalytic enzymes in the photosynthetic electron transport chain. Without photosynthetic enzymes, the activation energy barrier would prevent photosynthesis from moving forward. Proteins contain large amounts of nitrogen and ribosomes synthesize them. Ribosomes require large amounts of phosphorous (Sterner and Elser 2002). Thus, nitrogen or phosphorous can limit photosynthetic protein production. Photosynthetic proteins work at a certain rate at a given temperature. If light is saturating then the number of photosynthetic proteins or temperature are likely to be the next factors to limit photosynthesis. Under light saturating conditions, if the numbers of photosynthetic proteins are increased or temperature is increased, the photosynthetic rate will increase. Smith (1988) points out that multi--step reactions (photosynthesis) have one step that is slower than the others, thus the slowest step is the rate determining step. Falkowski and Raven (1997) state that under light saturating conditions, the rate limiting step is

somewhere in the electron transport chain. Unfortunately, the exact location of the rate limiting step on the electron transport chain is not known (Falkowski and Raven 1997).

Enzyme kinetics are usually described by the Michaelis--Menten equation:

$$V = \frac{V_{\max}[S]}{K_m + [S]} \qquad \text{(eq. 36)}$$

where V is the reaction rate of the enzyme and substrate, V_{max} is the maximum reaction rate of the enzyme and substrate, [S] is the substrate concentration, and K_m is the overall rate constant for the reaction (Falkowski and Raven 1997).

Discharge

Power and Stewart (1987) examined the effects of flooding on an algal community in an Oklahoma stream. They found that after a storm, algae persisted mostly on larger substrates.

Likewise, Uehlinger (1991) found substrate size and periphyton biomass were positively correlated in the Necker River. The Necker River is a flood--prone, sixth order, prealpine, gravel--bottom river. Thus, periphyton community resistance to damage from severe floods was contingent on substrate size.

In a follow--up study, Uehlinger et al. (1996) modeled periphyton dynamics in the Necker River. The periphyton model had several components: biomass--dependent growth rate, light, temperature, discharge, and catastrophic loss (bed--moving spate). The simplest accurate model included components for biomass--dependent growth rate,

discharge, and catastrophic loss. Light and temperature did not significantly affect model fit. Discharge dictates periphyton dynamics in the Necker River probably due to frequent bed--moving spates.

Biggs et al. (1999a) studied how velocity and sediment disturbance affect periphyton biomass. Their findings suggest that unstable sediments greatly increase periphyton disturbance. Thus, calculation of the bed movement threshold is important.

Metabolism and Disturbance

Fisher et al. (1982) studied succession in a desert stream after flooding. They measured algae, invertebrates, and metabolism. Metabolic recovery closely followed the recovery of algae and invertebrates. For five days after the flooding, respiration was greater than photosynthesis. After five days, photosynthesis was greater than respiration. Thus, respiration was more resistant to disturbance than photosynthesis, while photosynthesis was more resilient to disturbance than respiration.

Uehlinger and Naegeli (1998) tested how disturbance effects stream metabolism in the Necker River. After a spate, photosynthesis decreased more than respiration. The photosynthetic community, mostly located on the top portion of rocks, had greater exposure to shear forces and surface abrasion than the respiration community did, mostly located on the bottom portion of rocks and hyporheic sediments. Photosynthetic recovery rate was faster than respiration recovery rate. Again, respiration was more resistant to disturbance than photosynthesis, while photosynthesis was more resilient to disturbance than respiration.

Uehlinger (2000a) tested stream metabolism resistance and resilience to disturbances in the Necker and Thur Rivers. The Necker River is a tributary of the Thur River, with the Thur River being a major tributary to the Rhine. Like the Necker River, the Thur River is a flood--prone, prealpine, gravel--bottom river. In contrast, the Thur River receives more light, agricultural runoff, and sewage inputs than the upstream Necker River. Spates reduced photosynthesis and respiration by 53% and 24% in the Necker River, and 37% and 14% in the Thur River. Again, respiration was more resistance to disturbance than photosynthesis. Photosynthetic recovery rates were significantly greater in the Thur River, probably due to greater light, temperature, and nutrient concentrations. Respiratory recovery rates were similar between reaches. In both reaches, photosynthetic recovery rates were faster than respiratory recovery rates. Again, photosynthesis was more resilient than respiration. Uehlinger suggests that different energy bases of heterotrophic and autotrophic communities may account for the different recovery rates. Thus, the autotrophic energy base, light, recovers faster than the heterotrophic energy base, detritus.

Uehlinger (2000b) studied how spates and season influence stream metabolism in the River Glatt. The River Glatt is a gravel--bottom, step--pool, eutrophic, unshaded, flood--prone stream. Seasonal variation was apparent in photosynthesis and respiration. Spates had little effect on photosynthesis or respiration. Consequently, the researchers suggested that the disturbances were not severe enough to initiate bed--load transport.

Disturbance Effects on Algal Communities

Biggs and Thomsen (1995) tested stream periphyton resistance to disturbance by increases in shear stress. A laboratory flow tank simulated the spate. The researchers determined that nonfilamentous diatoms were more resistance to damage than filamentous algae. Thus, taxonomic community composition influenced how the stream reacted to disturbance; specifically, organism morphology affected its ability to withstand disturbance.

Uehlinger et al. (2003) studied how experimental floods influenced periphyton and stream metabolism below a dam in the River Spol. Periphyton biomass dynamics displayed high variation annually and seasonally. The structure of the diatom community exhibited persistent changes. Thus, Uehlinger concluded that the autotrophic community might take many years for periphyton to adapt to a new flow regime.

Power and Steward (1987) examined the effects of flooding on an algal community in an Oklahoma stream. Before the flood, the filamentous alga, *Rhizoclonium*, dominated riffles, while another filamentous alga, *Spirogyra*, dominated the pools. Immediately after the flood, *Rhizoclonium* occurrence decreased fourfold, whereas *Spirogyra* occurrence decreased twenty fold; furthermore, diatoms dominated the riffles while *Rhizoclonium* dominated the pools. A month after the flood, *Rhizoclonium* again dominated the riffles and *Spirogyra* dominated the pools. The authors suggest that *Rhizoclonium* has specialized basal attachment cells, which anchor the filaments to the substrate; in contrast, *Spirogyra* has no specialized basal attachment cells. Diatoms dominated the riffles immediately after the flood probably due to scour

resistant morphology. Thus, periphyton with stronger substrate attachment and greater scour resistant morphology are more resistant to disturbance.

Stevenson (1990) tested how spates affect benthic algal community dynamics in a stream. He found that benthic diatoms are quite well adapted to storms. He suggested that most spates have a positive effect on diatoms and only bed--moving spates would negatively affect diatoms.

Thus, disturbance magnitude and frequency, and algal attachment type, growth rate, and scour resistance are important factors in algal community dynamics.

Likewise, Fisher et al. (1982) showed that diatoms recover faster than filamentous algae. Fisher noted that life cycle differences might explain different recovery rates. Most filamentous algae can colonize another substrate only after existing cells produce mature filaments; whereas, every diatom cell is capable of attachment.

Biggs et al. (1999b) investigated how resource stress (low light and nutrients) modifies spate effects on periphyton. They found that high nutrient stress resulted in the lowest periphyton resistance while moderate light and low nutrient stress resulted in the strongest periphyton resistance. Chlorophyll *a* resilience was negatively correlated with resource stress, while taxonomic composition resilience was positively correlated with resource stress.

Peterson and Stevenson (1992) studied the importance of disturbance timing of epilithic algal communities growing in fast and slow currents in experimental outdoor stream channels. The control reach was left undisturbed for 33 days following a simulated spate. The experimental reaches were subjected to an additional spate after

either day 9, 18, 27, or 33. On day 33, all reaches were subjected to a final spate. Succession after disturbance started with diatoms and than ended with dense mats of filamentous algae by 21 -- 24 days. Resistance was lower in slow--current communities than in fast--current communities. Slow--current community resistance varied temporally; communities were least resistant on day 18 because community composition and physiognomy were transforming; communities were least resistance on day 33 because the filamentous algal mats senesced. Fast--current community resistance did not vary temporally. Slow--current communities had greater resilience taking only 3 -- 9 days for biomass and taxonomic structure to be similar to the control reach. The authors attributed greater resilience to enhanced reproduction because shear stress was lower and nutrients and light were less limiting. Thus, disturbance timing, successional state, and habitat affect epilithic algal response to disturbance.

Disturbance Effects on Moss Communities

Englund (1991) investigated disturbance effects on stream moss and invertebrate community structure. He found that moss was rare on small stones with the exception of small stones embedded in the substrate. Moss was abundant on large stones. Thus, he concluded that the stability of substrates affect moss distribution. Moss and invertebrate recovery rates were weak 14 months after a bed--moving spate. Thus, bed--moving spates have severe and prolonged effects on stream moss and benthic invertebrates.

Muotka and Virtanen (1995) studied bryophyte distribution in streams with different disturbance regimes. Fast colonizing bryophytes dominated the disturbed habitat while large perennial species (e.g. *Hygrohypnum*) dominated the stable habitat.

Shear Forces and Bed Movement

Under laminar flow, each fluid component travels in parallel streamlines with no mixing between adjacent layers. Thus, the thin layer in contact with the substrate has no forward velocity. Each successive layer away from the substrate has less resistance resulting in greater velocity.

However, laminar flow becomes unstable when velocity or depth exceeds a critical value. Thus, flow becomes turbulent; the fluid components mix between adjacent layers and follow irregular paths. Velocity near the streambed is faster during turbulent flow resulting in greater shear forces. Moreover, laminar flow rarely occurs in natural stream systems.

Velocity profiles of a specific cross--section are dependent on two variables. First, velocity increases with distance from the streambed. Second, velocity increases away from the stream bank towards the center of the stream. Stream velocity along the longitudinal stream gradient increases with slope, and depth, and decreases with streambed roughness.

Bed movement depends mostly on substrate size, shape, density, and arrangement. Knighton (1998) provided an equation to calculate bed movement threshold:

$$\tau_{cr} = kg(\rho_s - \rho)D \qquad \text{(eq. 37)}$$

where τ_{cr} is critical shear stress, k is a constant, g is gravity, ρ_s is sediment density, ρ is fluid density, and D is grain diameter. According to Komar and Li (1988), a k value of 0.045 is a good approximation on hydraulically rough beds. This equation accounts for both lift and drag forces. Unfortunately, substrates are heterogeneous; thus, bed movement threshold consists of a probability distribution not a singe value. Furthermore, mosses tend to colonize large boulders while algae colonize all rocks. In addition, Kuparuk River morphology consists of pool--riffle sequences so bed movement will differ according to morphology.

Metabolism from a Whole Ecosystem Perspective

Metabolism and The River Continuum Concept

Young and Huryn (1996) measured metabolism along a grassland river continuum for two years. Fourteen stations, spanning 310 km, were set up along Taieri River in New Zealand. The researchers found that photosynthesis was mostly dependent on water depth and turbidity. During average discharge, the headwater reaches were autotrophic while the reaches near the river mouth were heterotrophic. During periods of low discharge, autotrophic headwater river reaches would extend down the continuum towards the river mouth. When discharge was high, the heterotrophic river reaches would retreat up the continuum towards the headwaters. Thus, stochastic discharge can dictate longitudinal patterns of stream metabolism.

Meyer and Edwards (1990) also investigated stream metabolism and organic carbon turnover along a black--water river continuum in Georgia. The river was characterized as a warm, low gradient, swampy riparian, tea--colored stream. Along the river continuum, from second to sixth order stream size, GEP, ER, and GEP/ER increased with stream order.

Inter--biome Metabolism

Mulholland et al. (2001) studied whole--stream metabolism in eight streams from several different biomes in North America. The purpose of this experiment was to identify and compare factors that controlled stream metabolism in different biomes.

Whole--stream metabolism was measured by open--system, upstream--downstream diurnal oxygen changes. The factors investigated were discharge, water velocity, transient storage zone (A_s), A_s : A (total stream area), water uptake distance, hydraulic retention factor, photosynthetic active radiation (PAR), water temperature, soluble reactive phosphorous (SRP) concentration, dissolved inorganic nitrogen (DIN) concentration, autotroph biomass, and detritus standing crop.

Gross ecosystem production was significantly correlated with daily PAR and marginally correlated to total algal biomass. A multiple regression model with predictor variables: log PAR and SRP concentrations explained 90% of the variation in log GEP.

Ecosystem respiration was significantly correlated with SRP concentrations and marginally correlated to A_s; together, these predictor variables explained 73% of the variation in ER.

Net ecosystem metabolism was significantly correlated with PAR, with 53% of the variation in log NEM explained by log PAR.

Generally, streams could be grouped in three categories: (1) high GEP with positive NEM in early afternoon, (2) moderate GEP with a distinct peak during daylight but negative NEM at all times, and (3) little GEP during daylight and negative NEM at all times.

The only river to have positive NEM (GEP/ER>1) was Sycamore Creek, a desert stream. Thus, streams generally consume more organic matter than produced.

Hyporheic Zone and Respiration

Fellows et al. (2001) compared the differences in metabolism and hyporheic zone size between two streams. The researchers wanted to couple the measures of metabolism and surface--subsurface exchange. The authors wanted to provide links between hydrology and ecosystem processes. The researchers studied two headwater streams in north--central New Mexico. They conducted the study during baseflow conditions during the summer of 1996 and 1997. Each stream had two study reaches. Solute tracers, Br^{-1} or Cl^{-1}, were injected into the stream reach. Solute curves were visually fit using the OTIS storage model. The resulting parameters: stream cross--sectional area (A), storage zone cross--sectional area (A_s), dispersion (D), and storage zone exchange coefficient (α), were entered into the OTIS--P model for nonlinear least squares analysis. The output parameters from the OTIS--P model were used to calculate hydraulic residence time in the stream ($T_{str}=1/\alpha$) and storage zone ($T_{sto}=A_s/[A* \alpha]$); hydraulic uptake length in the stream channel ($S_{hyd}=Q/[A* \alpha]$); and the hydrologic retention factor ($R_h= T_{sto} / S_{hyd}$).

Dissolved oxygen (DO), water temperature, and light were measured at an upstream and downstream station during solute injection for 36 hours. DO values along with discharge (Q), reach travel time, and reaeration rate were used to calculate metabolism. Benthic metabolism was measured in light and dark incubation chambers. Column metabolism (no benthic sediments) was measured in light and dark incubation chambers. Sediment was analyzed for organic matter content and chl *a*. Hyporheic sediment respiration was measured in microcosms. Hyporheic zone respiration was calculated by the difference between whole--stream respiration and benthic chamber respiration. The area of the hyporheic zone (A_H) was calculated by dividing the average longitudinal hyporheic respiration (g O_2 m^{-1} d^{-1}) by the volumetric respiration from the sediment microcosm (g O_2 m^{-3} d^{-1}). The maximum depth of the hyporheic zone was calculated by dividing A_H by mean wetted width of the channel.

Gallina Creek had the greatest values of A_s, A_s/A, T_{sto}, R_h, and lowest values of S_{hyd}. Subsequently, Gallina Creek had the greatest whole--stream respiration and hyporheic respiration. A_H and hyporheic depth was much greater in Gallina Creek. Whole--stream respiration's and hyporheic respiration's correlation to A_s were significant ($R^2 = 0.93$, $p = 0.04$; $R^2 = 0.92$, $p = 0.04$). Both measures of respiration increased as A_s/A increased but were not significant ($R^2 = 0.87$, $p = 0.07$; $R^2 = 0.86$, $p = 0.04$). The fraction of whole--stream respiration contributed by the hyporheic zone was not significantly correlated with A_s or A_s/A ($R^2 = 0.57$, $p = 0.25$; $R^2 = 0.49$, $p = 0.30$).

Mulholland et al. (1997, 1999) studied two similar forest streams with different hyporheic zone sizes. The transient storage zone volume in Hugh White Creek (HWC)

was large (1.5 times that of the flowing water zone), while Walker Branch (WB) was low (0.1 times that of the flowing water). Respiration rate was 2.4 times greater in HWC than in WB. GEP was slightly higher in WB (0.32 g O_2 m^{-2} d^{-1}) than HWC (0.21 g O_2 m^{-2} d^{-1}). Phosphorous uptake rate was 2.6 times higher in HWC than in WB. Forty three percent of phosphorous uptake occurred in the transient storage zone of HWC while phosphorous uptake in the transient storage zone of WB was negligible. Thus, hyporheic zones increase heterotrophic metabolism and phosphorus uptake in streams.

Global Warming

Warming in the Arctic is an important global issue because scientists predict that temperature increases will be greatest in the Arctic (IPCC 2001, ACIA 2004). According to the Intergovernmental Panel on Climate Change (IPCC), over the next 100 years, air temperatures on the North Slope of Alaska are predicted to increase 5 -- 6°C while global air temperatures are predicted to increase 3°C. Further, the Arctic Climate Impact Assessment (ACIA) report predicts that Arctic air temperatures may increase 4 -- 7°C in 100 years (ACIA 2004). In the North Slope of Alaska, air temperatures have increased ~ 0.5°C per decade from 1961 to 1990 (Chapman and Walsh 1993). The ACIA report states that Arctic air temperatures rose ~ 1°C per decade between 1954 and 2003.

Rouse et al. (1997) investigated the effects of climate change on the freshwaters of Arctic and Sub--Arctic North America. The active layer lies between the soil surface and the true permafrost; the active layer melts in the summer and freezes in the winter. Rouse et al. (1997) predicted an increase in the permafrost active layer depth with increased air temperatures. Osterkamp and Romanovsky (1999) determined that

permafrost is warming and thawing in some areas of central Alaska. Permafrost on the North Slope is warming but has not yet thawed (Osterkamp and Romanovsky 1999). Thus, testing the effects of thawing permafrost on rivers of the North Slope will be valuable.

Both Rouse et al. (1997) and Hobbie et al. (1999) hypothesize that nutrient loading into Arctic streams should increase with global warming. First, the increased depth of the active permafrost layer will expose more soil to weathering. Moreover, soil weathering will increase with increased temperatures. Terrestrial primary production should increase with global warming (Le Dizes et al. 2003). Thus, allochthonous river matter will increase. Furthermore, terrestrial and aquatic decomposition rates will increase with temperature, increasing nutrient mineralization. An increase in active layer depth will increase soil moisture storage, and thereby decrease runoff. This decrease in runoff will lead to lower flushing rates and longer contact times with rock minerals (Rouse et al 1997). Therefore, runoff will have higher nutrient concentrations. In summary, nutrient concentrations are expected to increase with global warming.

Rouse et al. (1997) also suggest that an increase in the active layer depth may increase sediment erosion thereby increasing suspended sediment concentrations. In addition, dissolved organic carbon (DOC) concentrations may increase and water darkening may occur. Thus, light attenuation may increase and primary production may decrease if light is limiting.

With decreased runoff, river disturbances will decrease in magnitude. The intermediate disturbance hypothesis states that species diversity is greatest when

disturbance frequency and magnitude is at an intermediate level (Connell 1978). When disturbance frequency and magnitude is low, competitively strong organisms will out--compete competitively weak organisms thus lowering species diversity. Meanwhile, ecosystems with high disturbance frequency and magnitude prevent organisms from establishing viable populations. Ecosystems with intermediate disturbance frequency and magnitude prevent competitively strong organisms from dominating competitively weak organisms. Further, more organisms can establish viable populations in ecosystems with intermediate disturbances than in ecosystems with high disturbances. Since disturbance frequency and magnitude in Arctic streams are high, the intermediate disturbance hypothesis suggests that more organisms will be able to survive in a more moderate Arctic environment. Furthermore, organisms specially adapted to these harsh Arctic environments may become extinct from competition by invasive species. Rouse et al. (1997) predict that global warming will initiate a series fish immigrations and extinctions.

Rouse et al. (1997) also predict a longer ice--free season meaning autotrophic organisms will have a longer growing season.

Hobbie et al. (1999) predict that permafrost thawing will increase phosphorous runoff into streams near Toolik Lake. They were able to test thawing effects at a site near Toolik Lake where several meters of surface gravel were removed from glacial kames for road construction in the early 1970's. The stream that passes through one of the disturbed kames is turbid and extraordinarily high in phosphate and other nutrients. They concluded that permafrost near the glacial kame is melting thus increasing nutrient loads into the stream.

Le Dizes et al. (2003) modeled climate change of terrestrial tundra ecosystems in the Kuparuk River Catchment. They predicted that terrestrial net ecosystem production would increase; thus, C sequestration would increase. The Arctic tundra will act as a C sink. The vegetation C:N ratio should increase because increased net primary production will increase the carbon content of the vegetation. These scientists expect the vegetation to compensate for this increased carbon content by increasing N uptake from the soils.

Impacts of low--level phosphorus loading to Arctic streams have been a key component of the Arctic Long Term Ecological Research (LTER) research program at Toolik Lake, Alaska (Peterson et al. 1993, Slavik et al. 2004). For 20 years, the Kuparuk River has been the subject of an annual low--level phosphorous fertilization experiment. If global warming increases phosphorous loading in Arctic streams then this fertilization experiment may simulate the potential effects of global warming on these relatively pristine stream ecosystems.

Metabolism in the Kuparuk River

General Information

The Kuparuk River originates in the foothills of the Brooks Range on the North Slope of Arctic Alaska and drains north into the Arctic Ocean (Fig. 2). The experimental reaches of the Kuparuk River bestride the Dalton Highway (68° 38′ N, 149° 24′ W) (Fig. 3). This river is characterized as a cobble--bottom, fourth--order stream with meandering pool--riffle sequences. The average channel slope is 0.6% and the sinuosity is 1.5 (Kriet

et al. 1992, Slavik et al. 2004). The drainage basin area of the upper Kuparuk River is 143 km^2 and the main channel length is 25 km (Hershey et al. 1997). The vegetation in the upper Kuparuk drainage basin, consists mostly of upland heath communities on dry soils, moist tundra communities dominated by the tussock--forming cotton grass *Eriophorum vaginatum*, and wet sedge tundra dominated by *Carex aquatilus* (Hershey et al. 1997). The Kuparuk River is classified as a clear--water tundra river. This means it has no glacial input and very little input from springs (Craig and McCart 1975). The Kuparuk River has a mean summer discharge of 2.3 $m^3 s^{-1}$, width of ~17 m, and velocity is 0.30 m s^{-1} (Edwardson et al. 2003, Slavik et al. 2004). Thus, the mean depth is ~0.45 m. Stream bank vegetation is predominantly comprised of dwarf willows (*Salix spp.*), wet sedge (*Carex spp.*), and birches (*Betula nana*). The bank vegetation rarely exceeds 1 m in height so it does not shade the stream channel.

