Published in final edited form as:
J Am Water Resour Assoc. 2019 ; 55(6): 1479–1491. doi:10.1111/1752-1688.12797.

Benthic algal (periphyton) growth rates in response to nitrogen and phosphorus: Parameter estimation for water quality models

Travis S. Schmidt,
Colorado Water Science Center, U.S Geological Survey, Fort Collins, CO, USA

Christopher P. Konrad,
Washington Water Science Center, U.S. Geological Survey, Tacoma, WA, USA

Janet L. Miller,
Fort Collins Science Center, U.S Geological Survey, Fort Collins, CO, USA

Stephen D. Whitlock,
Office of Water, Environmental Protection Agency, Washington D.C., USA

Craig A. Stricker
Fort Collins Science Center, U.S Geological Survey, Fort Collins, CO, USA

Abstract

Nitrogen (N) and phosphorus (P) are significant pollutants that can stimulate nuisance blooms of algae. Water quality models (e.g., WASP, CE-QUAL-R1, CE-QUAL-ICM, QUAL2k) are valuable and widely used management tools for algal accrual due to excess nutrients in the presence of other limiting factors. These models utilize the Monod and Droop equations to associate algal growth rate with dissolved nutrient concentration and intra-cellular nutrient content. Having accurate parameter values is essential to model performance, however published values for model parameterization are limited, particularly for benthic (periphyton) algae. We conducted a 10-day mesocosm experiment and measured diatom-dominated periphyton biomass accrual through time as chlorophyll *a* (chl *a*) and ash-free dry mass (AFDM) in response to additions of N (range 5–11,995 μg NO_3-N/L) and P (range 0.89–59.51 μg SRP/L). Resulting half saturation coefficients and growth rates are similar to other published values, but minimum nutrient quotas are higher than those previously reported. Saturation concentration for N ranged from 150 to 2450 μg NO_3-N/L based on chl *a* and from 8.5 to 60 μg NO_3-N/L when based on AFDM. Similarly, the saturation concentration for P ranged from 12 to 29 μg-P/L based on chl *a*, and from 2.5 to 6.1 μg-P/L based on AFDM. These saturation concentrations provide an upper limit for streams where diatom growth can be expected to respond to nutrient levels and a benchmark for reducing nutrient concentrations to a point where benthic algal growth will be limited.

Correspondence to Schmidt: tschmidt@usgs.gov.

DATA AVAILABILITY

Data are available at: https://www.sciencebase.gov/catalog/item/5bc4a1eae4b0fc368eba0315

SUPPORTING INFORMATION

Additional supporting information may be found online under the Supporting Information tab for this article: Summary tables of various algal growth rate parameters for Monod and Droop equations derived from the literature and a photo-collage of mesocosm methods.

Keywords

nutrients; algal growth rate; diatoms; water quality model; Monod; Droop

INTRODUCTION

Nitrogen (N) and phosphorus (P) are two of the most broadly problematic chemical stressors in US streams and rivers (EPA 2016). Excess nutrients in fresh surface waters are positively related to algal biomass accrual (Biggs 2000; Dodds, Smith et al. 2002; Stevenson, Hill et al. 2008), which could become a nuisance or even harmful. Conversely, streams characterized by low N or P typically exhibit inhibited algal growth and are considered nutrient limited (Francoeur 2001; Rier and Stevenson 2006; Stevenson, Rier et al. 2006). Primary producers, such as benthic algae and macrophytes, are the most sensitive response indicators of nutrient pollution in streams (EPA 2014). Researchers have linked excess benthic algae (periphyton) to oxygen levels dropping below water quality standards and impaired recreation (Watson and Berlind 1990; Suplee, Watson et al. 2009). Hence, excess nutrients or algal biomass in the form of chlorophyll *a* (chl *a*) are causes of surface water impairment and the reason why 34 states, territories and the District of Columbia (D,C.) have adopted nutrient and chl *a* criterion (https://www.epa.gov/nutrient-policy-data/state-progress-toward-developing-numeric-nutrient-water-quality-criteria, accesses April 2019). While these standards are mostly for lakes and reservoirs, 5 states (Arizona, Washington, Montana, Oklahoma, Florida) have nutrient and chl *a* standards for some streams and rivers, and North Carolina, Oregon, and D.C. have chl *a* standards for some streams and rivers.

Factors such as temperature, light, grazing, and scouring often mask the effects of nutrients on algae growth, and these can vary within a stream as well as among streams. In addition to the confounding effects of these factors, the nutrient-algae relationship is often difficult to describe statistically because algal growth becomes independent of nutrient concentration above saturating concentrations. As Welch and Bergmann (1989) observed, these difficulties suggest that linking nutrient levels to periphyton biomass based on growth kinetics may be more productive than links based solely on empirical relationships. Additionally, modeling tools based on algal kinetics that distinguish the algal response due to changes in nutrient concentrations from variations in light, flow rates, grazing, and other factors can be helpful for restoring and maintaining the ecological and human resource potential of freshwater ecosystems.

Surface water quality models are used extensively to understand and predict the effects of dissolved nutrients in stream ecosystems. Model development is limited by available data for a particular system with respect to both the number of parameters that can be calibrated before reaching “equifinity” (multiple sets of parameter values that have the same likelihood) and the range in each independent variable that can be simulated. Many of the widely used models require the specification of algal growth rates as a function of nutrient concentrations. These models use either the Monod equation, which assumes fixed stoichiometry and relates algal growth to water column nutrient concentrations, or the Droop formulation, which simulates algal growth rate as a direct function of algal nutrient

stoichiometry and indirectly as aqueous nutrient concentrations (Droop 1974). Models that use the Monod formulation include the Water Quality Simulation Program, WASP (Martin, Ambrose et al. 2006), CE-QUAL-R1 (Laboratory 1995), Chesapeake Bay three-dimensional water quality model, CE-QUAL-ICM (Cerco and Cole 1994), and Hydrologic Simulation Program Fortran, HSPF (Bicknell, Imhoff et al. 2005). The Droop formulation is included in steady-state models such as QUAL2K (Chapra, Pelletier et al. 2008) and dynamic models such as WASP (Martin, Ambrose et al. 2006; Cerucci, Jaligama et al. 2010). Most of these models can simulate both phytoplankton, which is free-floating, and periphyton, which is attached to the substrate, in rivers, lakes and estuaries. Both periphyton and phytoplankton require nutrients and light, and both are subject to the same processes of growth, respiration, excretion, grazing, and mortality. Therefore, they are modeled with the same general equations, although the specific values of the model coefficients will vary (Bowie, Mills et al. 1985). Periphyton are different from phytoplankton in several ways. They are attached to the substrate and therefore do not transport with the flow, they receive only the light that penetrates to the bottom of the water column, they are subject to space limitation, and periphyton have losses due to scouring (Bowie, et al. 1985). These differences are handled through the transport, light extinction, space limitation and scouring equations specific to those processes. The nutrient requirements are similar in both phytoplankton and periphyton and models apply the same Monod and Droop nutrient limitation equations to both phytoplankton and periphyton. Since growth rate parameters can be quite different (Figure 1) between algal types, its incumbent on the people developing any of these models to choose model parameters most suitable for the algal community being investigated.

While measurement of algal growth rates has been a long-standing objective of laboratory and field investigations, significant gaps remain in terms of growth rates of *in-situ* benthic algal assemblages across stream types and the saturation of growth rates under high nutrient concentrations. A review of literature found two studies that reported half saturation concentration values for N (Bowie, Mills et al. 1985; Rier and Stevenson 2006) of which one (Rier and Stevenson (2006)) was for streams dominated by diatoms. Similarly, we found four studies (Rosemarin 1982; Bowie, Mills et al. 1985; Rier and Stevenson 2006; Hill and Fanta 2008) that reported half saturation constants for P, of which two (Rier and Stevenson 2006; Hill and Fanta 2008) were from streams dominated by diatoms (Fig. 1A, Table S1). Fortunately, all these studies reported growth rates (Fig. 1B, Table S1, S2). Finally, a review of the literature for benthic algae minimum cell quotas yielded three studies (Gerloff and Fitzgerald 1976; Wong and Clark 1976; Borchardt 1996) with reported values for N and five studies (Gerloff and Fitzgerald 1976; Wong and Clark 1976; Auer and Canale 1982; Borchardt 1994; Borchardt 1996) with reported values for P, none of which were measured for a diatom dominated stream assemblage (Fig. 1C, Table S3,S4).