Arctic LTER researchers have added phosphorous every year since 1983 from about mid--June to mid--August. They dripped phosphoric acid into the river with a peristaltic pump at relatively steady rate. The experimental zone in the Kuparuk River has been subject to several experimental manipulations. In 1983 and 1984, phosphoric acid was added at 0.0 k at 0.32 µM. From 1985 to 1995, phosphoric acid was added at 0.59 k at 0.32 µM. In 1986, phosphoric acid and ammonium sulfate was added at 1.11 k at 0.32 µM for phosphoric acid and 7.1 µM for ammonium sulfate. In 1989, ammonium sulfate was added at 1.11 k at 7.1 µM. In 1995 stable N--15 isotope was added at -1.5 k. From 1996 to 2003, phosphoric acid was added at 1.4 k at 0.32 µM. In 2004, there were two

phosphoric acid inputs. Phosphoric acid was added at 1.4 k at 0.32 µM and at 2.8 k at 0.96 µM.

The mean reference reach soluble reactive phosphorous (SRP) concentrations are 0.08 µM ± 0.01 µM; ammonium concentrations are 0.2 -- 0.35 µM; nitrate concentrations are 0.4 -- 5.0 µM (Slavik et al 2004).

Kuparuk Light Dynamics

The majority of photosynthesis in the Kuparuk River occurs on the benthos and not the water column (Arscott et al. 1998); thus, we need to know the amount of submerged light reaching the benthos. The amount of submerged light reaching the plant surface is calculated with the following equation:

$$I = I_o * e^{(-k_e * z)} \qquad \text{(eq. 38)}$$

where I is submerged light, I_o is surface PAR, k_e rate of light attenuation through the water column, and z is water depth (Carr et al. 1997).

The photoperiod is 24 hours during most of the summer field season at Toolik Lake Alaska. This could be problematic because WSM measurements assume that GEP is zero at solar midnight. However, there is a strong diurnal change in light intensity at the surface of most stream bottoms. At the summer solstice, the surface (PAR) ranged from a maximum of ~ 1500 µmole m^{-2} s^{-1} at solar noon to a maximum of ~ 66 µmole m^{-2} s^{-1} at solar midnight. Furthermore, light reflection at the water surface and light scatter in the water column will further diminish the light intensity at solar midnight.

Greater light reflection occurs at solar midnight than at solar noon in the Arctic summer because reflection increases with the incident light angle. A light reflection variable is not included in the submerged light equation above. The proportion of surface light reflected can be calculated by Fresnel's Law:

$$r_s = \left[\frac{\sin(\theta_1 - \theta_2)}{\sin(\theta_1 + \theta_2)}\right]^2 \qquad r_p = \left[\frac{\tan(\theta_1 - \theta_2)}{\tan(\theta_1 - \theta_2)}\right]^2 \qquad \text{(eq. 39)}$$

where r_s is the proportion of s--polarized light reflected, r_p is the proportion of p--polarized light reflected, θ_1 is the incident angle of sunlight, θ_2 is the angle of the refracted light inside water. The total proportion of reflected light is calculated with the following equation:

$$r_t = \frac{r_s + r_p}{2} \qquad \text{(eq. 40)}$$

The angle of the refracted light inside water is calculated with the following equation:

$$\theta_2 = \sin^{-1}\left(\frac{\sin\theta_1}{n}\right) \qquad \text{(eq. 41)}$$

where n is the refractive index of water (1.33). The sun's incidence angle at solar midnight during the summer solstice in Toolik Lake, Alaska is 85.33°. Thus, the

proportion of light reflected from the water surface is 60.5%. In contrast, the sun's incidence angle at solar noon during the summer solstice is 48.73° and the proportion of light reflected from the water surface is 3.2%. Thus, the maximum amount of light penetrating the water surface at solar midnight is ~ 26 µmole m^{-2} s^{-1} (i.e., ~ 66 µmole m^{-2} s^{-1} multiplied by the fraction of light not reflected [1 – 0.605]). The light level that actually reaches the stream bottom is less than this due to factors such as scattering, absorption, and bank shading. Thus, counter to expectation, light levels at the bottom of streams on the North Slope of Alaska are quite low at midnight, despite the fact that there is '24 hour sunlight'. This is essential for the whole--stream metabolism approach to work in these high latitude streams.

Kuparuk Temperature Dynamics

The Kuparuk River freezes from about late September to late May. The air temperatures range from ¯30 -- ¯40°C for winter lows to 10 -- 18°C for summer highs (Selkregg 1977, Scott 1978). The mean annual water temperature is 1.7°C (Laundre, unpublished data); the mean annual water temperature when unfrozen is 9°C. The North Slope receives about 18 cm of precipitation, mostly in the form of snowfall (Selkregg 1977, Scott 1978, Kriet et al. 1992).

Kuparuk Nutrient Dynamics

Carbon

Peterson et al. (1986) and Harvey et al. (1997) investigated carbon dynamics in the Kuparuk River. The carbon dynamics are grouped in three different categories: inputs, standing crops, and outputs.

Carbon inputs were divided into two categories: autochthonous and allochthonous. Autochthonous primary production was measured with the closed--system method in 1978 and 1980 (Peterson et al. 1986), 1984 and 1985 (Peterson et al. 1993), and 1989 (Bowden et al. 1992). GEP estimates for algae were 49 g C m^{-2} y^{-1}, hyporheos 5 g C m^{-2} y^{-1} and *S. agassizii* 55 g C m^{-2} y^{-1} (Harvey et al 1997; Bowden and Finlay, unpublished data). Allochthonous materials include peat and tundra plant fragments. Peat erodes mostly from the stream bank while tundra plant fragments enter when flows went over the banks and swept plant material into the river. Peat contributed 300 g C m^{-2} y^{-1} while tundra plant fragments contributed ~ 200 g C m^{-2} y^{-1} (Peterson et al. 1986). DOM and POM have not yet been intensively measured.

Carbon standing crops include course benthic organic matter (CBOM), fine benthic organic matter (FBOM), algae, bryophytes, invertebrates, and fish. CBOM was 48.5 g C m^{-2} and FBOM was 7.6 g C m^{-2}. Benthic algal standing crop was 1.1 g C m^{-2} and benthic bryophyte standing crop was 20 g C m^{-2} (Peterson et al. 1986, Bowden et al. 1992, Bowden et al. 1994). Invertebrate standing crop was roughly 1.3 g C m^{-2} and fish standing crop was 0.2 g C m^{-2} (Hershey unpublished data; Deegan & Peterson 1992).

Carbon outputs include FPOM, CPOM, and DOM, and respiration. FPOM transport was 4.5 x 10^4 kg y^{-1}, CPOM transport was 7.4 x 10^3 kg y^{-1}, and DOM transport was 6.4 x 10^5 kg y^{-1}. Respiration for algae was 24 g C m^{-2} y^{-1}, hyporheos was 4 g C m^{-2} y^{-1}, and *S. agassizii* was 16 g C m^{-2} y^{-1} (Bowden et al. 1994). Respiration for invertebrates and fish are unavailable.

Edwardson et al. (2003) compared benthic C uptake rates in the reference and fertilized reaches of the Kuparuk River. Benthic carbon uptake rates (mmol C m^{-2} h^{-1}) were greater in the fertilized reach (6.3) than in the reference reach (2.3).

Nitrogen

Ammonium enters the stream from surface and subsurface runoff (Harvey et al. 1997). In addition, in--stream ammonium evolution occurs from mineralization of organic matter. Nitrate enters by tributaries, seeps, and springs (Harvey et al. 1997). In--stream nitrate evolution occurs from nitrification of ammonium.

Peterson et al. (1997) did a ^{15}N--NH_4--tracer study in the reference reach of Kuparuk River. Wollheim et al. (2001) followed up that experiment with modeling analysis of nitrogen cycling. They found filamentous algae preferred NH_4 over NO_3 80% : 20%, diatoms 45% : 55%, and *S. agassizii* 20% : 80%. Epilithic N uptake rate was 30 mg N m^{-2} d^{-1}. They estimated lateral inputs of NH_4 and NO_3 as 12.9 and 4.1 mg N m^{-2} d^{-1} respectively. Further, areal NH_4 uptake rates were four times greater in the fertilized reach than in the reference reach.

Edwardson et al. (2003) compared benthic N uptake rates in the reference and fertilized reaches of the Kuparuk River. Benthic nitrogen uptake rates (mmol m^{-2} h^{-1}) were greater in the fertilized reach (0.95) than in the reference reach (0.34).

Phosphorous

Phosphorous enters the Kuparuk River by runoff from land and by mineral association of in--stream organic matter.

Slavik et al. (2004) reported that the Kuparuk River is oligotrophic and mostly phosphorous limited. However, Bowden et al. (1992) found that fertilization with ammonium and phosphorous increased epilithic chl *a*, photosynthesis, and respiration more than phosphorous fertilization alone. This suggests that the Kuparuk River may be close to co--limitation by nitrogen and phosphorus.

Edwardson et al. (2003) compared benthic phosphorous uptake rates in the reference and fertilized reaches of the Kuparuk River. Benthic phosphorous uptake rates (mmol m^{-2} h^{-1}) were greater in the fertilized reach (0.060) than in the reference reach (0.022).

Kuparuk River Nutrient--Discharge Dynamics

McDiffett et al. (1989) studied nutrient--discharge relationships in a first--order nutrient--rich river in Pennsylvania. Much of the nitrate and phosphate originated from the surrounding agriculture. Initially, nutrient concentrations increased during a spate; however, nutrient concentrations were eventually diluted below pre--spate levels.

Bond (1979) studied nutrient--discharge dynamics in a large undisturbed montane stream ecosystem in Utah. In this ecosystem, nitrate and phosphate concentrations had insignificant relationships with discharge. The ambient nitrate and phosphate concentrations were very low and there were no significant inputs from the surrounding watershed.

Slavik et al. (2004) report long--term results from an experiment in which the Kuparuk River was fertilized with a phosphoric acid dripper at a constant rate during the June to August periods for ~ 20 years (since 1983). Phosphorous in the fertilized zones of

the Kuparuk River is diluted with increased discharge. On the other hand, nitrate concentrations initially increase with discharge then decrease to pre--spate levels. This nitrate pulse probably comes from nitrate runoff from the landscape.

Extracellular nutrient dilution in the Kuparuk River will not instantaneously reduce photosynthetic or respiration rates (Strener & Elser 2002). Strener and Elser (2002) noted that primary producers undergo luxury consumption of nutrients and store these excess nutrients in their vacuoles. Thus, short-term extracellular nutrient deficiencies have no effect on photosynthesis or respiration. Instead, prolonged decreases in extracellular nutrient concentrations are necessary to decrease intracellular nutrient concentrations. After significant decreases in intracellular nutrient concentrations, protein production will decrease. Eventually, significant decreases in cellular protein concentrations will slow down photosynthetic rates in primary producers.

Kuparuk Discharge Dynamics

Permafrost underlies the Kuparuk River Catchment, which eliminates deep infiltration of water. The maximum thaw depth is < 1 m (Harvey et al. 1997). The Kuparuk River discharge can vary from 0.3 m^3 during dry periods to 100 m^3 during storms and spring snowmelt (Oatley 2002). Discharge can rapidly increase even during small rain events because infiltration is limited by permafrost.

Oatley (2002) studied bedload transport in the Kuparuk River. He calculated the reach--average median grain size to be 70 mm using the method described by Wolman (1954). Using stream channel cross--section data, he calculated the bed movement threshold to be $15 m^3 s^{-1}$.

Primary Producers of the Kuparuk River

The photosynthetic organisms of the Kuparuk River are mostly comprised of epilithic algae and bryophytes. Water column photosynthesis is negligible; therefore, photosynthesis occurs mostly in the benthos.

The reference reach of the Kuparuk River consists of two major primary producers: *S. agassizii*, and micro--epilithon. *S. agassizii* is a moss characterized by slow growth, small fronds, dense compaction, and tight adherence to the substrate. Micro--epilithon is algae that tightly adhere to rock substrates. Since *S. agassizii* and micro--epilithon adhere tightly to the substrate, they are adapted to frequent and severe disturbance. Micro--epilithon is adapted to severe bed--moving disturbance because they have a fast growth rate. While *S. agassizii* has a slow growth rate, a severe bed--moving disturbance will move all but the largest rocks. However, *S. agassizii* colonizes mostly boulders that will not move during a severe bed--moving spate.

The fertilized and ultra--fertilized reach of the Kuparuk River consists of three major primary producers: *S. agassizii*, *Hygrohypnum spp.*, and micro--epilithon. In contrast, the moss, *Hygrohypnum* is characterized by fast growth, long fronds, no compaction, and loose adherence to the substrate. Comparatively, *Hygrohypnum* is not well adapted to severe environments.

Miller et al. (1992) investigated the response of the epilithic diatom community to PO_4 fertilization in the Kuparuk River. This study occurred between 1983 -- 1987 before *Hygrohypnum* began to proliferate in the fertilized reach. During the first year of fertilization, species diversity and evenness decreased. By the second year, species

diversity and richness increased to maximum levels. From 1985 -- 1987 the epilithic biomass decreased by an order of magnitude. The reduction in epilithic biomass was attributed to the delayed population increase by grazing insects. The community became dominated by either fast--growing or prostrate species while some erect species declined.

Bowden et al. (1994) investigated the long--term effects of PO_4 fertilization on the bryophyte distribution in the Kuparuk River. After 7 years of fertilization, the investigators noted extensive bryophyte coverage in the fertilized reach. The investigators used plots and point transects to determine benthic bryophyte cover. The results suggested even distribution of *S. agassizii* in the fertilized and unfertilized reaches. In contrast, *Hygrohypnum* was found almost exclusively in the fertilized reach.

Finlay and Bowden (1994) hypothesized that bryophyte growth was limited by low phosphorous concentrations in the unfertilized reach and limited by epiphytes in the fertilized reach. *Hygrohypnum* stem tips elongated in the fertilized reach but not in the reference reach. Epiphyte biomass was over 4 times greater in the fertilized pools than in the fertilized riffles. In addition, epiphyte chl *a* was 4 times greater in the pools than in the riffles. The authors attributed these findings by increased detrital decomposition and reduced grazing by pool invertebrates.

Finlay and Bowden (1994) also measured N:P ratios for *Hygrohypnum* and *S. agassizii*. The initial N:P ratio for *Hygrohypnum* was 4.42. When *Hygrohypnum* was transplanted for a month the fertilized reach, its N:P ratio increased to 4.81 while the N:P ratio was 8.01 in the unfertilized reach. The initial *S. agassizii* N:P ratio was 5.25. In the

fertilized reach its N:P ratio increased to 5.64 and its N:P ratio increased to 7.03 in the unfertilized reach.

Slavik et al. (2004) measured epilithic stoichiometric ratios in the Kuparuk River. Reference reach C:N, C:P, and N:P ratios were 12.2, 232.2, and 20.3 respectively. Fertilized reach C:N, C:P and N:P ratios were 11.6, 153.8, and 14.1 respectively.

Arscott and Bowden (1998) compared epilithic algal and bryophyte metabolism in the Kuparuk River using the closed system method. They compared photosynthetic rates of epilithic algae, *S. agassizii*, and *Hygrohypnum* under unfertilized and fertilized conditions.

Percent cover was estimated using point transects. The dominant cover types in the reference reach were micro--epilithon and detritus in pools and micro--epilithon and *S. agassizii* in riffles. The dominant cover types in the fertilized reach were micro--epilithon, detritus, and *Hygrohypnum* in pools and micro--epilithon, *Hygrohypnum*, and *S. agassizii* in riffles. Micro--epilithon dominated the pools and riffles of the unfertilized reach while *Hygrohypnum* dominated the riffles of the fertilized reach. Moss coverage was greater in fertilized pools than unfertilized pools, although the mosses found in pools looked unhealthy.

Phosphorous had no effect on chl *a* of algal epilithon except for pools in late summer. There were higher standing stocks of chl *a* in early summer than late summer. Pools had greater chl *a* than riffles except for the unfertilized zone in late summer.

Corrected for chl *a*, P_{max} and α is greater in riffle micro--epilithon than pool micro--epilithon. The authors suggest that higher P_{max} rates in the riffle are a combination

of higher scour and grazing in riffles remove biomass and stimulate continuous growth. In addition, pool micro--epilithon accumulates senescent cells and detritus, which shade photosynthetically active cells. Thus, pool micro--epilithon may be shade adapted.

Areal NPP for pool epilithic algae (73.2 -- 102.3 mg O_2 m^{-2} h^{-1}) was slightly less although not significantly less than riffle epilithic algae (91.2 -- 112.5 mg O_2 m^{-2} h^{-1}). However, many storms occurred during the field season, thus, pool epilithon did not have a chance to build up. Bowden et al (1992) reported that areal rates of production by epilithic algae in pools were greater than riffles.

Areal production of epilithic algae in the fertilized reach was not clearly different from the unfertilized reach. Furthermore, areal epilithic algal production during the early season was not clearly different from the late season.

Higher P_{max} values in the fertilized reach were recorded for both moss species late in the season. In contrast, higher P_{max} values in the unfertilized reach were recorded for both moss species early in the season. The researchers believe PO_4 fertilization extends the optimal growing season for mosses. P_{max} decreases in the reference reach may be attributed to spring nutrient pulses and competition with epiphytic algae.

Primary production per unit chl *a* is greater in epilithic algae than both bryophytes. However, bryophyte biomass was much greater than epilithic algal biomass in the fertilized reach. Thus, chl *a* content per m^2 was greater for *Hygrohypnum* (362 -- 542 mg chl *a* m^{-2}) than epilithic algae (18 -- 38 mg chl *a* m^{-2}) in the fertilized reach. Integrated NPP in the unfertilized reach was estimated to be 2.28 g C h^{-1} with 90% of this production from epilithic algae and 10% from *S. agassizii*. In the fertilized reach,

integrated NPP estimations were 6.32 g C h^{-1} with 64% of this production from *Hygrohypnum*, 7% from *S. agassizii*, and 20% from epilithic algae.

Arscott et al. (1998) described the different bryophyte growth strategies. They classified *S. agassizii* as a stress tolerator. *S. agassizii*'s low photosynthetic rates reduce its need for nutrients. Furthermore, its short pincushion growth form and firm attachment to substrate reduce its probability of damage from disturbance. On the other hand, *Hygrohypnum* is classified as a competitor: higher photosynthetic rates, nutrient uptake rates, and tissue turnover rates. Thus, *Hygrohypnum* thrives in moderate/high nutrient environments.

Arscott et al. (2000) experimentally manipulated desiccation, irradiance, and temperature in *S. agassizii* and *Hygrohypnum* to test the hypothesis that *S. agassizii* is a stress tolerator while *Hygrohypnum* is a competitor. *S. agassizii* showed, rapid recovery from desiccation, low responses to increased light, and inhibition at high temperatures. In contrast, *Hygrohypnum* was vulnerable to desiccation but responded robustly to increased light and temperature.

Hyporheic Zone of the Kuparuk River

Although, the Kuparuk River is frozen solid for about 8 months of the year, the hyporheic zone is present when the river is thawed (Edwardson et al. 2003). Edwardson et al. (2003) measured nutrients, DO, and CO_2 at upwelling and downwelling sites in the Kuparuk River. NH_4 concentrations were generally higher in upwelling water than in channel water; intermediate NH_4 concentrations were found in downwelling water. Concentrations of NO_3 generally increased from channel water to upwelling water to

downwelling water. Concentrations of PO_4 were generally highest at upwelling sites and lower at downwelling sites. Concentrations of PO_4 were the lowest in channel water. Channel water had the highest DO concentrations followed by downwelling water; upwelling water had the lowest DO concentrations. Concentrations of CO_2 were the higher in upwelling sites than downwelling sites. During warm weather, temperature generally increases as water moves from the downwelling sites to the upwelling sites. The temperature gradually decreased when water moved along the longitudinal flow path of the parafluvial zone.

Food Web of the Kuparuk River

It is generally thought that bryophytes are not a food source for invertebrates or fish (but see, (Bowden 1999)). In the Kuparuk River, epilithic and epiphytic algae appear to be the major food source for invertebrates while invertebrates are the major food source for the fish (Benstead, personal communication).

Tables

Table 1. Photosynthesis-irradiance curves.

Equation Number	Equation	Source
21	$P = \begin{cases} \alpha * I, \rightarrow I \le P_{\max} / \alpha \\ P_{\max}, \rightarrow I > P_{\max} / \alpha \end{cases}$	Blackman (1905)
22	$P = \frac{P_{\max} * \alpha * I}{P_{\max} + \alpha * I}$	Baly (1935)
23	$P = \frac{P_{\max} * \alpha * I}{\left[(P_{\max})^2 + (\alpha * I)^2 \right]^{\frac{1}{2}}}$	Smith (1936)
24	$P = \alpha * I e^{\left(\frac{-\alpha * I}{P_{\max} e} \right)}$	Steele (1962)
25	$P = \begin{cases} \alpha * I e^{\left(\frac{-\alpha * I}{P_{\max} e} \right)}, \rightarrow I \le P_{\max} e / \alpha \\ P_{\max}, \rightarrow I > P_{\max} e / \alpha \end{cases}$	Steele (1962)
26	$P = P_{\max} * \left[1 - e^{\left(\frac{-\alpha * I}{P_{\max}} \right)} \right]$	Webb et al. (1974)
27	$P = \begin{cases} \frac{\alpha * I - (\alpha * I)^2}{4 P_{\max}}, \rightarrow I \le 2 P_{\max} / \alpha \\ P_{\max}, \rightarrow I > 2 P_{\max} / \alpha \end{cases}$	Platt et al.(1975)
28	$P = P_{\max} * \tanh\left(\frac{\alpha * I}{P_{\max}} \right)$	Jassby and Platt (1976)
29	$P = P_{\max} * \left(\frac{I}{K_m + I} \right)$	Carr et al. (1997)

Figure Legends

Figure 1. Oxygen budget for a stream reach.