The above summary of literature available to parameterize water quality models identified some shortcomings. Many of the experiments were conducted in lentic systems, in the eastern US, and some focused on a single green algae taxon (e.g., *Cladophora*, see Tables S2–S4). Since all experiments impart artifacts into the data conditional on the experimental environment (Schmidt, Rogers et al. 2018), it is important to observe similar findings under a variety of experimental conditions; in this way general behaviors of algal community response to nutrient addition or limitation can be identified and used in water quality

models. Further, algal communities in rivers are a diverse assemblage of green algae, cyanobacteria, and diatoms. Harmful and nuisance algal blooms are often dominated by cyanobacteria and green algae (Pan, Stevenson et al. 1996), with diatoms, dominant in lower nutrient headwater systems, considered one of the most sensitive classes of organisms to pollution, while also showing great variation in community composition across the continental US (Potapova and Charles 2002; Potapova, Charles et al. 2004; Potapova and Carlisle 2011). The abundance, diversity, and nutrient sensitivity of diatoms are reasons why they are used by many states to assess stream health and to develop numeric nutrient criteria (Zheng, Gerritsen et al. 2008; Smith and Tran 2010; Charles, Tuccillo et al. 2019). In the western US, diatoms can be the dominant algae in a river (Crayton and Sommerfeld 1979; Fisher, Gray et al. 1982) and nutrient enrichment is increasingly becoming a problem in the western US (Sickman, Melack et al. 2003; Baron, Driscoll et al. 2011), making the problem a national issue (EPA 2016; Amos, Miniat et al. 2018). Thus, to make generalized model parameters applicable to a wide variety of environmental conditions and assemblage composition, we set out to estimate growth rate parameters derived from an underrepresented type of algal community, a diatom-dominant community from a western US river. Also, this information could help managers prevent algal community regime shifts to filamentous green algae and cyanobacterial communities that contribute to harmful and nuisance blooms (*Didymosphenia geminate* an exception).

Our objective was to enhance predictive models of the effects of nutrients on diatom-dominated benthic algal communities through specific growth rate estimates. These model parameters would improve tools available to local resource managers addressing headwater streams with exceedances in nutrient or chl *a* standards. Specifically, we set out to estimate parameter values for the two common models of algal growth rates, Monod and Droop, that can be applied to benthic algal communities (diatom-dominated systems common to the US) over a wide range of dissolved nutrient concentrations. The Monod equation is based on Michaelis-Menten kinetics and expresses specific growth rate (μ) as a function of nutrient saturation:

$$\mu = \mu_{max}\frac{C}{(K_s + C)} \quad (1)$$

where (μ_{max}) is the maximum specific growth rate, C is the nutrient concentration, and (K_s) is the half-saturation concentration constant (Droop 1974). The Droop equation relates specific growth rate to the intra-cellular nutrient concentration, Q,

$$\mu = \hat{\mu}_{max}(1 - \frac{Q_{min}}{Q}) \quad (2)$$

where (Q_{min}) is minimum concentration needed for algal growth and ($\hat{\mu}_{max}$) is the maximum growth rate given unlimited intra-cellular nutrient content (Droop 1974; Borchardt 1996).

To estimate the parameter values for the Monod (μ_{max} and K_s) and for the Droop ($\hat{\mu}_{max}$ and Q_{min}) equations, we ran a 10-day stream mesocosm experiment and measured growth rates of natural algal assemblages exposed to a range of N and P concentrations. Mesocosms are

effective testing systems that bridge the artificiality of standard laboratory tests and the complexity and intractability associated with field studies (Lamberti and Steinman 1993). While some criticize mesocosms as being overly simplified versions of natural ecosystems (Carpenter 1996; Schindler 1998; Haag and Matschonat 2001), mesocosms provide clear advantages to observational field studies, mainly via the ability to manipulate variables of interest and identify cause and effect relationships (Odum 1984; McIntire 1993; Caquet, Lagadic et al. 1996). An additional advantage to using mesocosms for measuring algal growth is the ability to reduce ambient nutrient concentrations in the water, thereby allowing measurements of algal growth rates at very low nutrient concentrations (Mulholland, Steinman et al. 1991). Despite concerns of artificiality and scalability of mesocosm tests, Spivak et al. (Spivak, Vanni et al. 2011) showed that algal responses to nutrient enrichment in small scale experiments can be extrapolated to larger more natural aquatic systems. Therefore, we expect that the parameter values for algal growth derived from this mesocosm study can be applied to ecosystems with algal communities primarily composed of diatoms.

METHODS

Nutrient manipulation experiment

An annotated photo log of our methods is provided as Supplementary Information Fig. S1–S3. This experiment was conducted between April 1 and April 11, 2016 at the USGS Aquatic eXperimental Laboratory (AXL) mesocosm facility in Fort Collins, Colorado. AXL is described in detail by Schmidt et al. (Schmidt, Rogers et al. 2018). In brief, nutrient manipulations were carried out in 35 experimental stream units (n=35) constructed from 5-gallon plastic buckets outfitted with a standpipe to result in a stream volume of 4.7L, and a recirculation pump that generates a constant ~ 3 cm/s (calculated from pump rate 1325L/hr and cross-sectional area of mesocosm) water velocity across the bottom of the stream. The streams were distributed randomly among 4 Living Stream® bunks equipped with a chiller that maintained a water temperature of 20˚C (±2 ˚C). Each Living Stream® was illuminated with 4, 32-Watt natural spectrum fluorescent bulbs and 8, 54-Watt High Output natural spectrum fluorescent bulbs on a 16:8 light:dark cycle, which provided an average photosynthetically active radiation (PAR) of 79 μmol s^{-1} m^{-2}, a value while potentially sub-saturating for some diatom species (Hill, Fanta et al. 2009) is just below that expected in full sun (Hill, Roberts et al. 2011), and consistent with headwater streams which do not receive full sun all day due to riparian cover. Stream bottoms were covered with fifteen 22.1 cm^2 unglazed ceramic tiles for algal colonization.

Water was replaced continuously via two peristaltic pumps – one for unaltered river water and one for treatment water – at 3 ml/min each for a total replacement rate of 6 ml/min, or equivalent to a complete water turnover every ~12 hours. Water replenishment rates were measured and recorded daily. Clean river water was collected from the upper Cache La Poudre River in Northern Colorado, a relatively undisturbed stream northwest of Fort Collins, CO and stored in the lab in 600-gallon polyethylene Ace Roto-Mold® tanks.

The experiment consisted of 4 control streams and 31 treatment streams in a regression based design (Liber, Kaushik et al. 1992; Cottingham, Lennon et al. 2005) consisting of 8 N treatments (0, 0.035, 0.07, 0.1, 0.5, 1, 5,10 mg N/L) and 4 P treatments (0, 10, 50, 100 μg

P/L). Each N concentration was crossed with each P concentration but because we included replicated controls, there was no need for the 0N & 0P treatment cross, thus the total number of mesocosms was 35. Treatment water was prepared by adding stock solutions of $NaNO_3$ (CAS 7631–99-4) and KH_2PO_4 (CAS 7778–77-0) to 20L carboys of nutrient free deionized (DI) water. Carboys of DI water contributed to each treatment whether treated with a stock solution or not, thus diluting background N and P across all treatments. For example, background nutrient concentrations (0.09 mg N/L, 5μg P/L) in the river water were diluted by 50% (0.045 mg N/L, 2.5 μg P/L) in the controls. In addition, we added Na_2SiO_3 to each carboy to obtain a concentration of approximately 15 mg/L SiO_2 in each stream as a safeguard against silica (Si) limitation (Kilham 1971).

On day 0, we collected a large sample of periphyton from an upstream montane location of the Poudre River where algal assemblages are thinly dispersed on rocks and are diatom-dominated (as measured by BenthoTorch, but see (Echenique-Subiabre, Dalle et al. 2016)). Prior investigations (unpublished) using microscopy had determined low cyanobacteria counts and that algae communities were dominated by adnate species (Medley and Clements 1998). Rocks were scrubbed into buckets of river water, passed through a #18 sieve to remove macroinvertebrates, and diluted to 20 L. The periphyton was then transported back to AXL in coolers where it was homogenized with an immersion blender and kept in suspension using a motorized whisk. With the stream recirculation pumps halted, but renewal water replenishing steams continuously, we removed 1 L of water from each stream to prevent additions from overtopping stand pipes. Then, 500 ml aliquots of periphyton slurry were randomly delivered to each stream. Two aliquots were collected and processed for characterization of starting conditions chl *a*, particulate N and P as a measure of intra-cellular nutrient content, dry mass (DM), and ash free dry mass (AFDM). Recirculation was restored 2 hours after the addition of the algal inoculum, approximately simultaneous with the time when renewal water would begin to over top the stand pipe.

On days 3, 5, 7 and 10 we collected water samples from each stream and measured pH, specific conductance, temperature and PAR. Water samples were analyzed in situ for pH, specific conductance and temperature using a portable Hach® HQ40d field meter. PAR was measured using a Li-Cor Li-250A light meter held in the mesocosm at water level. Water samples were collected and filtered (0.45 μm) for nitrate (NO_3-N), soluble reactive phosphorus (SRP) and Silica (Si). Unfiltered water samples were collected for total nitrogen (TN), and total phosphorus (TP). Nitrate was analyzed on a Dionex™ ICS-3000 Ion Chromatograph by the Air, Water, and Aquatic Environments (AWAE, https://www.fs.fed.us/rm/boise/AWAE/labs/fortcollins.shtml) Biogeochemistry Lab in Fort Collins, CO. Ammonium was analyzed by EcoCore Analytical Services (https://ecocore.nrel.colostate.edu/), Colorado State University, Fort Collins, CO on an Alpkem Flow Solution IV. TN was analyzed on a Shimadzu TOC-V Combustion Analyzer by AWAE. SRP and TP were measured spectrophotometrically at AXL using standard methods (APHA 1998) on a Hach® DR6000. Si was analyzed spectrophotometrically at AXL using Hach® method 8185. Chl *a* was determined spectrophotometrically at AXL according to EPA method 446.0 (Arar and Collins 1997).