Figures

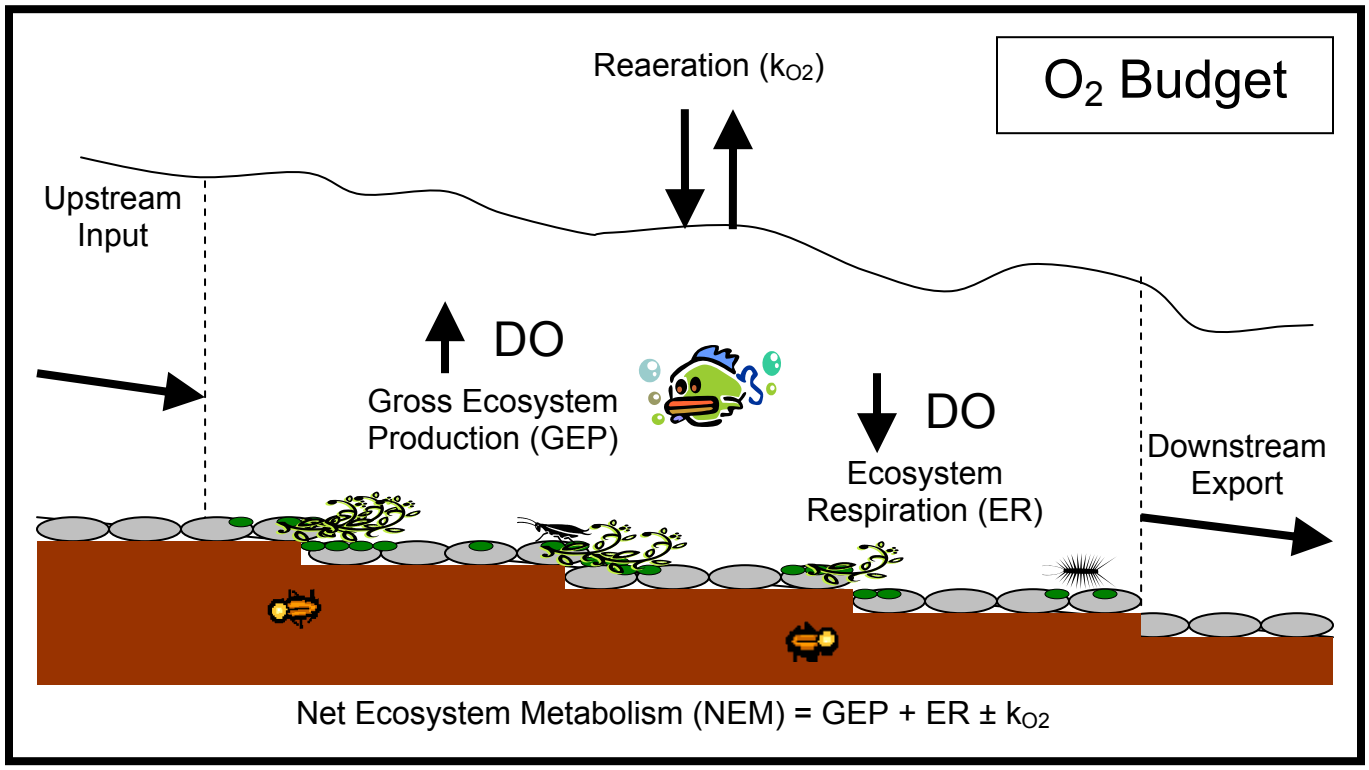

Figure 1.

Chapter 1: Modification and application of the whole--stream metabolism method for streams in Arctic environments

Abstract

Global warming may significantly alter whole--stream metabolism (WSM) in Arctic rivers, which may change net CO_2 fluxes on an ecosystem scale. The WSM method has not been applied in high--latitude regions because it has been assumed that the 24--hour photoperiod during the summer would preclude accurate estimate of ecosystem respiration (ER) in the dark and subsequent calculation of gross ecosystem production (GEP) in the light. We found that --- with some modification --- the WSM method could be reliably applied in Arctic streams near the Toolik Lake Field Station, Alaska (68^{o} N latitude). We measured WSM for 6 -- 9 days in 2001 and 2003 and for ~ 50 days in 2004 in the reference and fertilized reaches of the Kuparuk River. Ambient soluble reactive phosphorous (SRP) levels in the reference reach were ~ 0.08 μM, while addition of H_3PO_4 since 1983 in the fertilized reach increased SRP levels to a nominal concentration of ~ 0.30 μM at the mean annual flow of 2 m^3 sec^{-1}. We compared our past closed--system calculations (1989 -- 1994) with our WSM open--system calculations. Closed--system GPP calculations were not significantly different from the open--system GEP calculations, while closed--system CR calculations were ~ 28 times lower than the open--system ER calculations. This latter result is likely because closed--system estimates of respiration do not account for hyporheic respiration. Within the open--

system calculations, we compared single and dual station calculations. Single and dual station calculations of GEP and ER respectively, were not significantly different. As expected GEP was higher in the fertilized reach but unexpectedly, ER was not significantly different between reaches. The midnight metabolism correction is the metabolism correction for photosynthesis occurring at solar midnight. The results of corrected GEP and ER were similar to the uncorrected GEP and ER so the metabolism correction did not influence the overall results. On average, the midnight metabolism correction increased GEP by 13.0 % and 13.2 % of GEP in the reference and fertilized reaches, respectively, and ER by 1.1% and 2.0% of ER in the reference and fertilized reaches, respectively. Thus, the midnight metabolism correction proportionally influences GEP more than ER. Midnight surface sunlight deceased from late June to early August and this seasonal change influenced the midnight metabolism correction. We conclude that the WSM method, with simple modifications, can be applied reliably in Arctic streams during the summer months even when photoperiods are 24 hours long.

Introduction

Past studies show that Arctic Alaskan Rivers release substantial amounts of CO_2 into the atmosphere and influence the carbon budget on a landscape scale (Kling et al. 1991; Kling et al. 1992). Global warming may increase temperature, discharge, and phosphorous in Arctic rivers (Rouse et al. 1997, IPCC 2001, ACIA 2004). These physical and chemical changes may significantly alter whole--stream metabolism (WSM) in Arctic rivers, which may change net CO_2 fluxes on an ecosystem scale.

While open--system, WSM methods have been widely used to calculate gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) in temperate and tropical streams (Young and Huryn 1999, Mulholland et al. 2001, Uehlinger et al. 2003, Acuna et al. 2004), these method have not been used in Arctic streams. The Arctic ecosystem is unique because the summer photoperiod is 24 hours and so there is no "dark" period. The WSM method relies on a dark period to estimate ER, which is then used to calculate GEP from the net changes in oxygen measured in the stream. Thus, we had assumed that the WSM method would not work for our studies of Arctic streams.

However, we have found that with some modification the open--system WSM method works well in streams near the Toolik Lake Field Station in Arctic Alaska (68^{o}N latitude). The primary objective of this report is to explain the methods we have used to correct for the 24--hour photoperiod in these high--latitude streams. We also compared estimates of gross photosynthesis and respiration that we have derived for the Kuparuk River using both closed-- and open--system methods and for the open--system method

both dual-- and single--station methods. As a part of this analysis, we examined the differences in gross ecosystem production (GEP), and ecosystem respiration (ER) between reaches. Specifically, we hypothesized that:

- open and closed--system estimates of GEP would be similar,
- open and closed--system ER estimates would be different because the closed--system experiments did not include hyporheic respiration,
- dual and single station approaches would yield similar estimates of GEP and ER, and finally
- GEP and ER would be higher in the fertilized reach.

Methods

Site Description

The Kuparuk River originates in the foothills of the Brooks Range on the North Slope of Alaska and flows north into the Arctic Ocean (Fig. 2). The experimental reaches of the Kuparuk River are located near the Dalton Highway (68° 38′ N, 149° 24′ W). This river is a cobble--bottom, fourth--order stream with meandering pool--riffle sequences. The average channel slope is 0.6% and the sinuosity is 1.5 (Kriet et al. 1992, Slavik et al. 2004). The drainage basin area of the upper Kuparuk River is 143 km^2 and the main channel length is 25 km (Hershey et al. 1997). The Kuparuk River has a mean summer discharge of 2.3 $m^3 s^{-1}$ and width of 17 m (Slavik et al. 2004).

The vegetation in the upper Kuparuk drainage basin, consists mostly of upland heath communities on dry soils, moist tundra communities dominated by the tussock--forming cotton grass *Eriophorum vaginatum*, and wet sedge tundra dominated by *Carex aquatilus* (Hershey et al. 1997). Stream bank vegetation is mainly comprised of dwarf willows (*Salix spp.*), wet sedge (*Carex spp.*), and birches (*Betula nana*). The bank vegetation rarely exceeds 1 m in height so it does not shade the stream channel and the photoperiod is 24 hours during most of the summer field season thus, the Kuparuk River receives a plethora of light in the summer.

The Kuparuk River freezes from about late September to late May. The mean summer water temperatures of the Kuparuk River are 8 -- 10°C while occasionally reaching 21°C at low flow and 3°C at high flow (Hershey et al. 1997). On a diel timescale, the temperatures can change up to 10°C (Hershey et al.1997).

Permafrost underlies the Kuparuk River catchment and limits deep groundwater flow into the Kuparuk River. Further, there are no glacial inputs, so channel precipitation, overland flow, and shallow interflow feeds the Kuparuk River (McNamara et al. 1998). Interflow is water that flows above the permafrost in a shallow zone called the active layer which freezes and thaws annually to depths of ~ 25 -- 40 cm (Hinzman 1991). Since the active layer is shallow and generally saturated, discharge increases rapidly even during small rain events and during periods of summer drought the river almost stops flowing. Oatley (2002) reported that the Kuparuk River discharge could vary from 0.3 m^3 s^{-1} during dry periods to 100 m^3 s^{-1} during storms and spring snowmelt. Thus, the low

base flows and the rapid and high peak flows are reminiscent of an urban or desert catchment.

The Kuparuk River has low ambient nutrient concentrations and is limited by phosphorous in the reference reach (Fig. 3) while phosphorous and nitrogen are co--limiting in the fertilized reach (Bowden et al. 1992, Slavik et al. 2004). Over the last 16 years of study, the mean reference reach SRP concentrations were 0.08 μM ± 0.01 μM while the fertilized reach had a mean SRP concentration of ~ 0.30 μM at the mean annual flow of 2.3 m^3 sec^{-1} (Slavik et al. 2004). The Kuparuk River NH_4 levels were 0.20 -- 0.35 μM which were typically below the detection limit (Slavik et al. 2004). Nitrate levels were 0.4 -- 5.0 μM in the reference reach while nitrate levels were typically lower in the fertilized reach suggesting increased nitrate uptake rates in the fertilized reach (Slavik et al 2004).

The reference reach of the Kuparuk River has two major primary producers: *Schistidium agassizii*, and micro--epilithon (Diatoms) with micro--epilithon being the most dominant (Bowden et al. 1994, Arscott et al. 1998). In contrast, the fertilized reach of the Kuparuk River has three major primary producers: *S. agassizii*, *Hygrohypnum spp.*, and micro--epilithon with *Hygrohypnum* being the most dominant (Arscott et al. 1998). Compared to *S. agassizii*, *Hygrohypnum* grows faster, has much longer fronds, thus it is less compacted, and more loosely adhered to the substrate.

Field & Laboratory Methods

We measured dissolved oxygen (DO), surface light, water temperature, and discharge in the Kuparuk River in 2001, 2003, and 2004. In 2001, we took measurements

during the early (late June), middle (July), and late (late July/early August) season. In 2003, we took measurements in the early and late season and in 2004, we took measurements throughout the entire season (late June to early August). We established measuring stations at the bottom of the reference (0.5 km) and fertilized reaches (2.0 km; Fig. 3). For the dual station method in 2001 and 2003, we placed the upstream stations at 0.0 km for the reference reach and 1.4 km for the fertilized reach (Fig. 3). Each station included a DO, surface light, and water temperature sensor. We used a WTW 325 CellOx sensor to measure DO and temperature, and a Li--Cor LI--190SB light sensor to measure photosynthetic active radiation (PAR) at the water surface. We connected the sensors to a Campbell 10X datalogger to record the data every 5 seconds and averaged those measurements every 5 minutes. During the 2004 season, we checked the datalogging station about three times a week, re--calibrating sensors as necessary to ensure accurate sensor readings over the long--term measurement period.

We placed the DO and water temperature sensors in the thalweg of the stream; and we placed the datalogger on the floodplain and mounted the surface light sensor on a stake above the vegetation and next to the datalogger. A stage height recording gauge provided continuous estimates of discharge at 0.65 km and a new rating curve was calculated each year (Knighton 1998; Fig. 3). We estimated differences in discharge between reaches from empirical measurements of discharge between reaches (Peterson et al. unpublished data).

Phosphoric acid was added to the fertilized reach of the Kuparuk River with a peristaltic pump with a target fertilization concentration of 0.30μM SRP (Slavik et al.

2004). In 2001 and 2003, we sampled SRP, NH_4, and NO_3 two or three times during the season while in 2004 we sampled SRP, NH_4, and NO_3 twice a week for the entire season. . We analyzed SRP using colorimetric methods (Parsons et al. 1984) with a Varian Cary 50 spectrophotometer, NH_4 with a Turner Designs 10--Au fluorometer using the OPA method (Holmes et al. 1999), and NO_3 using colorimetric methods with a Lachet Quik--Chem 8000 (Diamond 2003).

Closed--system metabolism was calculated from 1989 -- 1994 in the reference and fertilized reaches of the Kuparuk River using the methods described in Bowden et al. (1992). Since the Kuparuk River contains approximately 50% riffles and 50% pools, we randomly collected rocks from riffles or pools within each reach. Contributions of gross primary production (GPP) and community respiration (CR) from riffles and pools were averaged for each reach.

Open--System Metabolism Calculation

Similar to non--Arctic ecosystems, we calculated net ecosystem metabolism (NEM) with a DO mass balance model described in Marzolf et al. (1994), and Young and Huryn (1998). We measured reaeration using the sound pressure method (Morse et al. in review). We used the single station method in all of our open--system calculations unless noted. While NEM is calculated with a DO mass balance model, the method to calculate ER and GEP described by Marzolf et al. (1994) and Young and Huryn (1998) are based on the premise that there is a long dark period. During this long dark period, GEP is assumed to be zero so nighttime NEM is equal to ER. Thus, the average nighttime NEM values are an estimate of that night's ER value. Then ER is interpolated between each

night's ER value to calculate ER during the daytime (Fig. 6A). Then ER calculations are subtracted from NEM to calculate GEP.

However, the Arctic summer does not have a prolonged dark period (Fig. 4A & B) so we cannot calculate ER and GEP using standard methods. The photoperiod around the Kuparuk River is 24 hours long from late May to late July while the photoperiod shortens to about 20 hours by early August. Although the photoperiod is 24 hours during much of the field season, light decreases substantially at solar midnight (Fig. 4A & B). Further, submerged light penetrating down to the benthic photosynthesizers is lower than the surface light because surface light reflects from the stream surface, and light absorption and scatter reduce light penetration to the benthos (Fig. 4B).

While the traditional methodology is adequate for calculation of NEM in Arctic ecosystems, the lack of a prolonged dark period during the Arctic summer prohibits calculation of ER and GEP based on the traditional methodology. Instead of calculating a night's ER value based on the average nighttime NEM values, we calculated a night's ER value based on the NEM value at solar midnight (02:00:00 for the Kuparuk River; Fig. 6B). Similar to the traditional methodology, we interpolate ER between each night's ER value. Then we calculate GEP by subtracting ER from NEM. While this methodology corrects for the lack of a prolonged dark period it does not correct for photosynthesis occurring at solar midnight when sunlight is greater than 0.

Around the summer solstice in the Kuparuk River, we observed a maximum of ~ 66 μmole m^{-2} s^{-1} of surface light at solar midnight. To correct for sunlight at solar midnight, we plotted surface light against GEP from solar noon to solar midnight to

create a photosynthesis--irradiance (PI) curve (Fig. 5A). We used surface light for our PI curves instead of submerged light because surface light exhibited less spatial variability and was available in all our long--term data sets. We fit a linear regression to the linear portion of the PI curve (Fig. 5B). If the y--intercept of the linear regression was 0 or positive, it meant that no GEP occurred at solar midnight and a correction was not necessary. If the y--intercept was negative then we used the absolute value of the y--intercept as an estimate of GEP at solar midnight. We subtracted the estimated GEP at solar midnight on each day – the *midnight correction* – from the daily value of uncorrected ER at solar midnight. We then interpolated the corrected ER from night to night and used this as the baseline to calculate corrected GEP as the difference between NEM and the corrected ER values (Fig 6C). We did not make a correction if the midnight surface light value was ≤ 1 μmole m^{-2} s^{-1}.

Statistical Analysis

The open--system WSM data were unbalanced because we took more samples in 2004 than in 2001 and 2003. To balance the data we took samples of the 2004 data during early, middle, and late field season. We evaluated ANOVA assumptions of normality with the Kolmogorov--Smirnov Test and equal variances with Levene's Test. We log transformed the data when necessary to comply with these assumptions.

We tested the null hypothesis that the response variables GEP/GPP and ER/CR were the same between the open and closed--system methodology. We tested this hypothesis with a one--way ANOVA using a general linear model (GLM in

MINITAB/14, Minitab Inc., State College) with one factor (method) with two levels (open--system and closed system) .

. We estimated WSM by single-- and dual--station methods in 2001 and 2003 and tested the null hypothesis that the response variables GEP and ER were the same when estimated by either methodology. We tested this hypothesis with a one--way repeated measures ANOVA using a GLM with one factor (method) having two levels (single station and dual station). We also examined a linear model of GEP and ER with the dual station values on the x--axes and the single station values on the y--axes.

We tested the null hypothesis that the response variables GEP and ER were the same between reaches with a one--way repeated measures ANOVA using a GLM with one factor (reach) and two levels (reference and fertilized). We used a similar model to test the null hypothesis that that the response variables uncorrected GEP, and uncorrected ER were the same between reaches.

We tested the null hypothesis that the response variables midnight metabolism correction and midnight surface light were the same between reaches and among seasons. We tested these response variables with a two--way ANOVA using a GLM with two factors (reach with levels of reference and fertilized and season with levels of early, middle, and late). If the ANOVA results were significant for season, we used multiple pairwise t--tests with the Bonferroni correction to examine pairwise differences in the response variables among season.

Results

GEP in the open system was not significantly different from GPP in the closed--system (F = 1.79, p = 0.19; Fig. 7A). ER in the open system was significantly higher than CR in the closed system (F = 1595, p < 0.01: Fig. 7B).

GEP and ER were not significantly different using either the dual or single station methodology (F = 1.23, p = 0.32; F = 0.46, p = 0.53; respectively). The linear relationships between dual and single station for GEP and ER were significant (r = 0.94, F = 183.8, p < 0.01; r = 0.63, F = 15.93, p < 0.01; respectively; Fig. 8)

GEP was significantly higher in the fertilized reach than in the reference reach (F = 48.67, p < 0.01; Fig 9A) while ER was not significantly different between reaches (F = 2.66, p = 0.15; Fig. 9B).

Similarly, uncorrected GEP was significantly higher in the fertilized reach (F = 39.14, p < 0.01) and uncorrected ER was not significantly different between reaches (F = 1.75, p = 0.23).

The midnight metabolism correction ranged from 0 to 74 mg O_2 m^2 h^{-1} with a mean of 12 (± 3 SE) mg O_2 m^2 h^{-1}. The midnight metabolism correction was not significantly different between reaches (F = 2.49, p = 0.12) but was significantly different among seasons (F = 11.57, p < 0.01; Fig. 10A). The midnight metabolism corrections was significantly higher during the early season than the late season (t = -4.81, p < 0.01) but was not significantly different between the early and middle season and middle and

late season (t = -1.89, p = 0.20; t = -1.96, p = 0.17; respectively). There were no significant interactions between the factors: reach and season (F = 0.97, p = 0.39).

Midnight surface light ranged from 0 to 66 µmole m^{-2} s^{-1} with a mean of 13 (± 2 *SE*) µmole m^{-2} s^{-1}. The midnight metabolism correction was not significantly different between reaches (F = 0.02, p = 0.90) but was significantly different among seasons (F = 32.90, p < 0.01; Fig. 10B). The midnight metabolism corrections was significantly higher during the early season than the middle and late seasons (t = -3.16, p < 0.01; t = -8.10, p < 0.01; respectively) and higher during the middle season than the late season (t = -3.56, p < 0.01). There were no significant interactions between the factors: reach and season (F = 0.01, p = 0.99).

Discussion

Bott et al. (1978) compared open and closed--system metabolism and found that the closed--system GPP was greater than open--system GEP while Marzolf et al. (1994) reported that the closed--system GPP was less than open--system GEP. In our study, the closed--system GPP estimates were not significantly different from the open system GEP estimates (6A). Our results suggest that open and closed--system methodologies provide similar estimates of photosynthesis in Arctic rivers.

In comparison to closed--system CR, open--system ER was over four times higher in Bott et al. (1978) and about 3 times higher in Marzolf et al. (1994). In our study, closed system CR was over 28 times lower then open--system ER (Fig. 7B). It is likely that the

differences in ER between the open-- and closed--system methods are due to the absence of the absence of hyporheic respiration in the closed--system approach. Our results are consistent with Fellows et al. (2001) who calculated the difference between open--system and closed--system ER to estimate hyporheic zone respiration and found that the hyporheic zone contributed from 40 -- 93% of the total ER. Likewise, Naegeli and Uehlinger (1997) performed a similar experiment in which the hyporheic zone contributed from 76 -- 96% of the total CR and Mulholland et al. (1997) noted that hyporheic zone size increased ER in a forested stream.

Assuming that closed--system CR is water column and benthic respiration and open system ER is water column, benthic, and hyporheic respiration, then hyporheic respiration is equal to ER minus CR. Thus hyporheic respiration was 730 and 754 mg O_2 m^{-2} h^{-1} in the reference and fertilized reaches, respectively. The proportion if total respiration that is hyporheic is 98% in the reference reach and 95% in the fertilized reach. The results suggest that the benthic mosses in the fertilized reach may be increasing benthic respiration because the proportion of hyporheic respiration to total respiration is lower in the fertilized reach.

Young and Huryn (1999) compared the dual and single station methodology and determined that the GEP estimates were more similar than the ER estimates ($r = 0.57$; $r = 0.17$; respectively). Likewise, our results suggest that dual-- and single--station estimates of GEP estimates were more congruent than were dual-- and single--station estimates of ER ($r = 0.94$; $r = 0.55$; respectively; Fig. 8).

The single station methodology is advantageous because the calibration correction for a second sensor is not necessary and the equipment can measure twice as many reaches. The disadvantage of the single station methodology is that the method relies on the upstream DO curves being the same as the downstream DO curve.

Guasch et al. (1995) and Mulholland et al. (2001) found that nutrients influence lotic open--system photosynthesis. Earlier closed--system metabolism experiments found GPP responding positively with increased SRP in the fertilized reach of the Kuparuk River (Peterson et al. 1985, Peterson et al. 1986, Bowden et al. 1992, Arscott et al. 1998). Likewise, GEP positively responded to increased SRP levels in the fertilized reaches of the Kuparuk River (Fig. 9A).

Guasch et al. (1995) and Mulholland et al. (2001) also found that nutrients can influence lotic open--system respiration and earlier closed--system metabolism experiments confirm that respiration responded positively with increased SRP in the fertilized reach of the Kuparuk River (Peterson et al. 1985, Bowden et al. 1992, Arscott et al. 1998). Surprisingly, in our study, ER was not significantly different between reaches (Fig. 9B). Further, the two reaches are geomorphically similar with only 1.5 km separating them and temperature and discharge were not significantly different between reaches. However, the prolific moss abundance in the fertilized riffles is a notable biological and physical difference between reaches as well as the difference in SRP. Biologically, we expected increased ER in the fertilized reach because the total biomass is probably larger in the fertilized reach; and chemically, more nutrients are available throughout the food web. However, physically, the mosses in the fertilized riffles may be

decreasing the water flowing into the hyporheic zone. Suren et al. (2000) found that bryophytes reduce the drag forces on rocks by reducing the force of the turbulent eddies and wakes formed around the rocks. Likewise, Nikora (1998) found that moss created hydraulically tranquil regions around the substratum in an experimental cobble--bed flume; and Scarsbrook and Townsend (1994) noted that experimentally added leaf litter lowered frictional forces between flowing water and the substratum. Thus, the mosses may be acting as a buffer reducing water flow into the hyporheic zone. In addition, Edwardson et al. (2003) reported that the ratio of transient storage zone area to stream area (As A^{-1}) in the Kuparuk River was about 50% higher in the reference reach although the differences were not significant. Therefore, this moss buffer may be physically decreasing ER in the fertilized reach enough to negate the favorable biological and chemical influences on ER.