On Day 1, we measured initial chl *a* and community composition by using a BenthoTorch (bbe moldaenke©) to sample one tile for chl *a*. That tile was removed from the stream to prevent re-sampling on subsequent days. These data were only used to verify the general community composition. Periphyton samples were collected from 5, 4, 3, and 2 randomly-selected tiles in each stream on days 3, 5, 7, and 10 respectively. The purpose of random selection of tiles from within our circular streams was to control for how within stream differences in velocity might affect algal accrual. The number of tiles removed at each time period decreased from start to finish as a way to improve detection of changes in biofilms during development. On sampling days, tiles were removed from the streams, placed in a petri-dish, covered with aluminum foil and kept on ice until processed. Samples were processed by scraping the periphyton off the top surface of each tile with a razor blade into a beaker with 250 mL of deionized (DI) water, homogenized and continually mixed on a stir plate, and subsampled (volumes recorded) onto two GF/F filters that were immediately wrapped in aluminum foil and frozen. One filter was later analyzed for chl *a*, particulate P, DM, and AFDM. The second filter was dried and ashed to measure DM and AFDM and particulate P. On each sampling day an aliquot of periphyton was collected from each experimental stream, dried and processed for total particulate N by an elemental analyzer interfaced to a mass spectrometer at USGS labs in Denver, CO (Johnson, Stricker et al. 2018).

Estimates of growth rate parameters

Growth rate parameters for the Monod and Droop models (equations 1 and 2) were calculated using 3 different methods: 1) a single stream specific growth rate (Stream) calculated from data collected on day 3 through day 10 of the experiments; 2) incremental growth rates (Incremental) calculated from data grouped into each time interval between samples (day 3–5, day 5–7, and day 7–10); and 3) incremental growth rates (Max growth) for days 3 and 5 (generally representing the maximum specific growth rate during the experiment). Growth rates for day 1–3 were not used because of high uncertainty when biomass was low.

For the (Stream) approach, specific growth rates (r) were calculated by a non-linear least-squares (R Core Team 2015) fit of an exponential growth model (constant specific growth rate) to biomass for day 3, 5, 7, and 10 of the experiment:

$$M_{s,d} = M_{s,3} exp(rt) \tag{3}$$

where ($M_{s,d}$) is biomass (chl *a* and AFDM) in stream (s) for (d) = days 5, 7, and 10, ($M_{s,3}$) is biomass on day 3, and (t) is time in days since day 3. Incremental specific growth rates (Incremental and Max growth) with units of per day were calculated for the change in AFDM and chl *a* in each sampling interval (i)

$$\mu_i = \frac{ln(M_{s+1}) - ln(M_s)}{t} \tag{4}$$

where (M_s) was the mass of AFDM or chl *a* per square meter for sample (s) and (t) is the time between samples in days.

The nutrient concentrations used to estimate the parameters correspond to samples used to calculate growth rates under each approach. The Stream approach used mean concentrations of nitrate as nitrogen (NO_3-N) and soluble reactive phosphorous (SRP) for days 3, 5, 7, and 10 to fit the model (n = 35 streams, Table 1). The (Incremental) approach related growth rates among time intervals (3–5, 5–7, 7–10) with mean nutrient concentrations for those time intervals while the (Max growth) approach related growth rates on days 3–5 to mean nutrient concentrations on those days. Nutrient concentrations less than the method detection limit (MDL) were set to 1/2 MDL (MDLs: SRP 1.78 μg/L, NO_3-N 10 μg/L). Model parameters are not sensitive to the MDL value.

The Monod and Droop equations (1 and 2 respectively) were fit to the stream specific growth rates and stream mean nutrient concentration using non-linear least squares fit (R Core Team, 2017). These equations rely on the presumption that growth rates are a function of a single (primary) nutrient and the other (secondary) nutrient is not limiting. We enforced this presumption by filtering streams with extremely high or low molar ratios of NO_3-N to SRP (Borchardt 1996); streams with N:P > 200 were excluded from the parameter estimates for growth rate as a function of N; streams with N:P < 1 were excluded from parameter estimates of growth rate as a function of P. We use molar ratios of dissolved N:P rather than threshold concentrations to retain streams with low concentrations of both nutrients and to exclude streams that may be saturated by the primary nutrient.

RESULTS

Photos of biofilm accrual across a gradient of treatments can be seen in Fig. S3. Dissolved nutrients in the experimental stream waters spanned a wide range of concentrations (Table 1) ranging from detection to ~12,390 μg/L NO_3-N and ~60 μg/L SRP. Intra-cellular particulate nutrient concentrations were more constrained: ranging ~30 – 80 μg/mg for N and ~2–10 μg/mg for P. Specific growth rates generally increased with dissolved nutrient concentration (Fig. 2) and intra-cellular particulate nutrient concentrations (Fig. 3). Water temperature and pH averaged 20.2 ˚C and 7.92 (Standard Units) across streams respectively. Specific conductance ranged from 52–158 μS/cm across streams, with variability explained by additions of $NaNO_3$ to achieve target N concentrations (R^2=0.998).

Maximum stream specific growth rates based on chl *a* were ~ 0.6/day when NO_3-N > ~500 μg/L (Fig. 2A) or SRP > ~7 μg/L (Fig. 2B). Lower maximum specific growth rates (<0.3/day) were observed when based on AFDM and saturation (constant growth rate) was indicated at lower nutrient concentrations than for chl *a*: $N0_3N$~100 μg/L (Fig. 2C) and SRP~10 μg/L (Fig. 2D).

Biomass generally varied with nutrient concentrations and maximum growth rate parameters, for both the Monod and Droop growth rates, maximum growth rate parameter estimates had standard errors generally less than 30% of parameter values (Table 2). Maximum growth rates estimated using the Stream approach, which averaged growth from day 3 to 10 of the experiments (7 days), were lower than the estimates using sample intervals, which included the 2- or 3-day interval with maximum growth rate in each stream. Estimates of the Monod half-saturation constant, K_s, had greater uncertainty with standard

errors ranging from 27% to 114% of parameter estimates. Estimates of minimum cellular quotas, Q_{min}, generally were more constrained for N than P (Table 2).

AFDM in streams with NO_3-N > 100 μg/L demonstrated saturation (constant growth rate despite increasing nutrient concentration indicated by an upper asymptote of the Monod equation, Fig. 2C). The other combination of nutrients and responses (NO_3-N/chl *a*; SRP/chl *a*, and SRP/AFDM) may have been close to saturation in streams with the highest respective nutrient concentrations (Fig. 2A, 2B, and 2D).

Relations between growth rate and the primary nutrient (NO_3-N in Fig. 2A and 2C and SRP in Fig. 2B and 2D) were limited in some streams by the availability of the secondary nutrient as expressed by the molar dissolved N:P ratio. Growth limitation was evident in streams with high concentrations of NO_3-N when molar N:P > 200 and in streams with high concentrations of SRP when N:P < 1. Specific growth rates for AFDM appeared to be more sensitive to nitrogen limitation in streams with high phosphorous availability (Fig. 2C) than they were to phosphorous limitation in streams with high nitrogen availability (Fig. 2D).

Growth rates for both chl *a* and AFDM demonstrated relations to intra-cellular particulate nutrients. The minimum intra-cellular nutrient quota for growth is ~ 34 μg particulate N/mg AFDM and ~ 1.7 μg P/mg AFDM for chl *a* (Fig. 3Aa and 3B). Very low specific growth rates for chl *a* force the x-intercepts of the Droop equation (~38 μg/mg AFDM of particulate N in Fig. 3A and ~ 1 μg/mg AFDM of particulate P in Fig. 3B) but lead to *under*-estimated Q_s at high nutrient concentrations (Fig. 3A and 3B). No streams had very low specific growth rates for AFDM, so estimates of Q_s are based on extrapolation of the Droop equation and, thus, have greater uncertainty.

Intra-cellular (particulate) P availability did not appear to affect the relation between specific growth rates and intra-cellular N (Fig. 3A and 3C, gray points fall on the regression line), but intra-cellular (particulate) N availability may have limited growth rates in some streams despite ample intra-cellular P (Fig. 3B and 3D, gray points fall below regression line).