Closed--system metabolism experiments were performed in the reference and fertilized reaches of the Kuparuk River before *Hygrohypnum* grew abundantly in the fertilized reaches (Peterson et al. 1985; Peterson et al. 1986; Bowden et al. 1992). Peterson et al. (1986) found that closed--system GPP was 33 mg O_2 m^{-2} h^{-1} (± 29 *SE*) and CR was 13 mg O_2 m^{-2} h^{-1} (± 12 *SE*) in the reference reach. In comparison, Bowden et al. (1992) found that GPP was < 50 mg O_2 m^{-2} h^{-1} and CR was ≤ 20 mg O_2 m^{-2} h^{-1} in the reference reach and increased GPP and CR by 20% in the fertilized reach during the 1989 season. The reference closed--system GPP values were similar to our open--system GEP values, while the fertilized closed--system GPP values were lower. We hypothesize that

the lower GPP values in the fertilized reach was due to the lack of abundant *Hygrohypnum* cover in the fertilized reach at the time these studies were performed.

After *Hygrohypnum* substantially inhabited the fertilized reach, Arscott et al. (1998) estimated NPP (net primary production) in the Kuparuk River using the closed--system method. They found that reference NPP was 73 mg O_2 m^{-2} h^{-1} and fertilized NPP was 202 mg O_2 m^{-2} h^{-1}, which is close to our open--system GEP values although NPP includes autotrophic respiration meaning the actual GPP values are greater than the NPP values reported.

Benstead et al. (2005) and Harvey et al. (1998) fertilized 2 other Arctic streams near the Kuparuk River with nitrogen and phosphorous. Benstead et al. (2005) found that epilithic chl *a* was significantly higher in the fertilized reach after a month of fertilization and Harvey et al. (1998) found that GPP and CR was higher in the fertilized reach during all four years of the experiment. Thus, fertilization of other Arctic Rivers has had similar results as the Kuparuk River.

Likewise, the uncorrected GEP was significantly higher in the fertilized reach and ER was not significantly different between reaches so the metabolism correction did not influence the overall results.

The midnight metabolism correction was significantly higher in the early season (late June) then in the late season (late July/early August) because midnight sunlight is greater during the early season. The midnight metabolism correction was higher in the fertilized reach than in the reference reach although not significant (Fig 10A). On average, the midnight metabolism correction increased GEP by 13.0 % and 13.2 % of

GEP in the reference and fertilized reaches, respectively, and ER by 1.1% and 2.0% of ER in the reference and fertilized reaches, respectively. Thus, the midnight metabolism correction proportionally influences GEP more than ER.

Midnight surface sunlight decreased from late June to early August and this seasonal change influenced the midnight metabolism correction (Fig. 10B). The midnight surface sunlight was not different between reaches most likely because they are only 1.5 km apart so the light availability is similar.

Compared to other streams, both reaches of the Kuparuk River had similar GEP values and high ER values (Table 2). We found that GEP was similar to other rivers despite the very low nutrient levels in the Kuparuk River. However, the high light availability due to the lack of shading and 24--hour photoperiod likely offset the very low nutrient levels.

Compared to other rivers, the Kuparuk River has high ER values with most ER a result of hyporheic respiration. Continuous permafrost in this Arctic environment would seem to limit the importance of hyporheic processes. However, Edwardson et al. (2003) found that biogeochemical processes in the hyporheic zone of Arctic streams are at least as important as temperate stream ecosystems. We hypothesize that the high ER levels in the Kuparuk River are the result of fresh organic matter running off the landscape during snowmelt in late spring. This organic matter replenishes the hyporheic zone each year for processing during the summer.

Conclusions

We conclude that the WSM method, with simple modifications, can be applied reliably in Arctic streams during the summer months even when photoperiods are 24h long. On average, the midnight metabolism correction increased GEP by 13.0% and 13.2% of GEP in the reference and fertilized reaches, respectively, and ER by 1.1% and 2.0% of ER in the reference and fertilized reaches, respectively. Thus, the midnight metabolism correction proportionally influences GEP more than ER. Midnight surface sunlight decreased from late June to early August and this seasonal change influenced the midnight metabolism correction. Compared to other streams, both reaches of the Kuparuk River had similar GEP values and high ER values. Kuparuk River GEP was similar to other rivers despite the very low nutrient levels, which may be offset by the high light availability due to the lack of shading and 24--hour photoperiod. Meanwhile, compared to other rivers, the Kuparuk River has high ER values with most ER a result of hyporheic respiration. We hypothesize that the high ER levels in the Kuparuk River are the result of fresh organic matter running off the landscape during snowmelt in late spring, which replenishes the hyporheic zone each year for processing during the summer.

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Tables

Table 2. GEP and ER values from rivers in different biomes using the open--system oxygen method.

Stream	Reference	Biome/landuse	GEP ($g\ O_2\ m^{-2}\ d^{-1}$)	ER ($g\ O_2\ m^{-2}\ d^{-1}$)
Kuparuk River, Alaska (reference)	This study	Arctic tundra	1.5	-18.0
Kuparuk River, Alaska (fertilized)	This study	Arctic tundra	2.8	-19.0
Sutton Stream, New Zealand	Young & Huryn 1999	Grassland	0.8	-4.6
Powder Creek, New Zealand	Young & Huryn 1999	Native forest	0.6	-5.4
Lee Stream, New Zealand	Young & Huryn 1999	Pasture	1.3	-2.0
Big Stream, New Zealand	Young & Huryn 1999	Exotic forest	1.5	-2.3
Three O'Clock Stream, New Zealand	Young & Huryn 1999	Grassland and pasture	3.7	-2.7
Quebrada Bisley, Puerto Rico	Mullholland et al. 2001	Tropical forest	< 0.1	-7.8
Sycamore Creek, Arizona	Mullholland et al. 2001	Sonaran desert	15.0	-8.3
Walker Branch, Tennessee	Mullholland et al. 2001	Deciduous forest	1.2	-5.4
Gallina Creek, New Mexico	Mullholland et al. 2001	Montane coniferous forest	0.4	-6.7
South Kings Creek, Kansas	Mullholland et al. 2001	Grassland	1.8	-2.4
Eagle Creek, Michigan	Mullholland et al. 2001	Deciduous forest	0.8	-6.4
Mack Creek, Oregon	Mullholland et al. 2001	Coniferous forest	1.9	-11
Bear Brook, New Hampshire	Mullholland et al. 2001	Deciduous forest	0.2	-6.9
Fuirosos, Spain	Acuna et al. 2004	Deciduous forest	0.8	-4.6
Sively 3, Organ Cave, West Virginia	Simon and Benfield 2002	Natural Cave	0.0	-0.2
Aguera Stream Site 5, Spain	Elosegui and Pozo 1998	Deciduous forest/agriculture	4.6	-5.4
Aguera Stream Site 7, Spain	Elosegui and Pozo 1999	Deciduous forest/agriculture	5.0	-3.1

Figure Legends

Figure 2. Map showing the location of Toolik Lake Field Station.

Figure 3. Diagram displaying the experimental reaches of the Kuparuk River.

Figure 4. Typical surface and subsurface light levels in the Kuparuk River. A. Continuous light values throughout each day. B. Magnification of midnight light values.

Figure 5. Example of a daily PI curve used to estimate the midnight correction when residual light levels still exist. A. Differentiation of the linear and curvilinear portions of the photosynthesis irradiance curve for a single day. B. Regression of the linear portion of the photosynthesis irradiance curve from Panel A. The absolute value of the y--intercept is the value used for the midnight correction to ER.

Figure 6. Arctic metabolism correction: A. Temperate metabolism measurement. B. Arctic metabolism measurement uncorrected for midnight sunlight. C. Arctic metabolism measurement corrected for midnight sunlight.

Figure 7. Closed versus open system metabolism: A. Comparison of closed--system GPP versus open--system GEP (mean ± 1 *SE*). B. Comparison of closed--system CR versus open--system ER (mean ± 1 *SE*).

Figure 8. Dual versus single station: A. Linear regression of dual versus single station GEP. B. Linear regression of dual versus single station ER.

Figure 9. Single station open--system GEP and ER between reaches. A. Gross ecosystem production (mean ± 1 *SE*). B. Ecosystem respiration (mean ± 1 *SE*).

Figure 10. A. Daily midnight metabolism corrections (mean ± 1 *SE*) for early, mid, and late seasons, and reference and fertilized reaches. B. Daily midnight light intensity (mean ± 1 *SE*) for early, mid, and late seasons, and reference and fertilized reaches.

Figures

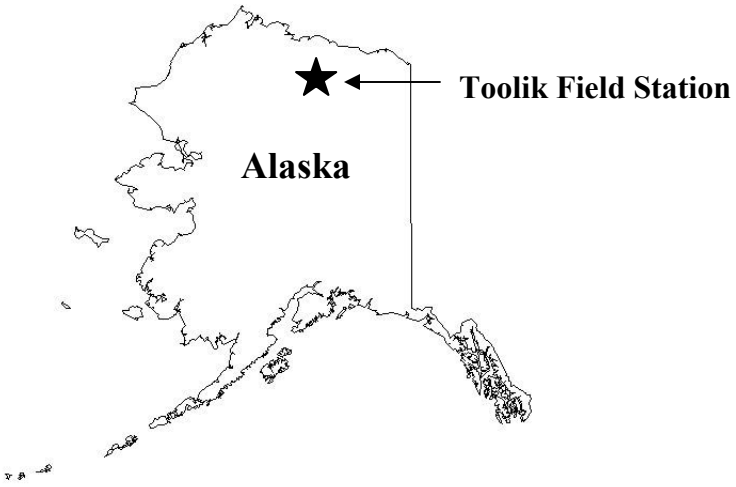

Figure 2.

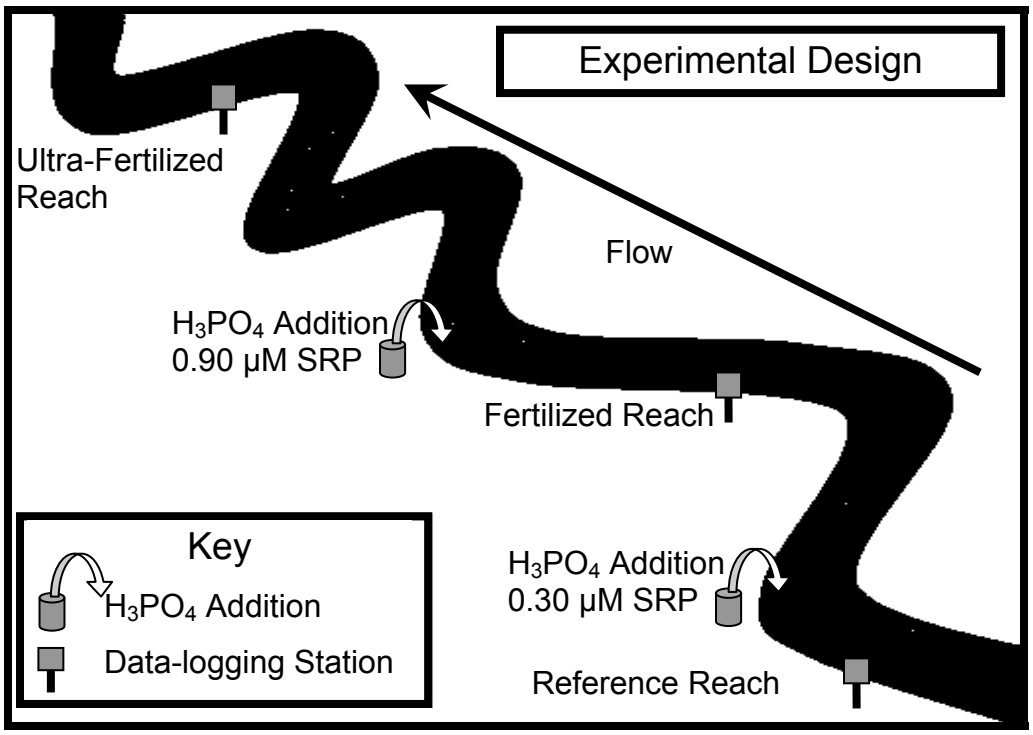

Figure 3.

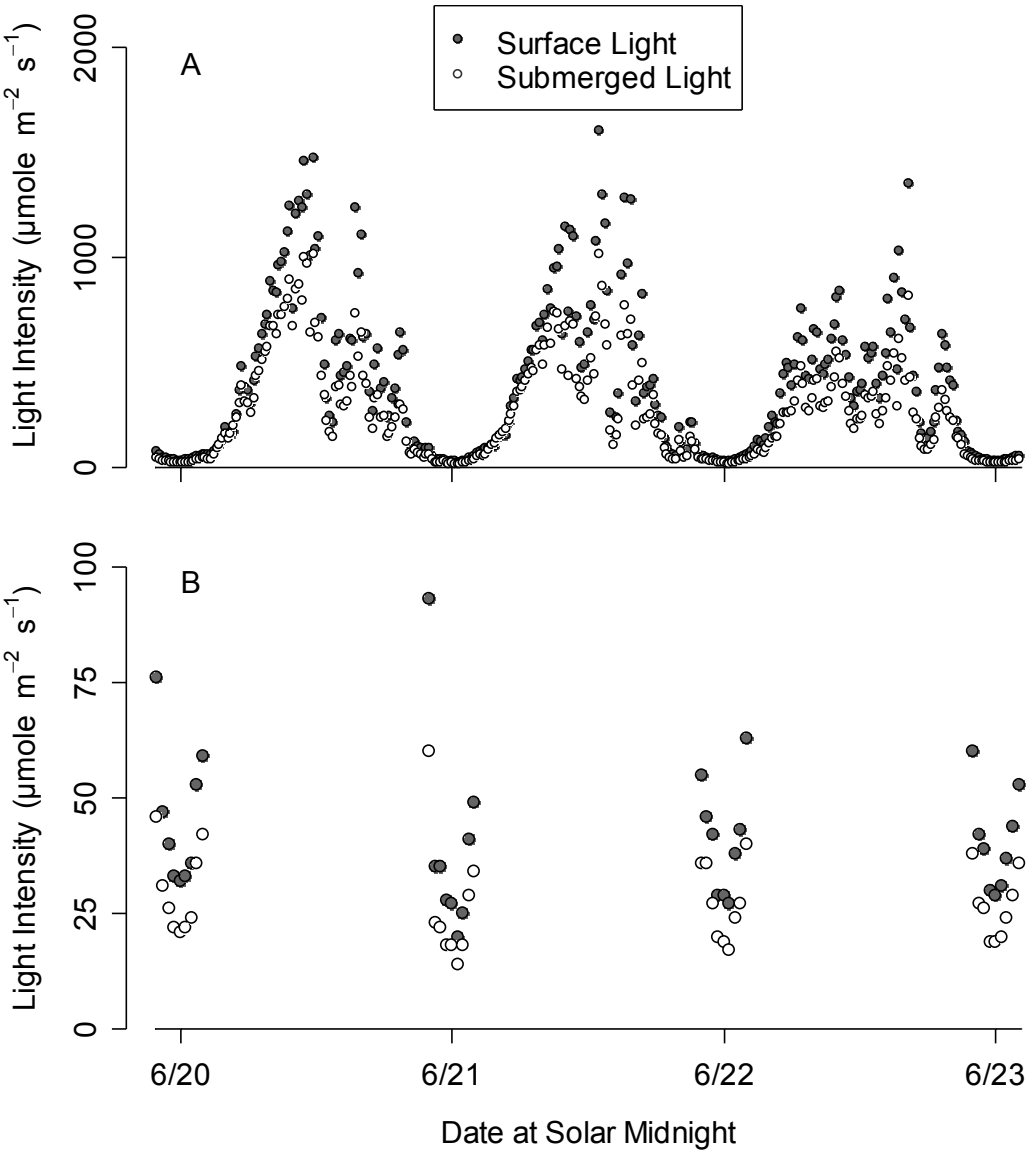
Surface Light
Submerged Light
A
B
Light Intensity (µmole m^{-2} s^{-1})
0
1000
2000
0
25
50
75
100
6/20
6/21
6/22
6/23
Date at Solar Midnight

Figure 4.

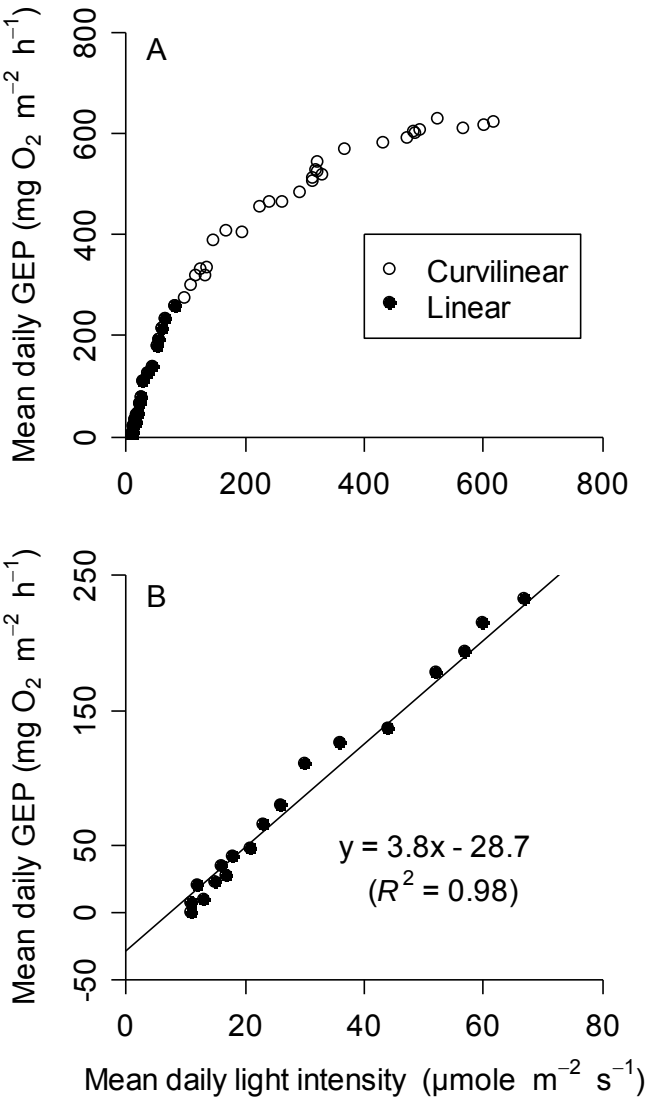
A
Curvilinear
Linear
Mean daily GEP (mg O_2 m^{-2} h^{-1})
0
200
400
600
800
B
y = 3.8x - 28.7
(R^2 = 0.98)
-50
0
50
150
250
0
20
40
60
80
Mean daily light intensity (µmole m^{-2} s^{-1})

Figure 5.

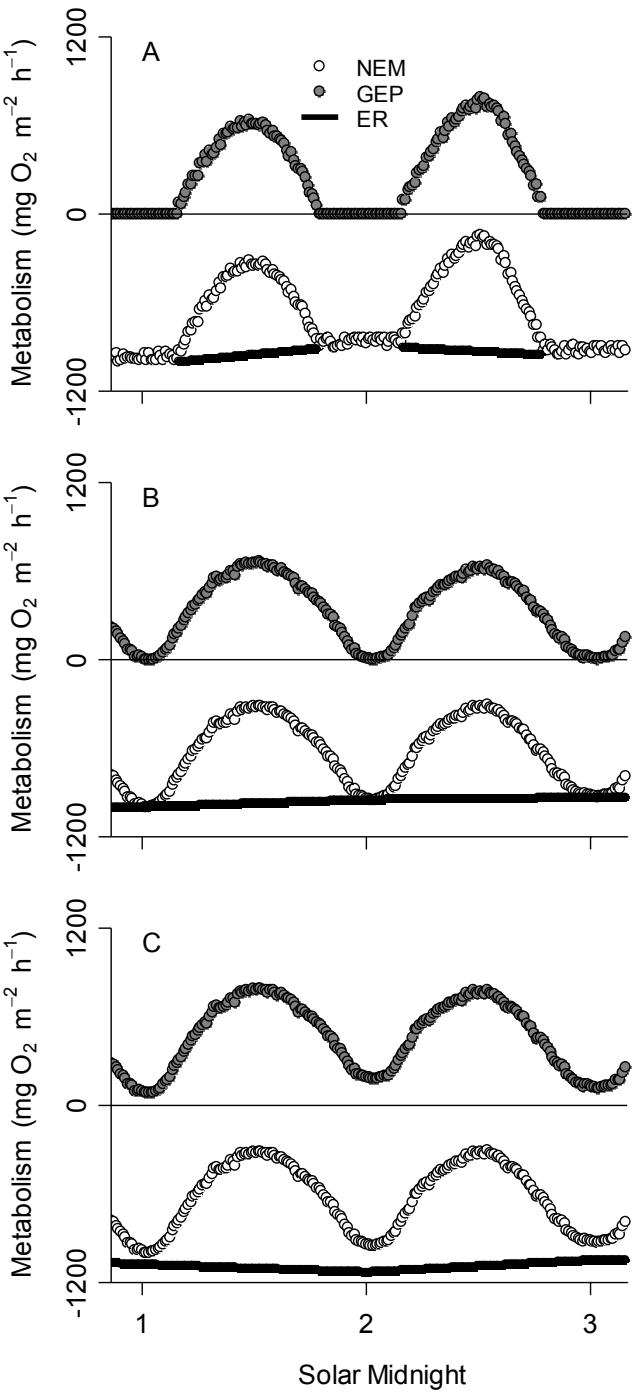
A
B
C
NEM
GEP
ER
1200
0
-1200
Metabolism (mg O_2 m^{-2} h^{-1})
1
2
3
Solar Midnight

Figure 6.