Discussion

To be useful tools for maintaining the integrity of US freshwaters and help prevent nuisance algal blooms, kinetic models must be applied with knowledge of the underlying equations and accurate model parameters. The stream experiment presented here provided a much-needed dataset to augment the limited number of empirical studies from which important model variables have been derived. Our experiment demonstrated the dependence of early growth rates of benthic algae (up to 10-days after colonization) on dissolved concentrations of N and P (Fig. 2). The highest growth rates depended on the availability of both nutrients indicated by a range of molar dissolved N:P from about 1 to 200. Growth rates as a function of nutrient concentration for streams with N:P outside of this range were generally lower than the growth rates of streams inside this range. Strong correlation of TN and TP to NO_3-N and SRP respectively (Pearson correlation 0.99 for NO_3-N, TN and SRP, TP) indicate that total nutrients could be used as the basis for modeling algal growth with a simple, linear transformation: SRP = TP/1.09 – 6.8 and NO_3-N = TN/1.05 – 54. In natural streams and

rivers, however, correlations between dissolved inorganic nitrogen and TN or SRP and TP will not be as strong because of the multiple sources (e.g., wastewater, agricultural runoff, natural sources) of N and P to these ecosystems. AFDM had lower maximum specific growths rates than chl *a*, suggesting models parameterized on growth rates derived from chl *a* may over-predict algal accrual as compared to those parameterized based on AFDM derived growth rates. For AFDM these rates ranged from 0.25 to 0.44 d^{-1} and for chl *a* they ranged from 0.31 to 0.97. These rates fell within those observed by others (Fig. 1, Table S1 and S2).

The higher chl *a* based growth rates may be due to the ability of diatoms (but true of algae in general) to regulate chl *a* content (i.e., changes in per cell chl *a* content) as conditions dictate (Jøsrgensen 1969). This variation in chl *a* is observed in the AFDM:chl *a* across these experiments which ranged from 67 to 2260 with our highest AFDM:chl *a* (mg AFDM/mg chl *a*) observed in day 10 and in the experiments with the lowest nitrogen doses. As nutrient levels were increased, chl *a* increased more quickly than AFDM resulting in higher growth rates based on the former, and indicating that the periphyton was able to increase chl *a* faster than they multiplied. Literature C:chl *a* ranges of 20 to 100 have been cited for general phytoplankton (Chapra 1997), and from 18 to 500 for diatoms (Bowie et al. 1985), similar to what we observed (Table 1), lending further support to the case that this variation in chl *a* would introduce inaccuracies to rates estimated from chl *a*. Because of this, the parameters estimated with AFDM may be more accurate for estimating biomass than the parameters estimated with chl *a*. Although algal chl *a* content is known to vary with conditions, many water quality models hold the C:chl *a* ratio constant, thus limiting the ability of these models to accurately track algal biomass through time. Even though the rates from AFDM are likely more accurate, in these models with constant C:chl *a*, the rates derived from chl *a* may compensate for this limitation and produce better model results. Finally, in the field setting, estimates of chl *a* could be more accurate than estimates of AFDM as the latter could be confounded by sediment accumulation into biofilms.

Specific growth rates declined over the course of the experiments with the maximum typically between day 3 and day 5, similar to Rier and Stevenson (2006). Applying the Monod growth constants based on this 3 to 5-day period could tend to overstate the expected growth at low nutrient concentrations without other limiting effects for long term, continuous modeling. This is especially true for steady state modeling where flow and nutrient concentrations remain constant over long periods. Thus, for long term steady state model simulations and time varying modeling where nutrient concentrations remain steady for days, using parameters estimated from the Stream approach, which are based on growth from day 3 to day 10, would yield more accurate results. This does not appear to be an issue with the Droop model, as minimum cell quotas are not very different based on the Stream approach compared to the day 3–5 approach. Thus, the time-scale of application should be consistent with time-scale of data when using a linear model (e.g., constant specific growth rate). The Stream approach provides parameter values for applications where model time scale is about a week for periods of initial biomass accrual. Models with a longer time scale (e.g., monthly time step) would likely need to lower *Gmax* from the values estimated from our experiments (Table 2).