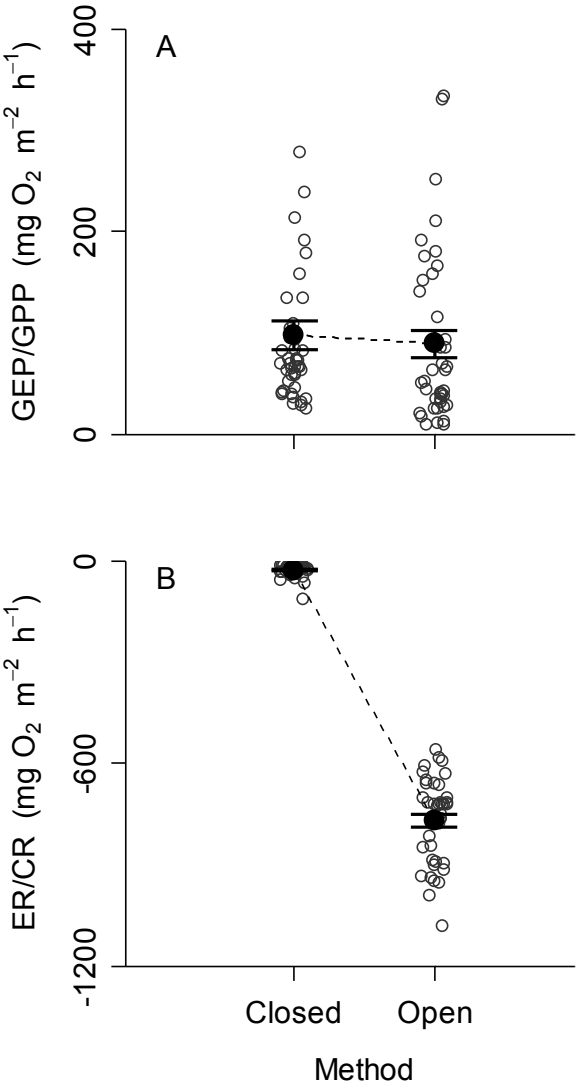
A
B
GEP/GPP (mg O_2 m^{-2} h^{-1})
ER/CR (mg O_2 m^{-2} h^{-1})
400
200
0
0
-600
-1200
Closed
Open
Method

Figure 7.

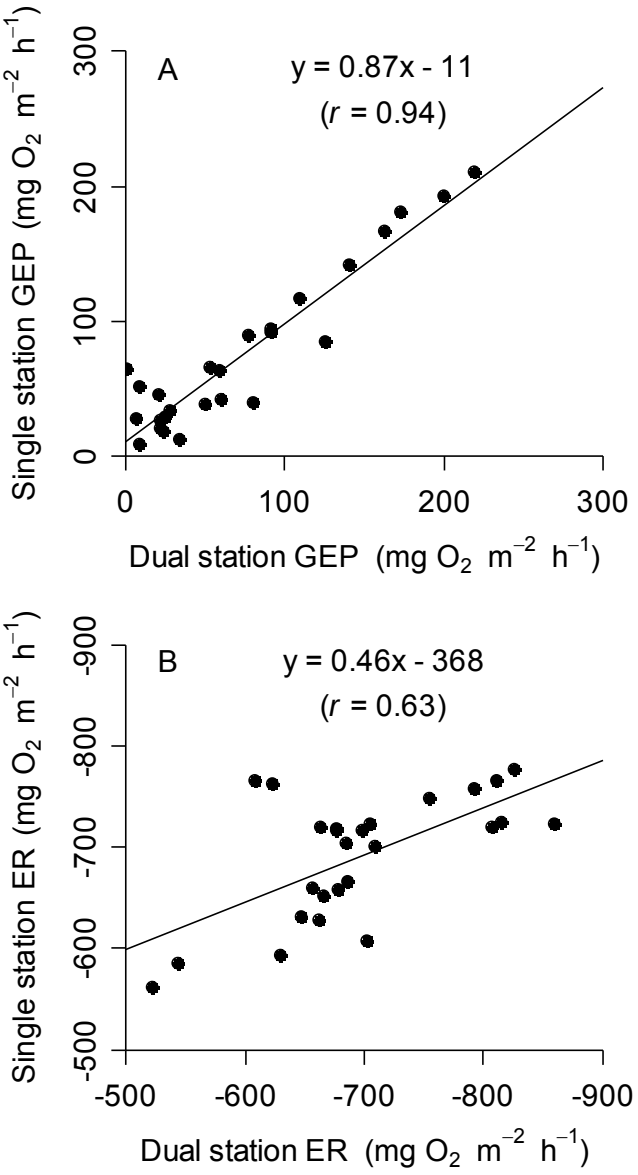
A
y = 0.87x - 11
(r = 0.94)
Single station GEP (mg O2 m−2 h−1)
Dual station GEP (mg O2 m−2 h−1)
0
100
200
300
B
y = 0.46x - 368
(r = 0.63)
Single station ER (mg O2 m−2 h−1)
Dual station ER (mg O2 m−2 h−1)
-500
-600
-700
-800
-900

Figure 8.

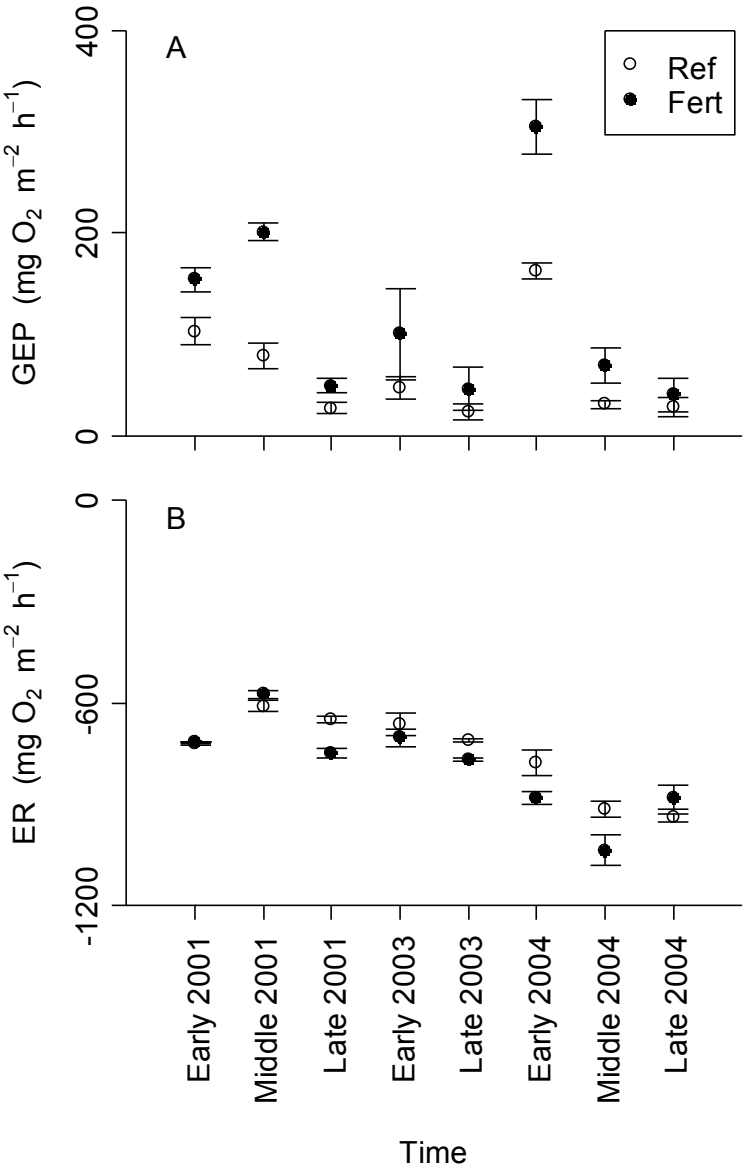
A
B
Ref
Fert
GEP (mg O2 m-2 h-1)
ER (mg O2 m-2 h-1)
400
200
0
0
-600
-1200
Early 2001
Middle 2001
Late 2001
Early 2003
Late 2003
Early 2004
Middle 2004
Late 2004
Time

Figure 9.

.

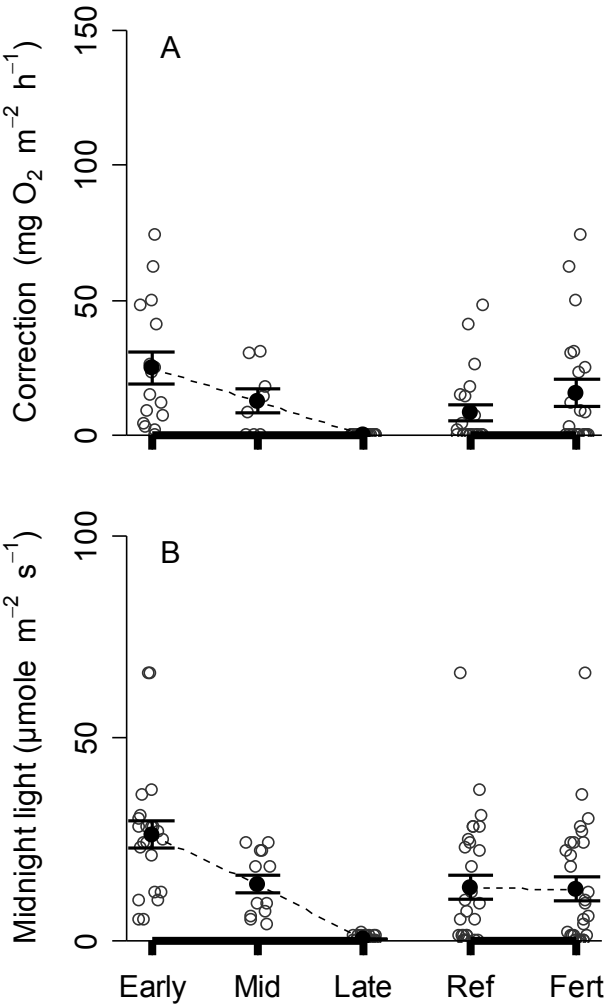
A
B
Correction (mg O_2 m^{-2} h^{-1})
Midnight light (µmole m^{-2} s^{-1})
0
50
100
150
Early
Mid
Late
Ref
Fert

Figure 10.

Chapter 2: The influence of physical, biological, and chemical variables on photosynthesis and respiration in an Arctic tundra river

Abstract

Global warming may significantly alter ecosystem metabolism in Arctic rivers, which may change net CO_2 fluxes on an ecosystem scale. Global warming will likely increase water temperatures, discharge, and SRP (soluble reactive phosphorous) in Arctic rivers.

We examined the influence of light, temperature, discharge, photosynthetic biomass, and nutrients on whole--stream metabolism (WSM) in three experimental reaches of the Kuparuk River, in Arctic Alaska, using the open--system, single--station method. Ambient SRP levels in the reference reach were ~ 0.05 μM. Phosphoric acid has been added to the fertilized reach of the Kuparuk River since 1983 to raise the SRP level to an average concentration of ~0.30 μM at the mean discharge of 2.3 m^3 sec^{-1}. In 2004, we created an ultra--fertilized reach below the historic fertilized reach in which we increased the SRP levels to 0.90 μM or 3 times the historic treatment level.

Gross ecosystem production (GEP) was significantly higher in the fertilized reaches where bryophytes (mosses) and associated epiphytic algae have established a large autotrophic biomass, than in the reference reach, which is dominated by epilithic diatoms only. Among all reaches, GEP was positively correlated with light, temperature, photosynthetic biomass, and SRP and negatively correlated with discharge. Two different

modeling approaches (information theoretic and mechanistic) showed that submerged light, temperature, and photosynthetic biomass were the most important variables influencing GEP in all reaches.

Ecosystem respiration (ER) was not significantly different among any of the study reaches. In all reaches, ER was weakly correlated with temperature, discharge, and SRP. However, ER showed a positive response to temperature and a negative response to discharge in the fertilized reaches, most likely due to the extensive bryophyte and epiphyte biomass that have accumulated there. Analysis of multiple linear models using information theory suggests that ER in the fertilized reach was best described by temperature; ER in the reference reach was less well explained by temperature. SRP was of low to moderate importance among all reaches as a descriptor of ER.

The combined influence of increased water temperature, discharge, and SRP will decrease NEM, meaning that carbon sequestration in streams is expected to increase, although not substantially, in the future. This means that the net CO_2 flux out of these rivers into the atmosphere will likely decrease.

Introduction

Past studies show that Arctic Alaskan Rivers release substantial amounts of CO_2 into the atmosphere and influence the carbon budget on a landscape scale (Kling et al. 1991; Kling et al. 1992). Global warming may increase temperature, discharge, and phosphorous in Arctic rivers (Rouse et al. 1997, IPCC 2001, ACIA 2004). These physical and chemical changes may significantly alter whole--stream metabolism (WSM) in Arctic rivers, which may change net CO_2 fluxes on an ecosystem scale. By examining the influence of light, temperature, discharge, photosynthetic biomass, and nutrients on WSM, we can develop predictive models of photosynthesis and respiration based on which driving variables are important.

The long--term (20+ years) phosphorous fertilization experiment in the Kuparuk River near Toolik Lake, Alaska, provides a unique opportunity to examine the key environmental variables that affect whole system photosynthesis and respiration (Peterson et al. 1993, Slavik et al. 2004). This phosphorous fertilization simulates the phosphorous increase due to global warming for rivers in the foothills of the North Slope of Arctic Alaska. Phosphorus --- which is typically the limiting nutrient in these rivers (Peterson et al. 1993) --- has been added to Kuparuk River at low, but ecologically notable levels, during summer open--flow season of every year since 1983. Several key changes in the biology have occurred in the fertilized reach: *Hygrohypnum* spp. (mosses) have overtaken *Schistidium agassizii* (a moss) and epilithic diatoms as the dominant primary producers (Arscott et al. 1998); photosynthetic biomass has increased (Arscott et

al. 1998); insect abundance has increased and species composition has changed (Lee and Hershey 2000); and fish growth rates have increased (Deegan and Peterson 1992).

We have previously used closed--system methods to examine metabolic processes in the Kuparuk River (Peterson et al. 1985, Bowden et al. 1992, Arscott et al. 1998, Arscott et al. 2000). Closed--system stream metabolism experiments measure changes in dissolved oxygen (DO) that occur as a result of photosynthesis and respiration in chambers that recirculate water around a sample of benthos (McIntire et al. 1964). The closed--system method is well suited to studies of isolated taxa or communities (Bott et al. 1978, Bott et al. 1997). For example, Arscott et al. (1998) isolated *S. agassizii*, *Hygrohypnum*, and micro--epilithon (Diatoms) from the Kuparuk River and examined the metabolism of these key autotrophs in the reference and fertilized reaches. Arscott et al. (2000) also examined the influence of light, temperature, and desiccation on metabolism of *S. agassizii* and *Hygrohypnum*. While closed--system metabolism experiments provide good experimental control, they are subject to nutrient depletion and other unnatural changes (Bott et al. 1978, Bott et al. 1997). Furthermore, closed--system methods usually underestimate whole--system respiration because they do not normally include hyporheic sediments (Grimm and Fisher 1984, Mulholland et al. 1997, Naegeli and Uehlinger 1997, Fellows et al. 2001) although new chamber methods have included hyporheic sediments (Uzarski et al. 2001, Uzarski et al. 2004).

Open--system experiments of stream metabolism are based on measurements of DO in open stream channels (Odum 1956). Changes in DO are the result of photosynthesis and respiration but also include corrections for oxygen exchange with the

atmosphere (or reaeration, Kilpatrick et al. 1989) and in some cases, oxygen dilution caused by groundwater (e.g., McCutchan et al. 2002, Hall and Tank 2005). The open--system method offers the opportunity to measure stream metabolism in natural settings, in the field. In addition, the open--system approach can be used to measure metabolism continuously for long periods and integrates metabolism in the water column, benthos, and hyporheos.

Until recently, we thought that the open--system method could not be used in the Arctic, where there is 24--hour sunlight, because the open--system method relies on a 'dark' period to estimate ecosystem respiration. Recently, we showed that with some minor modification the open system method could be used successfully at high--latitude sties such as the Kuparuk River (Chapter 1, Cappelletti and Bowden in review). We initiated this study to determine how important driving variables --- light, temperature, discharge, photosynthetic biomass, and nutrients --- influence whole--system primary production and respiration in Arctic streams. This information is necessary to understand the potential influences of climate warming in the Arctic and to calibrate stream process models.

The specific objectives of this study were:

- to measure whole--stream metabolism in the reference, fertilized and ultra--fertilized reaches of the Kuparuk River continuously over the 2004 field season,
- to measure and model key environmental driving variables (surface light, submerged light, temperature, discharge, photosynthetic biomass, and nutrients) for whole--stream metabolism in this environment, and

- to apply a combination of information theoretic and mechanistic models to identify the statistical significance of the key driving variables on stream metabolism in the Kuparuk River.

Methods

Site Description

The Kuparuk River originates in the foothills of the Brooks Range on the North Slope of Alaska and flows north into the Arctic Ocean (Fig. 2). The experimental reaches of the Kuparuk River are located near the Dalton Highway (68° 38′ N, 149° 24′ W). The reference reach is located upstream of the fertilized and ultra--fertilized reaches and the SRP levels (~0.05 μM) are similar to other streams and rivers in the area (Fig. 3). Since 1983, we have added phosphoric acid in the fertilized reach to achieve a target concentration of ~ 0.30 μM SRP at an average discharge of 2.3 m^3 sec^{-1}. In 2004, we established an ultra--fertilized reach downstream of the fertilized reach, where we increased the SRP levels to ~ 0.90 μM.

This Kuparuk River at the location of the experimental reaches is a cobble--bottom, fourth--order stream with meandering pool--riffle sequences. The average channel slope is 0.6% and the sinuosity is 1.5 (Kriet et al. 1992, Slavik et al. 2004). The drainage basin area of the upper Kuparuk River is 143 km^2 and the main channel length is 25 km (Hershey et al. 1997). The Kuparuk River has a mean summer discharge of 2.3 m^3 s^{-1} and width of 17 m (Slavik et al. 2004).

The vegetation in the upper Kuparuk drainage basin, consists mostly of upland heath communities on dry soils, moist tundra communities dominated by the tussock--forming cotton grass *Eriophorum vaginatum*, and wet sedge tundra dominated by *Carex aquatilus* (Hershey et al. 1997). Stream bank vegetation is mainly comprised of dwarf willows (*Salix* spp.), wet sedge (*Carex* spp.), and birches (*Betula nana*). The bank vegetation rarely exceeds 1 m in height so it does not shade the stream channel and the photoperiod is 24 hours during most of the summer field season.

The Kuparuk River freezes from about late September to late May. The mean summer water temperatures of the Kuparuk River are 8 -- 10°C while occasionally reaching 21°C at low flow and 3°C at high flow (Hershey et al. 1997). On a diel timescale, the temperatures can change up to 10°C (Hershey et al.1997).

Permafrost underlies the Kuparuk River catchment and limits deep groundwater flow into the Kuparuk River. Further, there are no glacial inputs, so channel precipitation, overland flow, and shallow interflow feeds the Kuparuk River (McNamara et al. 1998). Interflow is water that flows above the permafrost in a shallow zone called the active layer which freezes and thaws annually to depths of ~ 25 -- 40 cm (Hinzman et al. 1991). Since the active layer is shallow and generally saturated, discharge increases rapidly even during small rain events and during periods of summer drought the river almost stops flowing. Oatley (2002) reported that the Kuparuk River discharge could vary from 0.3 m^3 s^{-1} during dry periods to 100 m^3 s^{-1} during storms and spring snowmelt.

The reference reach of the Kuparuk River has two major primary producers: *S. agassizii* and micro--epilithon (Diatoms) with micro--epilithon being dominant (Bowden

et al. 1994, Arscott et al. 1998). In contrast, the fertilized reach of the Kuparuk River has three major primary producers: *Hygrohypnum*, *S. agassizii*, and micro--epilithon with *Hygrohypnum*. being dominant (Arscott et al. 1998). Compared to *S. agassizii*, *Hygrohypnum* grows faster, has much longer fronds, is less compacted, and accumulates much higher biomass.

The Kuparuk River has low ambient nutrient concentrations and is limited by phosphorous in the reference reach while phosphorous and nitrogen are co--limiting in the fertilized reach (Bowden et al. 1992, Slavik et al. 2004). The epilithic C:N ratios are 12.2 and 11.6, the C:P ratios are 232.2 and 153.8, and the C:N ratios are 20.3 and 14.1 in the reference and fertilized reaches, respectively (Slavik et al. 2004).

Field & Laboratory Methods

We measured DO, surface light, submerged light, turbidity, water temperature, and discharge in the Kuparuk River from late June 2004 to early August 2004. We established measuring stations at the bottom of the reference (0.5 km), fertilized (2.0 km), and ultra--fertilized reaches (4.0k; Fig. 3). We used a WTW 325 CellOx sensor to measure DO, a Li--Cor LI--190SB light sensor to measure photosynthetic active radiation (PAR) at the water surface, a Li--Cor LI--192SA light sensor to measure PAR underwater, a D & A OBS--3 sensor to measure turbidity, and a Campbell 107 sensor to measure temperature. We connected the sensors to a Campbell 10X datalogger to record the data every 5 seconds and averaged those measurements every 5 minutes. During the 2004 season, we checked the datalogging station about three times a week, re--calibrating

sensors as necessary to ensure accurate sensor readings over the long--term measurement period.

We placed the DO, submerged light, turbidity, and water temperature sensors in the thalweg of the stream; and we placed the datalogger on the floodplain and mounted the surface light sensor on a stake above the vegetation and next to the datalogger.

We measured the depth of the light sensor and corrected submerged light based on the differences between the light sensor depth and the mean river depth with the light extinction equation:

$$I_{Sub\ measured} = I_{Surf} * e^{(ktd_{sensor})} \quad \text{(Eq. 1)}$$

where $I_{sub\ measured}$ is the measured submerged light intensity (µmole m^{-2} s^{-1}), I_{surf} is surface light intensity (µmole m^{-2} s^{-1}), k is the extinction coefficient, t is turbidity (NTU), and d_{sensor} is depth of the light sensor (m) (Carr et al. 1997). We fitted Equation 1 to light extinction data we obtained at each site and solved for the parameter, k. We calculated the corrected submerged light level for the mean river depths as follows:

$$I_{Sub\ corrected} = I_{Surf} * e^{(ktd_{river})} \quad \text{(Eq. 2)}$$

where $I_{Sub\ corrected}$ is the corrected submerged light intensity (µmole m^{-2} s^{-1}) and d_{river} is the mean depth (m) which varies with discharge.

A stage height recording gauge provided continuous estimates of discharge at 0.65 km and a new rating curve was calculated each year (Knighton 1998; Fig. 3). We calculated the rate of increase in discharge downstream from 11 discharge measurements upstream and downstream taken on different dates (Peterson. unpublished data). We used

hydraulic geometry from cross sectional measurements to calculate depth (Leopold et al. 1992).

Phosphoric acid was added to the fertilized and ultra--fertilized reaches of the Kuparuk River with a peristaltic pump. The target fertilization concentration was 0.30 µM SRP in the fertilized reach (Slavik et al. 2004) and 0.90 µM SRP in the ultra--fertilized reach (Benstead et al. in press). We sampled SRP, NH_4, and NO_3 twice a week for the entire season. We analyzed SRP using colorimetric methods (Parsons et al. 1984) with a Varian Cary 50 spectrophotometer, NH_4 with a Turner Designs 10--Au fluorometer using the OPA method (Holmes et al. 1999), and NO_3 using colorimetric methods with a Lachet Quik--Chem 8000 (Diamond 2003).

Epilithic chlorophyll *a* was measured weekly in one pool and one riffle from each stream reach. Three replicates were taken from each location. We used standard methods employed by the Arctic Long--Term Ecological Monitoring program to sample chl *a.* We placed a small template (an empty photographic slide mount) of known area on top of a rock and scrubbed the area within the template with a metal brush. The scrubbed rock area was rinsed and the resulting epilithic slurry was placed in a sample vial of known volume. A subsample of the epilithic slurry was filtered onto a glass--fiber filter and then extracted in 90% acetone buffered with $MgCO_3$ at 4°C for ~24 hours (Arar and Collins 1997). Extracted chl *a* concentrations were measured with a Turner Designs 10--AU fluorometer and converted to area--specific values (mg chl *a* m^{-2}).

We estimated moss cover using the point transect method (Bowden et al. 1994). We only examined moss cover in riffles because moss cover is sparse in Kuparuk River

pools; these environments are dominated by detritus and epilithic algae (Bowden et al. 1992, Arscott et al. 1998). At each riffle, we took five random transects across the river. We recorded selected taxa or vegetation type at 5 cm intervals along each transect. The taxa or vegetation type included *S. agassizii*, *Hygrohypnum*, *Lamanea* sp. (a red alga), and filamentous algae. If no visible macroflora was present, then the point was labeled as micro--epilithon, which is comprised of a biofilm of epilithic diatoms (Miller et al. 1992). Percent cover was calculated by the number of times a cover type was recorded divided by the total number of points in each riffle times 100.

We calculated net ecosystem metabolism (NEM) by the methods described in Marzolf et al. (1994), and Young and Huryn (1998) with modifications described in Chapter 1 and by Cappelletti and Bowden (in review) to account for the 24--hour photoperiod in this high--latitude environment. We calculated reaeration using the sound pressure method developed by Morse et al. (in review) for these sites. We calculated the bias in our GEP and ER calculations due to groundwater (McCutchan et al. 2002, Hall and Tank 2005) and compared the bias with uncertainty in metabolism calculations due to reaeration coefficient, temperature, travel time, metabolic rate, and DO instruments (McCutchan et al. 1998). We used measurements of lateral discharge and hyporheic DO from Edwardson et al. (2003) to calculate groundwater bias in our GEP and ER calculations.

Statistical Analysis

We tested the null hypothesis that the response variables (SRP, NH_4, NO_3, epilithic chl *a*, *S. agassizii* cover, *Hygrohypnum* cover, GEP, and ER) were the same

among reaches, using analysis of variance (ANOVA). We did not evaluate surface light, submerged light, temperature, and discharge because they were essentially identical among reaches, although temperature and discharge did increase slightly downstream. We evaluated ANOVA assumptions of normality with the Kolmogorov--Smirnov Test and equal variances with Levene's Test. We log--transformed the data when necessary to comply with these assumptions. If the ANOVA results were significant, we then used multiple pairwise t--tests with the Bonferroni correction to examine pairwise differences in the response variables among reaches.

We could not analyze the influence of photosynthetic biomass in the same way that we analyzed the influences of light, temperature, and discharge because measurements of photosynthetic biomass were taken on different timescales than these other variables. We used the photosynthetic model developed by Uehlinger et al. (1996) to estimate daily photosynthetic biomass as a function of carrying capacity, discharge, and catastrophic discharge:

$$\frac{dX}{dt} = \underbrace{\mu_{\max,0} X}_{1a} \; \underbrace{\frac{1}{1 + k_c X}}_{1b} - \underbrace{c_{\det} Q\left(X - X_0\right)}_{2a} - \underbrace{k_{flood}\left(Q\right)\left(X - X_0\right)}_{2b} \qquad \text{(Eq. 3)}$$

with

$$k_{flood}\left(Q\right) = \begin{cases} 0 & for \quad Q < Q_{crit} \\ k_{flood} & for \quad Q \geq Q_{crit} \end{cases}$$

where $\mu_{max,0}$ is the maximum specific growth rate(day^{-1}), X is mean daily chl *a* (mg chl *a* m^{-2}), k_c is a half--saturation constant for carrying capacity (mg chl *a* m^{-1}), c_{det} is an empirical detachment coefficient (s m^{-3} d^{-1}), X_0 is the minimum biomass (so the model

does not crash), Q is discharge (m^{-3} s^{-1}), k_{flood} is a catastrophic loss coefficient (s m^{-3} d^{-1}), and Q_{crit} is the discharge at the onset of bedload transport (m^{-3} s^{-1}).

Term 1a in Equation 3 represents exponential chl *a* growth; term 1b is a carrying capacity function that limits growth; term 2a represents the detachment rate of chl *a* as a function of discharge and the existing amount of chl *a*; term 2b represents the catastrophic loss of chl *a* during bed--moving spates. Oatley (2002) reported that the bed--moving threshold in the Kuparuk River is 15 m^{-3} s^{-1}.

This photosynthetic biomass model does not include the chl *a* contribution from *S. agassizii* and *Hygrohypnum*. Further, we averaged the weekly epilithic chl *a* values within each reach and then averaged those values among reaches so we have one chl *a* value among all reaches. We used this model to simulate the general temporal trend in epilithic photosynthetic biomass among all reaches to be used as a predictor of photosynthesis. We also reasoned that due to the small sample size (*n* = 8 sample dates) and the reaches are all exposed to the same discharge regime averaging the epilithic chl *a* values would make the model more robust and reliable.

We modeled daily nutrient levels based on discharge and concentration versus discharge relationships derived from our twice--weekly nutrient samples. We examined linear and nonlinear responses of soluble reactive phosphorous (SRP), NH_4, and NO_3 to discharge. If the nutrients had weak or no relationship with discharge then we did not include that nutrient in any further analyses

Photosynthetic enzyme concentrations within algal cells may not respond to short--term nutrients fluxes in stream water because these organisms can store excess nutrients

in vacuoles and are able to "cash out" stored nutrients when needed (Rhee 1973, Greenwood 1976, Siderius et al. 1996). Greenwood (1976) reported that nitrogen limited plants generally took 72 hours to fully respond to increased nitrogen levels. Thus, instantaneous nutrient levels may not be as a good a predictor of photosynthesis and respiration as a moving nutrient average of nutrient levels for several days. Thus, equation 4 uses a four--day moving average to account for this lagged response:

$$N_{x\ time\ lagged} = \frac{N_{x-3} + N_{x-2} + N_{x-1} + N_x}{4} \qquad \text{(eq. 4)}$$

where N is the nutrient level, and x is the day.

Phosphorous is the limiting nutrient in the reference reach of the Kuparuk River (Peterson et al. 1993, Bowden et al. 1992, Slavik et al. 2004), while phosphorous and nitrogen are co--limiting in the fertilized reaches. Thus, SRP is potentially the only nutrient predictor of photosynthesis and respiration in the reference reach and SRP, NH_4, and NO_3 are potentially the nutrient predictors of photosynthesis and respiration in the fertilized reaches, pending the adequacy of the nutrient models (Bowden et al. 1992, Slavik et al. 2004).

Bivariate--ANCOVA Models

We examined the response of mean daily GEP to mean daily surface light, submerged light, temperature, discharge, epilithic chl *a*, and SRP, and the response of mean daily ER to mean daily temperature, SRP, and discharge using a bivariate analysis. We used this analysis to exclude any predictor variables in the multivariate analysis that had weak to no relationship with the response variables. The discharge variable was log--

transformed to provide a linear fit. Among reaches, we also compared the response of GEP and ER to each predictor variable by using analysis of covariance (ANCOVA).

We examined the correlation among surface light, submerged light, temperature, discharge, chl *a*, and SRP within each reach. If any predictors were highly correlated ($r > 0.90$) then we removed the highly correlated predictor variables from the multivariate analysis (Graham 2003).

Multiple Linear Models

Step--wise multiple regression has been used to select the most important variables from a set of candidate variables that might influence photosynthesis and respiration (Young and Huryn 1996, Uehlinger et al. 2000, Mulholland et al. 2001, Acuna et al. 2004). However, evidence suggests that step--wise multiple regression can arbitrarily include or exclude predictor variables (Dersken and Keselman 1992, Burnham and Anderson 2002, Graham 2003). As an alternative, we used information theory (Burnham and Anderson 2002) to evaluate and rank all possible model subsets for our multiple linear models. Information theory selects the "best" model based on goodness--of--fit and penalizes for increased model complexity. Goodness--of--fit is calculated by minimizing the negative log--likelihood of each model. Then each model is penalized based on the number of estimable parameters using either Akaike's Information Criterion (AIC) or small sample Akaike's Information Criterion (AIC_c). Each model was scored (w_i) from a scale of 1 to 0 with the sum of all the models equaling 1. The better models had higher scores (w_i). We calculated the importance of each variable by summing the

model scores in which the variable was included in the model. Variable importance scores varied from 0 to 1, with higher scores meaning greater variable importance.

The form of the multiple linear photosynthesis model was:

$$GEP = \beta_o + \beta_1(I) \text{ or } (I_{Sub}) + \beta_2(chl\,a) + \beta_3(T) + \beta_4(Q) + \beta_5(N_{x\ time\ lagged}) \quad \text{(Eq. 5)}$$

where GEP is gross ecosystem production (mg O_2 m^{-2} h^{-1}), I is surface light intensity (μmole m^{-2} s^{-1}), I_{Sub} is submerged light intensity (μmole m^{-2} s^{-1}), chl *a* is modeled chl *a* (mg chl *a* m^{-2}), T is water temperature (°C), Q is log discharge (m^3 s^{-1}) and $N_{x\ time\ lagged}$ is the relevant lagged nutrient/s (μM).

The form of the multiple linear respiration model was:

$$ER = \beta_o + \beta_1(T) + \beta_2(Q) + \beta_3(N_{x\ time\ lagged}) \quad \text{(Eq. 6)}$$

were ER is ecosystem respiration (mg O_2 m^{-2} h^{-1}), T is water temperature (°C), Q is log discharge (m^3 s^{-1}), and $N_{x\ time\ lagged}$ is the relevant lagged nutrient/s (μM).

The temporal scale of the variables was in mean daily values and the β's were the estimable coefficients. Each predictor variable was added and subtracted from the model until each possible combination was evaluated, including a null model. We evaluated this model for each reach and we calculated the variable importance of each predictor variable for each reach.

Mechanistic Photosynthesis Models

Mechanistic photosynthesis models typically utilize photosynthesis--irradiance (PI) curves to model photosynthesis as a function of light intensity. Typically, photosynthesis increases linearly with light until light saturates the photosynthetic process whereby further increases in light do not increase photosynthesis. Generally, the

PI curves include two parameters and one light variable. The first coefficient, P_{max}, represents the maximum photosynthetic rate where the photosynthetic process is saturated with light. The second coefficient is usually α (the slope of the linear portion of the PI curve) or I_k (the half--saturation coefficient of the PI curve). Most lotic open--system PI curves use surface light as the light variable (Young and Huryn 1996, 1999, Uehlinger et al. 2000, Mulholland et al. 2001) while some use submerged light (Uehlinger 1993).

PI curves have primarily been developed in laboratory environments where the environmental conditions were controlled (Pfeifer and McDiffett 1975, Jassby and Platt 1976, McBride 1992). Rapid changes in temperature, photosynthetic biomass, discharge, and nutrients characterize natural lotic environments and each of these variables may have a strong influence on photosynthesis. Consequently, standard PI curves with surface light as the only predictor may not accurately estimate photosynthesis in natural lotic systems over a long time. Thus, we developed several mechanistic photosynthesis models that incorporate other important variables.

Research has suggested that temperature can substantially influence light--saturated photosynthetic rates because temperature is limiting (Cote and Platt 1984, Cota et al. 1994) but has little influence on light--unsaturated rates because light is limiting (Malone and Neale 1981, Tilzer et al. 1986). Thus, in the Jassby--Platt PI formula, the P_{max} coefficient is more sensitive to changes in temperature than the α or I_k.

We evaluated the mechanistic photosynthesis models with information theory approach, as for the multivariate models described above. However, the mechanistic

models are more complicated and hundreds of different model combinations are possible. Consequently, we selected a limited number of models for analysis. The mechanistic models all followed a Michaelis--Menten model structure (Table 6). The first model included surface light as a predictor of photosynthesis while the second model included submerged light (Table 6; Model 1 & 2). The third model included submerged light as a predictor of photosynthesis and it includes temperature and chl *a* as variables influencing the P_{max} coefficient (Table 6; Model 3). The data entered into these models had a time step of 15 minutes.

Future Predictions

The ACIA (2004) predicts increased air temperatures of 4°C and a 20% increase in precipitation in the Arctic region. We developed a air--water temperature relationships for each reach and found that a for 4°C increase in air temperatures would increase water temperatures by ~ 2°C for each reach. We increased discharge by 20% using two methods. The first method increased discharge by 20% throughout the hydrograph while the second method used a sliding scale so that discharge increases mostly during peak flow and least during base flow. Increases in SRP were also predicted (Rouse et al. 1997; Hobbie et al. 1999), so the fertilized and ultra--fertilized reaches represent the nutrient conditions for the future. Using the calibrated best multiple linear models, we predicted what GEP, ER, and NEM would be with increased water temperature, discharge, and SRP.

Results

Key macronutrient concentrations were measured in each experimental reach as independent variables in the analyses of GEP and ER. Soluble reactive phosphorous levels were significantly different among reaches ($F = 13.16$, $p < 0.01$). The SRP levels were higher in the ultra--fertilized reach than in the reference and fertilized reaches ($t = 4.46$, $p < 0.01$, $t = 3.61$, $p < 0.01$) and higher in the fertilized than the reference reach ($t = 0.85$, $p < 0.01$; Fig. 11A). Ammonium levels were not significantly different among reaches ($F = 0.10$, $p = 0.91$; Fig. 11B). Nitrate levels were significantly different among reaches ($F = 4.51$, $p < 0.05$). The NO_3 levels were significantly higher in the reference than the ultra--fertilized reach ($t = -3.23$, $p < 0.05$) while there were no significant differences between the reference and fertilized reaches and fertilized and ultra--fertilized reaches ($t = 1.32$, $p = 0.59$; $t = -1.91$, $p = 0.15$; Fig. 11C).

Estimates of epilithic autotrophic biomass were required to assess the effects of this variable on stream GEP. Epilithic chl *a* was significantly different among reaches ($F = 8.67$, $p < 0.01$). Epilithic chl *a* was significantly higher in the ultra--fertilized reach than in the reference reach ($t = 2.46$, $p < 0.01$) while there were no significant differences between the reference and fertilized reaches and fertilized and ultra--fertilized reaches ($t = 2.33$, $p = 0.22$; $t = 0.13$, $p = 1.00$; Fig. 11D). Cover for the bryophyte *S. agassizii* was not significantly different among reaches ($F = 3.82$, $p = 0.05$; Fig. 11E). Cover for *Hygrohypnum* was significantly different among reaches ($F = 49.36$, $p < 0.01$). *Hygrohypnum* cover was significantly higher in the fertilized and ultra--fertilized reaches

than in the reference reach (t = 7.83, p < 0.01; t = 5.29, p < 0.05) while there were no significant differences between the fertilized and ultra--fertilized reaches (t = -2.54, p = 1.00; Fig. 11F).

The primary dependent variables in this study were gross ecosystem production (GEP) and ecosystem respiration (ER). Gross ecosystem production was significantly different among reaches (F = 28.26, p < 0.01). GEP was significantly higher in the fertilized and ultra--fertilized reaches than in the reference reach (t = 6.76, p < 0.01; t = 10.41, p < 0.01), and was significantly higher in the ultra--fertilized reach than the fertilized reach (t = 4.55, p < 0.01; Fig. 11G). Ecosystem respiration was not significantly different among reaches (F = 1.10; p = 0.35; Fig. 11H).

To model surrogate daily chl *a* values from the weekly epilithic chl *a* samples, we used a mechanistic chl *a* growth model devised by Uehlinger et al. (1996). The chl *a* model fit the data well (R^2 = 0.86; Fig. 12) and we used modeled chl *a* in the subsequent analyses.

To model daily nutrient values from our twice--weekly nutrient sampling, we devised relationships to estimate concentration from discharge. Soluble reactive phosphorus responded negatively and strongly with discharge among all reaches (R^2 = 0.61, 0.94, 0.97 in the reference, fertilized, and ultra--fertilized reaches, respectively; Fig 13A, B, & C). Since discharge was a good predictor of SRP, we used modeled SRP in the subsequent analyses. In contrast, neither ammonium nor nitrate correlated will with discharge in any reach. The R^2 values for the relationships between ammonium concentration and discharge were 0.27, 0.00, 0.13 in the reference, fertilized, and ultra--

fertilized reaches, respectively (Fig. 13D, E, & F). The R^2 values for the relationships between nitrate concentration and discharge were 0.13, 0.13, 0.30 in the reference, fertilized, and ultra--fertilized reaches, respectively (Fig. 13G, H, & I). Because the goodness--of--fit was weak for modeled NH4 and NO3, these nutrients were not evaluated in subsequent analyses.

Gross ecosystem production responded positively to surface light, subsurface light, temperature, chl *a*, and SRP and negatively to discharge. Gross ecosystem production responded positively to surface light among all reaches (Fig. 14A, B, & C) and the slope coefficients of the linear regression were not significantly different between reference and fertilized reaches, reference and ultra--fertilized reaches, or fertilized and ultra--fertilized reaches ($t = 0.54$, $p = 0.59$; $t = 0.83$, $p = 0.41$; $t = 0.27$, $p = 0.79$; respectively). The response of GEP to submerged light was similar and positive among all reaches (Fig. 14D, E, & F). However, unlike surface light, the slope coefficients of the linear regression with submerged light were significantly higher in the fertilized and ultra--fertilized reaches than in the reference reach ($t = 2.62$, $p < 0.05$; $t = 3.89$, $p < 0.01$; respectively) while there were not significant differences between the fertilized and ultra--fertilized reaches ($t = 0.80$, $p = 0.43$). Gross ecosystem production responded positively with temperature in all reaches (Fig. 14G, H, & I). The slope coefficients of the linear regression were significantly higher in the fertilized and ultra--fertilized reaches than in the reference reach ($t = 4.57$, $p < 0.01$; $t = 4.77$, $p < 0.01$; respectively) but there were not significant differences between the fertilized and ultra--fertilized reaches ($t = 0.55$, $p = 0.58$). Gross ecosystem production responded positively to modeled chl *a* (Fig. 15D, E, &

F) and the slope coefficients of the linear regression were significantly higher in the fertilized and ultra--fertilized reaches than in the reference reach ($t = 3.01$, $p < 0.01$; $t = 3.68$, $p < 0.01$; respectively) while there were no significant differences between the fertilized and ultra--fertilized reaches ($t = 0.42$, $p = 0.67$). Gross ecosystem production responded positively to modeled SRP (Fig. 15G, H, & I). The slope coefficient was significantly higher in the reference reach than in the fertilized and ultra--fertilized reaches ($t = 7.55$, $p < 0.01$; $t = 7.84$, $p < 0.01$; respectively) and in the fertilized reach than in the ultra--fertilized reach ($t = 8.83$, $p < 0.01$).

Discharge was the only measured variable to which GEP responded negatively. Log discharge had a negative relationship with GEP in all reaches (Fig. 15A, B, & C). The slope coefficients of the linear regression were significantly higher in the reference reach than in the fertilized and ultra--fertilized reaches ($t = 4.80$, $p < 0.01$; $t = 4.39$, $p < 0.01$; respectively) while there were not significant differences between the fertilized and ultra--fertilized reaches ($t = 0.51$, $p = 0.61$).

Ecosystem respiration responded negatively with temperature in the reference reach but positively in the fertilized and ultra--fertilized reaches (Fig 16A, B, & C). The relationship between respiration and temperature should be positive, meaning higher respiration with higher temperature. The slope coefficients of the linear regression were significantly higher in the fertilized and ultra--fertilized reaches than in the reference reach ($t = 2.87$, $p < 0.01$; $t = 4.24$, $p < 0.01$; respectively) while there were no significant differences between the fertilized and ultra--fertilized reaches ($t = 1.80$, $p = 0.08$).

Ecosystem respiration responded positively to increases in discharge in the reference reach but responded negatively in the fertilized and ultra--fertilized reaches (Fig. 16D, E, & F). The slope coefficients of the linear regression were significantly higher in the in the reference reach than in the fertilized and ultra--fertilized reaches (t = 3.20, $p < 0.01$; t = 4.40, $p < 0.01$; respectively) while there were no significant differences between the fertilized and ultra--fertilized reaches (t = 1.75, p = 0.08).

Ecosystem respiration responded negatively with modeled SRP in the reference reach while there was a positive response in the fertilized and ultra--fertilized reaches (Fig. 16G, H, & I). The slope coefficients of the linear regression were not significantly different between the reference and fertilized, reference and ultra--fertilized, and fertilized and ultra--fertilized (t = 1.08, p = 0.28; t = 1.08, p = 0.28; t = 0.04, p = 0.97; respectively).

To reduce the complexity of the models we tested, we examined correlation among all of the independent variables and eliminated variables that were highly correlated with another variable in the set of independent variables. The correlation among predictor variables for each reach is listed on Table 3. We found that temperature and log discharge were highly correlated ($r > 0.90$) among all reaches and decided to drop log discharge from the multivariate models because temperature directly influences biological rates while discharge does not. We also excluded surface light from the multivariate models because submerged light was a better predictor of photosynthesis.

We used two different approaches to find the best model of GEP and ER in each stream reach. In the first approach, we tested all possible linear models of the

independent variables and identified the variables that best explained GEP and ER in each reach using information theoretic methods. The relative importance (Akaike weights) of each of the variables in the best model for GEP is listed in Table 4 and in Fig. 17A. The best multiple linear photosynthesis model for the reference reach included submerged light, temperature, and modeled chl *a*. For the fertilized reach, the best multiple linear photosynthesis model included temperature and modeled chl *a*; submerged light was of low importance in this reach. The best multiple linear photosynthesis model for the ultra--fertilized reach included submerged light, temperature, modeled chl *a*, as in the reference reach. There was no model in which SRP was deemed important.

We repeated this analysis for ecosystem respiration (Table 5, Fig. 17B). The best multiple linear respiration model for the reference reach was the null model, which included no predictor variables. This is not surprising because ER in the reference reach was relatively invariant. For the fertilized reach, the best multiple linear respiration model included temperature and SRP. Temperature was highly important while SRP was moderately important. The best multiple linear respiration model for the ultra--fertilized reach included only temperature.

In a second approach, we tested a series of mechanistic models that explain GEP based on key driving variables. Among all reaches, the best mechanistic photosynthesis model included submerged light, temperature, and chl *a* (Table 6; model 3), which explained 82 -- 86% of the variation in GEP. Among all reaches, the mechanistic model with submerged light explained 51 -- 70% of the variance in GEP (Table 6; model 2) and

was ranked higher than the models with surface light which explained 33 -- 47% of the variance in GEP (Table 6; model 1).

Table 7 displays the results of the predictions for GEP, ER, and NEM with increased, temperature, and discharge, and SRP. Future water temperatures and SRP levels increased GEP while future discharge decreased GEP. Gross ecosystem production increased with the combination of future changes in water temperature, discharge, and SRP.

Ecosystem respiration did not respond to elevated temperature in the reference reach or elevated SRP levels. However, ER responded positively to the combination of elevated temperature and SRP.

Net ecosystem metabolism decreased with temperature and SRP but did not respond to discharge. With the combined influence of increased water temperature, discharge, and SRP resulted in a decrease in NEM.

Hall and Tank (2005) suggest that if the ER bias due to effects of groundwater seepage is >1.30, then corrections need to be made for this seepage effect. We found that the ER bias due to groundwater seepage in our study was 1.16 in the reference and ultra--fertilized reaches and 1.15 in the fertilized reach; thus, we did not correct for groundwater seepage bias. Following McCutchan et al. (1998), we concluded that a GEP bias of <0.80 due to groundwater seepage would require correction. The GEP bias encountered was 0.91 in the reference reach and 0.92 in the fertilized and ultra--fertilized reaches and so we did not correct for GEP bias either.

Discussion

We manipulated SRP levels in the fertilized reaches of the Kuparuk River so that SRP was highest in the ultra--fertilized reach, intermediate in the fertilized reach, and lowest in the reference reach (Figure 11A). Ammonium concentrations did no change in response to the added SRP in the fertilized reaches (Fig 11B). However, we did observe NO_3 was highest in the reference reach, intermediate in the fertilized reach and lowest in the ultra--fertilized reach (Fig. 11C). These findings are consistent with the conclusions reported by Slavik et al. (2004). The concentrations of NH_4 are so low in this river that organisms may not be capable of efficiently remove it or our techniques may not be able to detect it reliably at such low levels (Holmes et al. 1999).

Epilithic chl *a* levels and *Hygrohypnum* cover were higher in the fertilized and ultra--fertilized reaches than in the reference reach while *S. agassizii* cover was not different among any reaches (Fig. 11D, E, & F). These results are entirely consistent with previous results presented by Bowden et al. (1992) and Slavik et al. 2004).

Guasch et al. (1995) and Mulholland et al. (2001) found that nutrients influence lotic open--system photosynthesis. We also found that GEP responded positively to increased SRP levels in the fertilized reaches of the Kuparuk River (Fig. 11G). These results are consistent with results from earlier closed--system metabolism experiments in which it was found that GPP responded positively to increased SRP in the fertilized reach of the Kuparuk River (Peterson et al. 1985, Bowden et al. 1992, Arscott et al. 1998).

Guasch et al. (1995) and Mulholland et al. (2001) also found that nutrients can influence lotic open--system respiration and earlier closed--system metabolism experiments (which exclude hyporheic influences) showed that respiration responded positively to increased SRP in the fertilized reach of the Kuparuk River (Peterson et al. 1985, Bowden et al. 1992, Arscott et al. 1998). However, in this study, overall ER in the fertilized reaches of the Kuparuk River did not respond to increased SRP levels (Fig. 11H), despite the higher respiration in the bryophyte--epiphyte community in these reaches. Mosses in the fertilized riffles may interfere with ER in the fertilized reaches by physically blocking a substantial portion of the hyporheic exchange that would normally occur in this zone. Suren et al. (2000) found that bryophytes reduce the drag forces on rocks by reducing the force of the turbulent eddies and wakes formed around the rocks. Likewise, Nikora (1998) found that moss created hydraulically tranquil regions around the substratum in an experimental cobble--bed flume; and Scarsbrook and Townsend (1994) noted that experimentally added leaf litter lowered frictional forces between flowing water and the substratum. Edwardson et al. (2003) reported that the ratio of transient storage zone area to stream area (As A^{-1}) in the Kuparuk River was about 50% higher in the reference reach, although the differences were not significant. These results suggest that it is plausible that extensive bryophyte growth might interfere with hyporheic exchange and so, might reduce the component of ER that is contributed by hyporheic respiration.

We found that Uehlinger's epilithic chl *a* model fit our data well (Fig. 12). The mathematics of the model were logical for the Kuparuk River because this river is flood

prone and discharge typically influences the amount of photosynthetic biomass in these rivers (Grimm and Fisher 1989, Uehlinger 1991, Uehlinger et al. 1996, Elosegui and Pozo 1998). Meanwhile, artificial stream channels with regulated flows are typically influenced by many factors including light, temperature, nutrients, and herbivores (Bothwell 1986, 1988, Anderson et al. 1999, Wellnitz and Ward 2000). Therefore, this model may not work well for rivers with moderately fluctuating flows. This model is useful because it is logistically and economically unfeasible to measure chl *a* levels of moss and epilithon at daily intervals.

Discharge was a good predictor of SRP but not NH_4 or NO_3 (Fig. 13). Soluble reactive phosphorous was modeled on a daily time scale so it could be included into our multiple linear models.

The bivariate results suggest that submerged light is a better predictor of photosynthesis than surface light; submerged light (Fig. 14), temperature, log discharge, chl *a*, and SRP are good predictors of GEP (Figs. 14 & 15); and the GEP response to SRP was greatest under low SRP levels (Fig 15).

Ecosystem respiration responded positively to temperature and SRP while ER responded negatively to log discharge in the fertilized reaches (Fig. 16). Conversely, ER responded negatively to temperature and SRP while ER responded positively to log discharge in the reference reach. Although the reference reach responded differently, the responses were very weak. The ER response to temperature and discharge was greater in the fertilized reaches than in the reference reach while the ER response to SRP was not significantly different among reaches. Interestingly, ER showed an increasing response to

changes in temperature and discharge as SRP levels increased. It is possible that the weak response by ER to temperature and discharge was because hyporheic respiration dominanted epilithic respiration and was buffered from changes in water column temperature and disturbance.

Temperature was highly correlated ($\underline{r} > 0.90$) with log discharge among all reaches so log discharge was dropped from the multiple linear models because discharge does not directly influence biological rates while temperature does (Graham 2003; Table 3). Further, discharge influences submerged light, chl *a*, and SRP so eliminating discharge greatly reduces intercorrelation of the predictor variables.

We evaluated the combined influence of submerged light, temperature, chl *a*, and SRP with multiple linear models using information theory. Submerged light, temperature, and chl *a* were very important predictors of GEP while SRP was less important (Fig. 17A). The same variables were important in all reaches expect that submerged light only of low importance in the fertilized reach.

Uehlinger (1993), Young and Huryn (1996), and Acuna et al (2004) all found that light and temperature were important variables influencing photosynthesis. However, none of these studies use chl *a* as a predictor of lotic open--system photosynthesis with daily time scales. Chlorophyll a was weakly to moderately correlated with submerged light and temperature in all reaches. The bivariate analysis we did suggests that chl *a* is a good predictor of GEP. This means that chl *a* predicts photosynthesis in a way that is not predicted by submerged light and temperature. Conversely, submerged light and

temperature are highly to very highly correlated with log discharge. Thus, discharge is a redundant variable in this analysis.

Temperature was more important than SRP among all reaches (Fig. 17B). Temperature was an important predictor of ER in the fertilized reaches but was of low importance in the reference reach, which is similar to our findings from the ANCOVA analysis. Since the hyporheic zone is buffered from changes in water column temperature, we hypothesize that temperature's weak influence on ER in the reference reach is due to the dominance of hyporheic respiration while the fertilized reaches are less dominated by hyporheic respiration and therefore have greater responses to temperature.

Submerged light was a better predictor of GEP than surface light for mechanistic models among all reaches (Table 6). Similarly, the bivariate analysis suggests that submerged light a better predictor of GEP than surface light. Light scatter and absorption increases with turbidity and light attenuation increases with depth thus, increased turbidity and depth increase the likelihood of light scatter or absorption. Generally, the benthos contributes more to photosynthesis than the water column in low to middle order reaches (Vannote et al. 1980). The majority of photosynthesis in the Kuparuk River occurring on the benthos and not the water column (Arscott et al. 1998), thus surface light has to penetrate through the water column to the benthos. Young and Huryn (1996) found that light attenuation because of depth and turbidity was an important predictor of photosynthesis during a high flow year but not during a low flow year. On the other hand, Uehlinger (1993) found that light attenuation was not an important predictor of

photosynthesis because there is little variation in depth or turbidity during their study. Turbidity and river depth varied considerably in the Kuparuk River during the 2004 field season. Submerged light accounts for changes in turbidity and depth so it is a better measure of light and predictor of GEP in the Kuparuk River.

The best mechanistic photosynthesis model in all reaches included submerged light, temperature, and chl *a* among, like the multiple linear models. The best mechanistic models explained 82 -- 86% of the variance in GEP in each reach while the mechanistic model with surface light only explained 33 -- 47 % of the variance in GEP. These results are consistent with our understand of metabolic processes in rivers. Photosynthesis is dependent on light reaching the photosynthesizers (submerged light) and the photosynthetic biomass (chl *a*) that harnesses the light. Temperature regulates both light unsaturated and light saturated photosynthetic rates although the latter is more important (Malone and Neale 1981, Cote and Platt 1984, Tilzer et al. 1986, Cota et al. 1994). At some levels, nutrients certainly influence photosynthetic rates (Rhee 1973, Greenwood 1976, Siderius et al. 1996). However, fluctuations in SRP levels within the stream reaches we studied were not an important influence on photosynthesis.

The combined influence of increased water temperature, discharge, and SRP will increase GEP by 141 -- 196% and ER by 11 -- 12% while NEM decreases by 1 -- 7%. The decrease in NEM means that carbon sequestration in streams is expected to increase, although not substantially, in the future. Studies by Kling et al. (1991) and Kling et al. (1992) suggest that Arctic Alaskan Rivers released substantial amounts of CO_2 into the atmosphere. These results are consistent with our results that ER in much greater than

GEP in the Kuparuk River. Thus, climate change may decrease the amount of CO_2 emitted into the atmosphere, although the decrease is small and there is uncertainty because we only examined one river.

The North Slope of Alaska contains glacial rivers, spring rivers, tundra rivers, and hybrids of all three (Craig and McCart 1975). The Kuparuk River is a 4th order tundra river and is representative of the many Arctic rivers flowing through the North Slope because the flow characteristics and benthic invertebrate abundance are intermediate to that of a glacial and spring river (Craig and McCart 1975).

Conclusions

While long--term phosphorous fertilization increased GEP in the fertilized reaches of the Kuparuk River, short--term fluctuations in SRP levels within the stream reaches was not an important influence on GEP. Phosphorous fertilization did not increase ER in the fertilized reaches of the Kuparuk River and fluctuations in SRP levels within the stream reaches was not an important influence on ER. Uehlinger's model was useful for modeling chl *a* on a daily time scale while limiting nutrients can be modeled based on biological principles. The bivariate and mechanistic analysis suggested that submerged light was a better predictor of GEP than surface light. The results from the multiple linear models suggest that submerged light, temperature, and chl *a* were important variables influencing GEP within each reach while temperature was an important variable influencing ER in the fertilized reaches. The best mechanistic explained 82 -- 86% of the variance in GEP and may be a useful photosynthesis model for other streams. The combined influence of increased water temperature, discharge, and

SRP will decrease NEM, meaning that carbon sequestration in streams is expected to increase, although not substantially, in the future. This means that the net CO_2 flux out of these rivers into the atmosphere will likely decrease.

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Tables

Table 3. Pearson correlation matrix of predictor variables in each stream reach.

Ref	I_{Surf}	I_{Sub}	T	log Q	Chl *a*	SRP
I_{Surf}	1	--	--	--	--	--
I_{Sub}	0.87	1	--	--	--	--
T	0.53	0.78	1	--	--	--
log Q	-0.37	-0.71	-0.90	1	--	--
Chl *a*	0.09	0.20	0.33	-0.48	1	--
SRP	0.19	0.40	0.47	-0.62	0.54	1

Fert	I_{Surf}	I_{Sub}	T	log Q	Chl *a*	SRP
I_{Surf}	1	--	--	--	--	--
I_{Sub}	0.80	1	--	--	--	--
T	0.42	0.79	1	--	--	--
log Q	-0.25	-0.72	-0.92	1	--	--
Chl *a*	0.05	0.24	0.38	-0.50	1	--
SRP	0.09	0.48	0.71	-0.84	0.83	1

Ultra--Fert	I_{Surf}	I_{Sub}	T	log Q	Chl *a*	SRP
I_{Surf}	1	--	--	--	--	--
I_{Sub}	0.81	1	--	--	--	--
T	0.38	0.77	1	--	--	--
log Q	-0.20	-0.70	-0.93	1	--	--
Chl *a*	0.13	0.47	0.59	-0.67	1	--
SRP	0.09	0.53	0.76	-0.85	0.90	1

Table 4. Multivariate linear models of GEP with Akaike weight ($\underline{w_i}$) greater than 0.01 in each reach. The best model is boldfaced for each reach.

Reference Models	$\underline{w_i}$
$\beta_0+\beta_1*I_{Sub}+\beta_2*$Chl $\underline{a}+\beta_3$SRP	0.04
$\beta_0+\beta_1*I_{Sub}+\beta_2*T+\beta_3*$Chl $\underline{a}$	**0.56**
$\beta_0+\beta_1*I_{Sub}+\beta_2*T+\beta_3*$Chl $\underline{a}+\beta_4$SRP	0.40

Fertilized Models	$\underline{w_i}$
$\beta_0+\beta_1*T+\beta_2*$Chl $\underline{a}$	**0.54**
$\beta_0+\beta_1*T+\beta_2*$Chl $\underline{a}+\beta_3*$SRP	0.16
$\beta_0+\beta_1*I_{Sub}+\beta_2*T+\beta_3*$Chl $\underline{a}$	0.23
$\beta_0+ +\beta_1*I_{Sub}+\beta_2*T+\beta_3*$Chl $\underline{a}+\beta_4*$SRP	0.07

Ultra--Fertilized Models	$\underline{w_i}$
$\beta_0+\beta_1*T+\beta_2*$Chl $\underline{a}$	0.12
$\beta_0+\beta_1*T+\beta_2*$Chl $\underline{a}+\beta_3*$SRP	0.14
$\beta_0+\beta_1*I_{Sub}+\beta_2*T+\beta_3*$Chl $\underline{a}$	**0.48**
$\beta_0+\beta_1*I_{Sub}+\beta_2*T+\beta_3*$Chl $\underline{a}+\beta_4*$SRP	0.41

Table 5. Multivariate linear models of ER with Akaike weight ($\underline{w_i}$) greater than 0.01 in each reach. The best model is boldfaced for each reach.

Reference Models	$\underline{w_i}$
β_0	**0.37**
$\beta_0+\beta_1*T$	0.32
$\beta_0+\beta_1*$SRP	0.21
$\beta_0+\beta_1*T+\beta_2*$SRP	0.18

Fertilized Models	$\underline{w_i}$
β_0	0.02
$\beta_0+\beta_1*T$	0.38
$\beta_0+\beta_1*$SRP	0.21
$\beta_0+\beta_1*T+\beta_2*$SRP	**0.52**

Ultra--Fertilized Models	$\underline{w_i}$
$\beta_0+\beta_1*T$	**0.76**
$\beta_0+\beta_1*$SRP	0.01
$\beta_0+\beta_1*T+\beta_2*$SRP	0.23

Table 6. Akaike weights ($\underline{w_i}$), goodness--of--fit ($\underline{R^2}$), and model rank for each mechanistic photosynthesis models in each reach.

Mechanistic Photosynthesis Model	Akaike Weight ($\underline{w_i}$)			$\underline{R^2}$			Rank		
	Ref	Fert	UFert	Ref	Fert	UFert	Ref	Fert	UFert
Model 1: $GEP = P_{\max} * \left(\frac{I_{Surf}}{I_k + I_{Surf}} \right)$	0.00	0.00	0.00	0.34	0.33	0.47	3	3	3
Model 2: $GEP = P_{\max} * \left(\frac{I_{Sub}}{I_k + I_{Sub}} \right)$	0.00	0.00	0.00	0.51	0.55	0.70	2	2	2
Model 3: $P_{\max} = k_{Chl\ a} * Chl\ a * k_t^{\ T}$ $GEP = P_{\max} * \left(\frac{I_{Sub}}{I_k + I_{Sub}} \right)$	1.00	1.00	1.00	0.82	0.86	0.85	1	1	1

Table 7. Actual and predicted GEP, ER, and NEM (mean ± SE) based on increased SRP, temperature, and precipitation in the year 2100. The baseline conditions are boldfaced and the value inside the parentheses is the percent change of the predicted value from the actual value.

GEP (mg C m^{-2} h^{-1})	Actual	↑T	↑$Q_{+20\%}$ (↓Chla)	↑Q_{SS} (↓Chla)	↑T + ↑$Q_{+20\%}$ (↓Chla)	↑T + ↑Q_{SS} (↓Chla)
Reference	**23 ± 3 (+0%)**	29 ± 2 (+22%)	20 ± 2 (-15%)	23 ± 2 (-1%)	25 ± 2 (+8%)	28 ± 3 (+28%)
Fertilized	42 ± 5 (+81%)	63 ± 5(+167%)	36 ± 5 (+54%)	42 ± 5 (+77%)	57 ± 5 (+141%)	62 ± 5 (+163%)
Ultra-Fertilized	54 ± 5 (+132%)	70 ± 5 (+200%)	49 ± 5 (+109)	54 ± 5 (+128)	65 ± 5 (+177)	70 ± 5 (+196)

ER (mg C m^{-2} h^{-1})	Actual	↑T
Reference	**259 ± 6 (0%)**	259 ± 6 (0%)
Fertilized	277 ± 6 (+7%)	290 ± 2 (+12%)
Ultra-Fertilized	260 ± 9 (0%)	288 ± 5(+11%)

NEM (mg C m^{-2} h^{-1})	Actual	↑T	↑$Q_{+20\%}$ (↓Chla)	↑Q_{SS} (↓Chla)	↑T + ↑$Q_{+20\%}$ (↓Chla)	↑T + ↑Q_{SS} (↓Chla)
Reference	**235 ± 7 (0%)**	230 ± 7 (-2%)	239 ± 7 (+1%)	236 ± 7 (0%)	234 ± 8 (-1%)	230 ± 8 (-2%)
Fertilized	234 ± 7 (0%)	227 ± 3 (-3%)	240 ± 7 (+2%)	235 ± 3 (0%)	233 ± 7 (-1%)	228 ± 3 (-3%)
Ultra-Fertilized	206 ± 9 (-13%)	218 ± 2 (-7%)	211 ± 8 (-10%)	206 ± 2 (-12%)	223 ± 9 (-5%)	219 ± 2 (-7%)

Figure Legends

Figure 11. Season of 2004 summary of nutrients, biological variables, and GEP and ER among reaches (mean ± 1 *SE*).

Figure 12. Temporal dynamics of actual epilithic chl *a*, modeled chl *a*, and discharge. The goodness--of--fit for Uehlinger's model was $R^2 = 0.86$.

Figure 13. Relationships between nutrients and discharge in each reach. A, D, and G are reference reach; B, E, and H are fertilized reach; and C, F, and I are ultra--fertilized reach nutrient--discharge relationships.

Figure 14. The response of GEP to surface light, submerged light, and temperature in each reach. A, D, and G are reference reach; B, E, and H are fertilized reach; and C, F, and I are ultra--fertilized reach GEP relationships.

Figure 15. The response of GEP to log discharge, modeled chl *a*, and modeled SRP in each reach. A, D, and G are reference reach; B, E, and H are fertilized reach; and C, F, and I are ultra--fertilized reach GEP relationships.

Figure 16. The response of ER to temperature, log discharge, and modeled SRP in each reach. A, D, and G are reference reach; B, E, and H are fertilized reach; and C, F, and I are ultra--fertilized reach ER relationships.

Figure 17. The variable importance (w_i) of each predictor variable in the multivariate linear models for GEP and ER in each reach. A. Predictor variable importance for GEP. B. Predictor variable importance for ER.

Figures

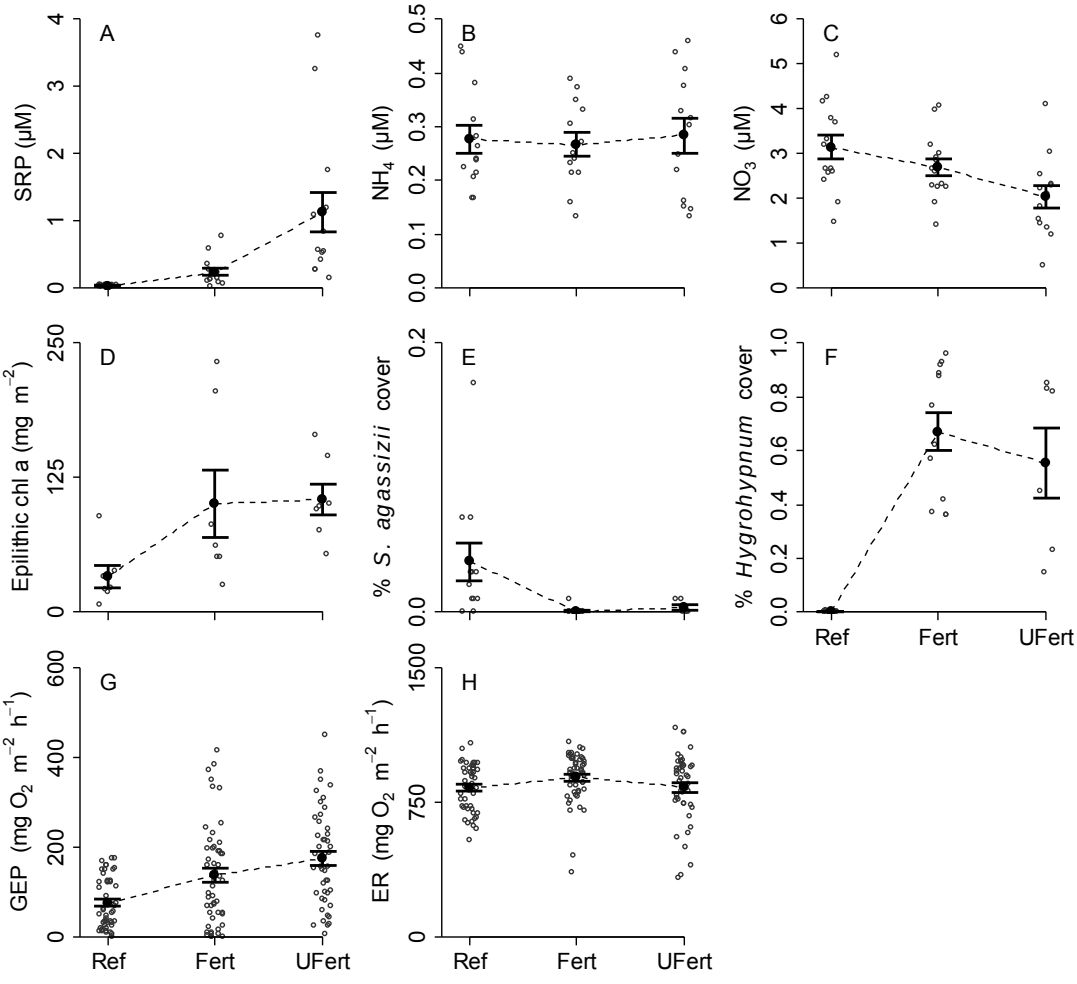

Figure 11.

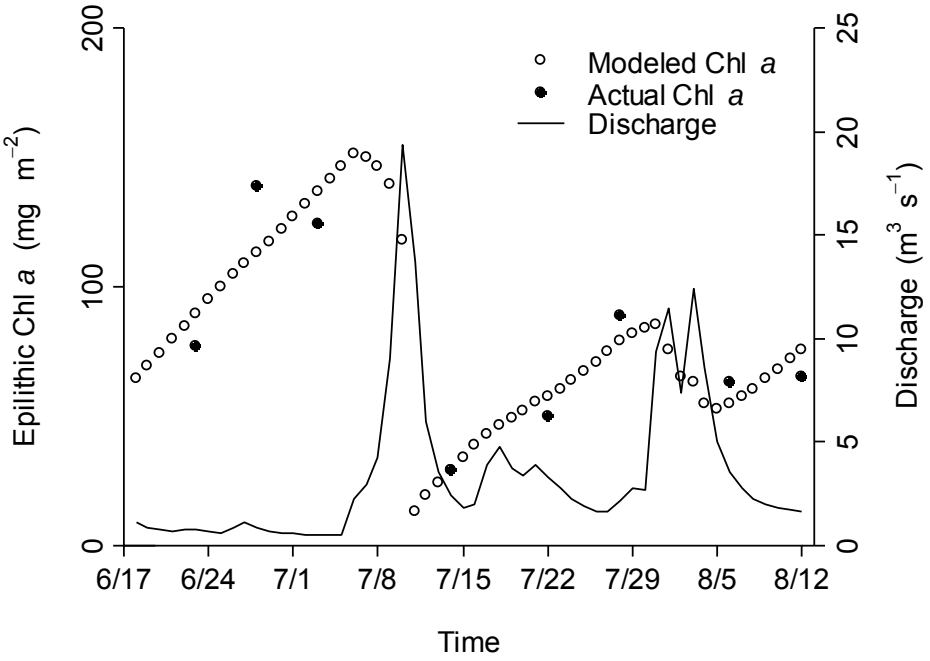
Modeled Chl a
Actual Chl a
Discharge
Epilithic Chl a (mg m^{-2})
Discharge (m^3 s^{-1})
0
100
200
0
5
10
15
20
25
6/17
6/24
7/1
7/8
7/15
7/22
7/29
8/5
8/12
Time

Figure 12.

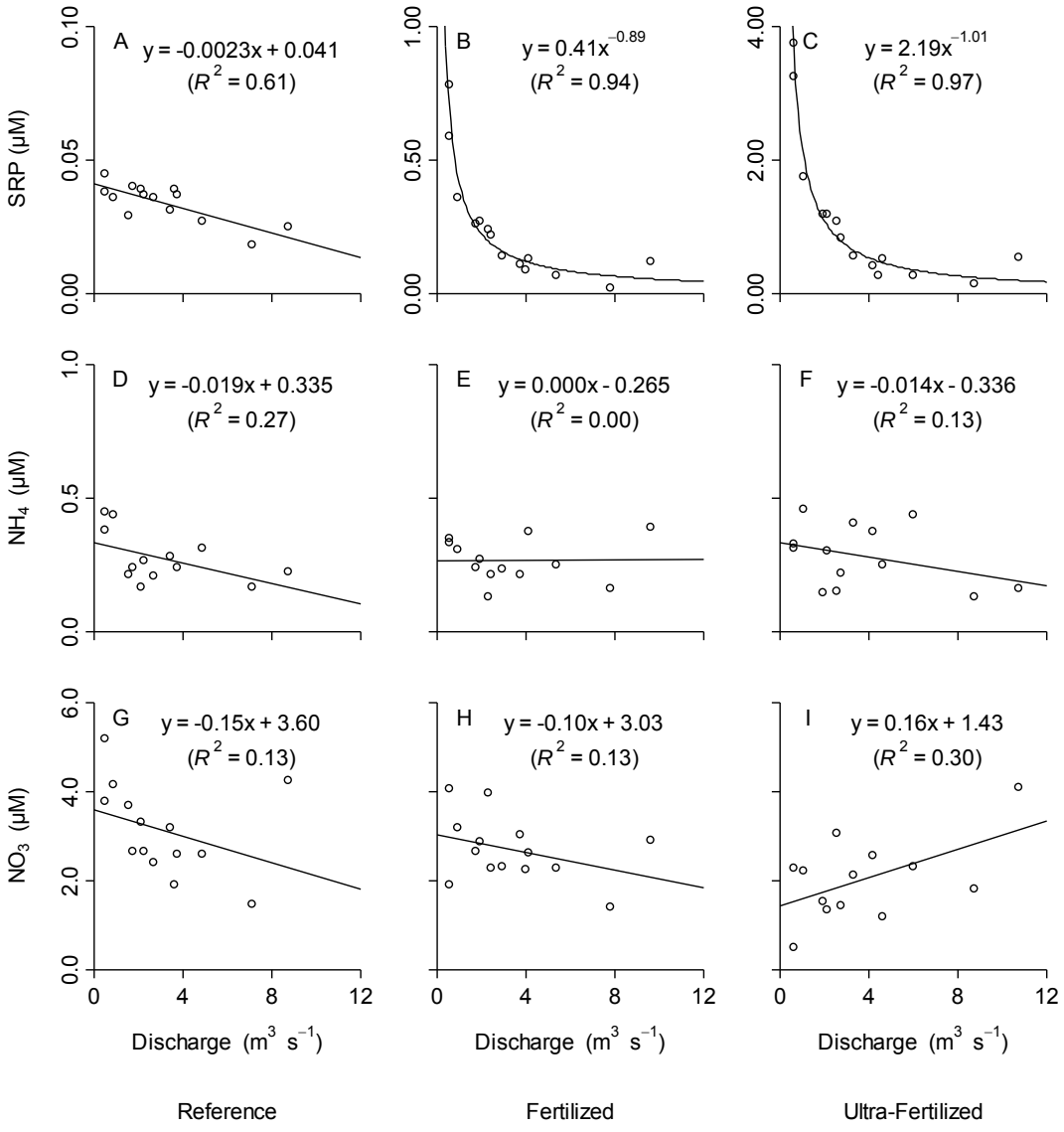
A
y = -0.0023x + 0.041
(R^2 = 0.61)
B
y = 0.41x$^{-0.89}$
(R^2 = 0.94)
C
y = 2.19x$^{-1.01}$
(R^2 = 0.97)
D
y = -0.019x + 0.335
(R^2 = 0.27)
E
y = 0.000x - 0.265
(R^2 = 0.00)
F
y = -0.014x - 0.336
(R^2 = 0.13)
G
y = -0.15x + 3.60
(R^2 = 0.13)
H
y = -0.10x + 3.03
(R^2 = 0.13)
I
y = 0.16x + 1.43
(R^2 = 0.30)
SRP (µM)
NH_4 (µM)
NO_3 (µM)
Discharge (m^3 s^{-1})
Reference
Fertilized
Ultra-Fertilized

Figure 13.

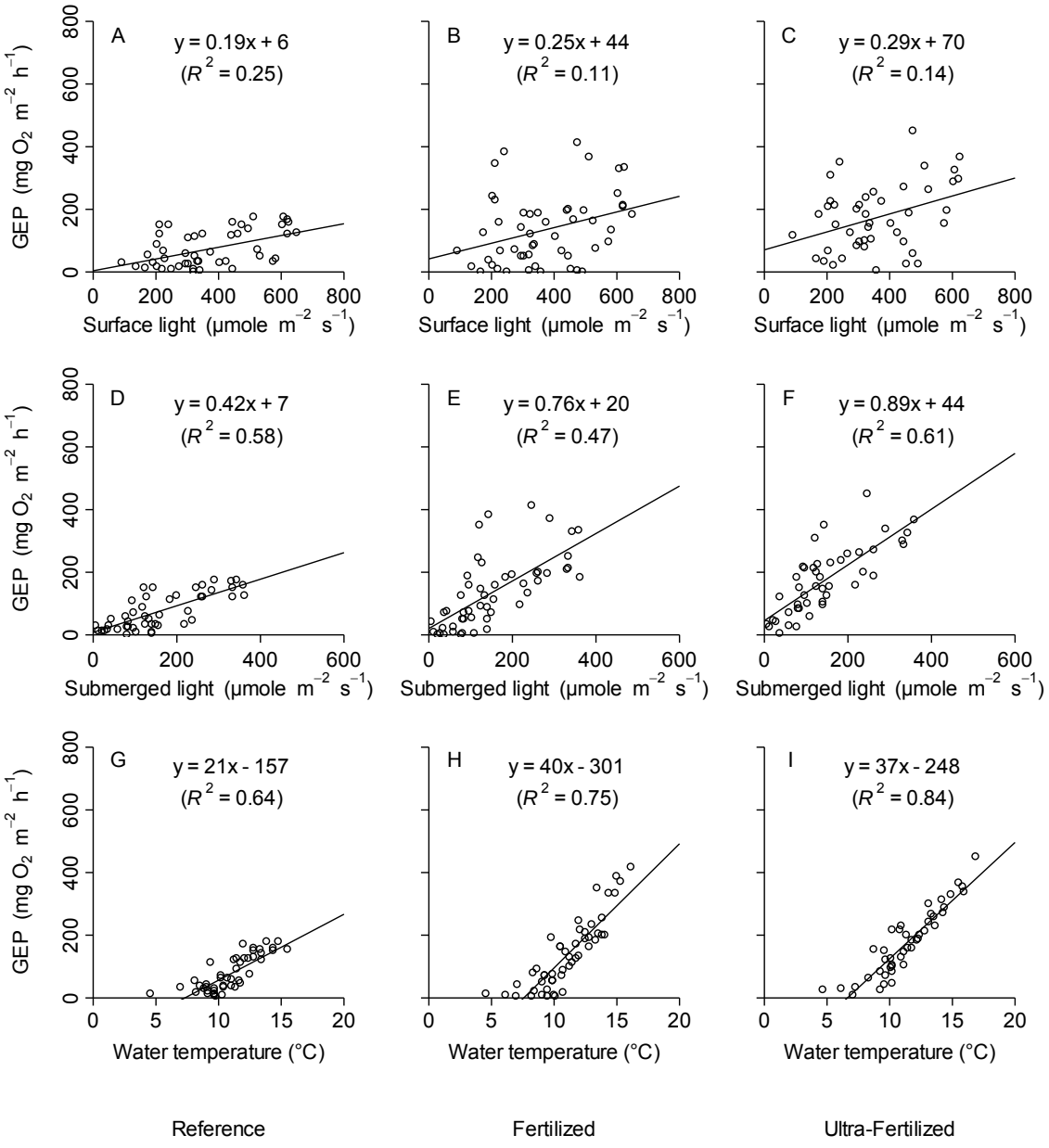
A
y = 0.19x + 6
(R^2 = 0.25)
B
y = 0.25x + 44
(R^2 = 0.11)
C
y = 0.29x + 70
(R^2 = 0.14)
D
y = 0.42x + 7
(R^2 = 0.58)
E
y = 0.76x + 20
(R^2 = 0.47)
F
y = 0.89x + 44
(R^2 = 0.61)
G
y = 21x - 157
(R^2 = 0.64)
H
y = 40x - 301
(R^2 = 0.75)
I
y = 37x - 248
(R^2 = 0.84)
GEP (mg O_2 m^{-2} h^{-1})
Surface light (µmole m^{-2} s^{-1})
Submerged light (µmole m^{-2} s^{-1})
Water temperature (°C)
Reference
Fertilized
Ultra-Fertilized

Figure 14.

.

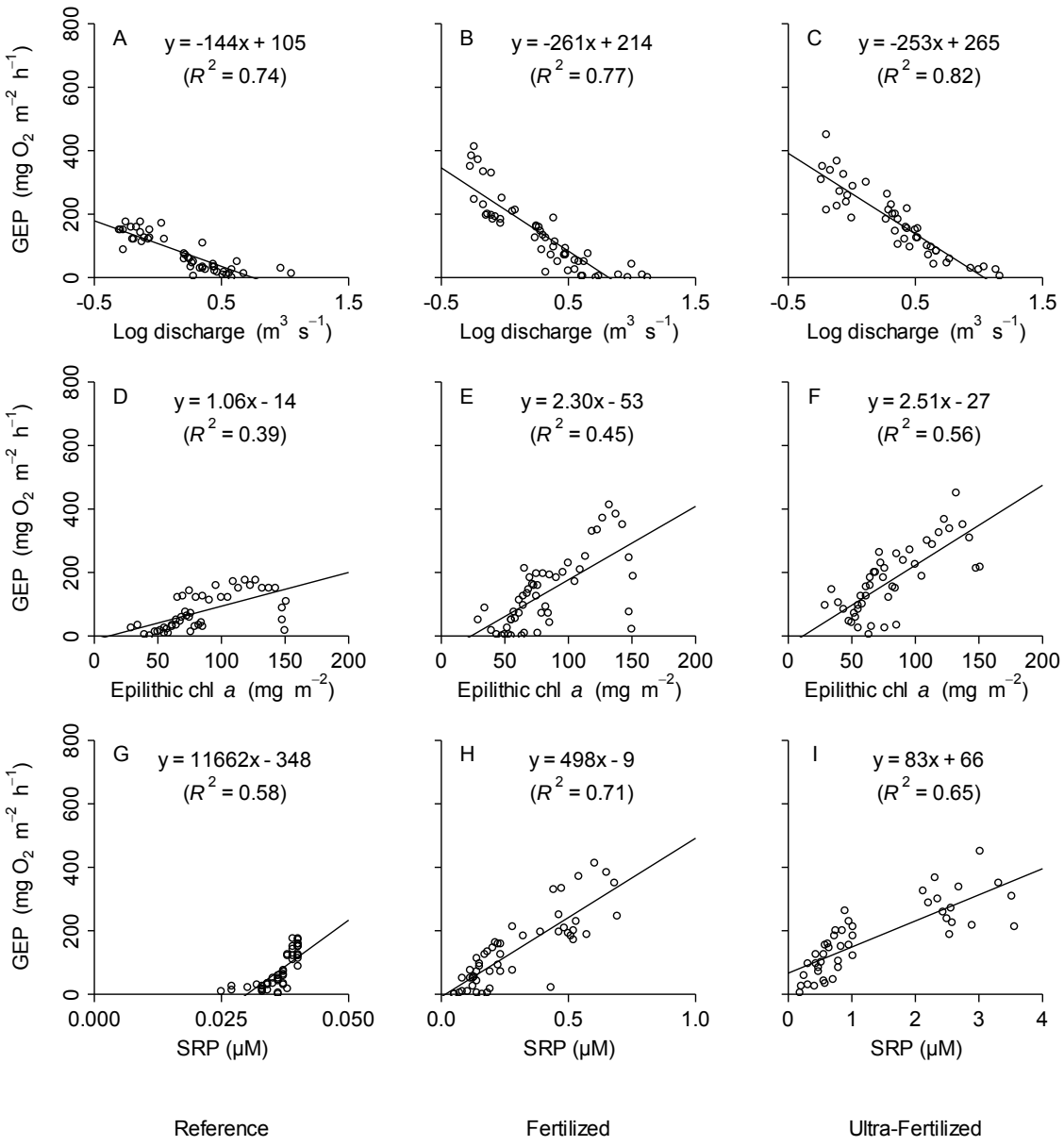
A
y = -144x + 105
(R^2 = 0.74)
B
y = -261x + 214
(R^2 = 0.77)
C
y = -253x + 265
(R^2 = 0.82)
D
y = 1.06x - 14
(R^2 = 0.39)
E
y = 2.30x - 53
(R^2 = 0.45)
F
y = 2.51x - 27
(R^2 = 0.56)
G
y = 11662x - 348
(R^2 = 0.58)
H
y = 498x - 9
(R^2 = 0.71)
I
y = 83x + 66
(R^2 = 0.65)
GEP (mg O_2 m^{-2} h^{-1})
Log discharge (m^3 s^{-1})
Epilithic chl *a* (mg m^{-2})
SRP (µM)
Reference
Fertilized
Ultra-Fertilized

Figure 15.

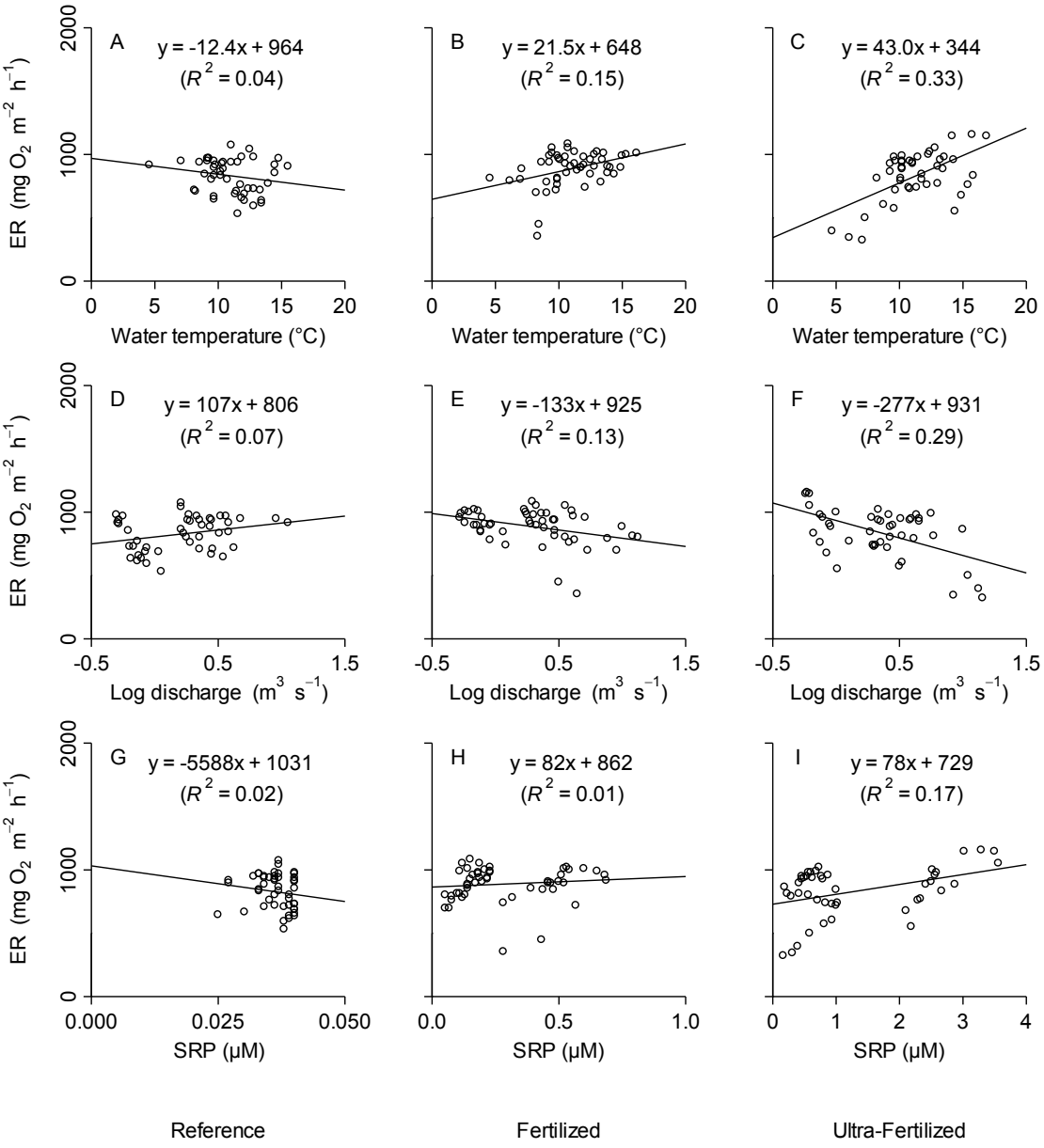
A
y = -12.4x + 964
(R^2 = 0.04)
B
y = 21.5x + 648
(R^2 = 0.15)
C
y = 43.0x + 344
(R^2 = 0.33)
D
y = 107x + 806
(R^2 = 0.07)
E
y = -133x + 925
(R^2 = 0.13)
F
y = -277x + 931
(R^2 = 0.29)
G
y = -5588x + 1031
(R^2 = 0.02)
H
y = 82x + 862
(R^2 = 0.01)
I
y = 78x + 729
(R^2 = 0.17)
ER (mg O_2 m^{-2} h^{-1})
Water temperature (°C)
Log discharge (m^3 s^{-1})
SRP (µM)
Reference
Fertilized
Ultra-Fertilized

Figure 16.

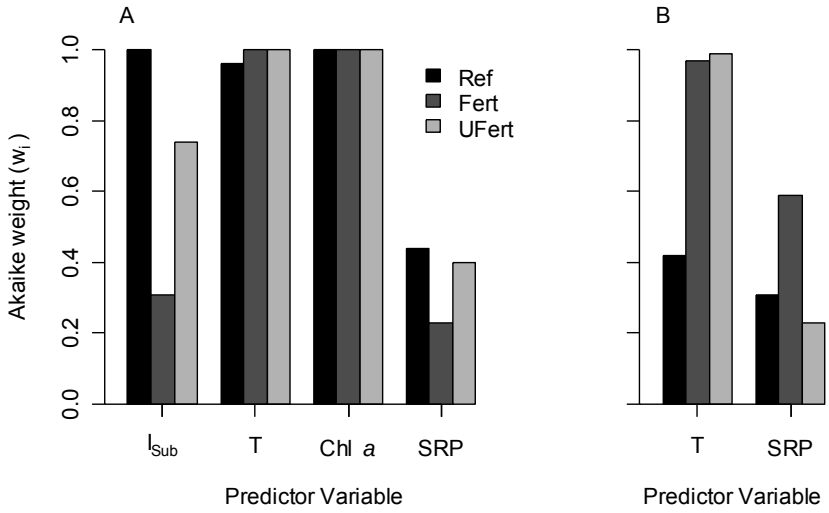
A
B
Akaike weight (w_i)
0.0
0.2
0.4
0.6
0.8
1.0
Ref
Fert
UFert
I_{Sub}
T
Chl *a*
SRP
Predictor Variable
T
SRP
Predictor Variable

Figure 17.

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