Excess nitrogen under dissolved phosphorous limitation (Fig. 3A, gray points) is not expressed by increased intra-cellular particulate N (Fig. 3A); whereas intra-cellular particulate P does indicate "luxury consumption" without an immediate growth benefit when N:P <1 (Fig. 3B). Nutrient limitation and saturation can have significant management implications because of diminished sensitivity in algal growth rates to changes in nutrient concentration. By defining nutrient saturation when the growth rate is ninety percent of the maximum growth rate, $\frac{\mu_{sat}}{\mu_{max}} = 0.9$, the saturation concentration for a nutrient can be computed from the Monod formulation as $9K_s$ (i.e. nutrient saturation occurs at about nine times the half saturation concentration). Applying a factor of nine to the Monod equation, the saturation concentration for nitrogen ranges from 150 to 2450 μg-N/L based on chl *a* and from 8.5 to 60 μg-N/L based on AFDM. Similarly, for phosphorus the saturation concentration ranges from 12 to 29 μg-P/L based on chl *a*, and from 2.5 to 6.1 μg-P/L based on AFDM. The wide range of saturation values reflects differences in the methods used. The max growth method resulted in the lowest saturation values and is comparable to the method used by Rier and Stevenson (2006). The stream approach used the growth rate over day 3 to 10 to represent growth over this longer period and is comparable to the approach by Stevenson, Hill et al. (2008). The stream approach saturation values are much higher (1700 vs 150 μg-N/L and 29 vs 12 μg-P/L) than the max growth approach, especially for nitrogen.. The higher saturation values indicate that nutrient management may be effective in limiting algal growth at higher concentrations than previously thought.

Algal growth rates in streams will be high where nutrient concentrations are above these saturation concentrations, unless other factors (light, substrate stability, water quality, diffusion limitation) inhibit growth. Moreover, growth rates will be insensitive to variation in concentrations greater than saturation concentrations. These saturation concentrations provide an upper limit for streams where diatom growth can be expected to respond to nutrient levels and a benchmark for reducing nutrient concentrations to a point where algal growth is limited. However, we should note that little is known about how differences in community composition might cause changes in these upper and lower limits to saturation concentrations. Moreover, if the ambient concentration of a nutrient is greater than the saturation concentration, and nutrient reductions are implemented to a degree that results in concentrations below saturation values, algal growth will begin to decline, resulting in a potential water quality improvement (Hilton et al., 2006). For streams where water quality is impaired because of algal growth in response to nutrient enrichment (rather than light or water clarity, for instance), nutrient criteria would need to be less than these values to affect algal growth. In cases where downstream loading is a concern, however, reduction in nutrient concentration can be beneficial even if the concentration remains above saturation levels for algal growth.

Most models developed to predict nutrient concentrations or algal biomass in freshwater have utilized the Monod formulation due to its simplicity and often the lack of data on luxury (intra-cellular nutrient concentrations) nutrient uptake (Cerucci, Jaligama et al. 2010). However, utilizing the Droop formulation can improve prediction because of the important role luxury uptake plays in regulating algal growth and nutrient removal from the

environment under nutrient limitation conditions (Cerucci, Jaligama et al. 2010; Chyan, Zhang et al. 2014). Thus, the publication of the estimated half-saturation constants, growth rates, and intra-cellular nutrient concentrations observed for diatom-dominated benthic algae in this study should make it easier for model developers to parameterize Droop models. Such a tool would provide more accurate predictions to decision makers who implement strategies to improve water quality and prevent nuisance algal blooms.

Our combination of experimental conditions and the use of a diatom dominant western US river algal assemblage produced model parameters both consistent with the literature as well as some values distinct from the literature. For example, the half saturation constants are very similar to those produced by Rier and Stevenson (2006), who used a stream side mesocosm approach and a diatom-dominated assemblage from the eastern US; whereas our growth rate parameters are nearly a factor of 2 lower. It is not suspected that diffusion gradients or self-shading from the accrual of thick algal mats limited our growth rates (possible exceptions include day 10 observations at high nutrient exposures, Fig. S3), as our experiments were conducted for a short duration targeting maximum growth rates of thin film formation (Bothwell 1988; Bothwell 1989), nor that light limited growth rates as PAR in our experiments were near saturation (Hill, Roberts et al. 2011). Finally, our minimum cell quota for P and N were both higher than any reported. Given the paucity of data it is unknown if our experimental conditions or our unique algal assemblage were the driver of these differences, though perhaps it was a combination of both. Nonetheless, more studies like these would be useful to help develop a more generalized understanding of how these water quality model parameters change across experimental designs and types of algal assemblages.

Conclusions

We applied nutrient-dose, mesocosm experiments on diatom-dominated periphyton from a Northern Colorado stream to estimate growth rates, kinetic constants and saturation values. The growth rates and parameters were determined from chl *a* and AFDM across growth periods of 10-days and 2-day increments. Rates calculated from day 3 to 10 were lower than rates calculated based on the maximum growth increment. This indicates that rates from days 3–10 are more appropriate for longer term modeling, as models parameterized based on the algal maximum growth period could overstate the longer term expected algae accrual. Rates calculated from chl *a* were higher than AFDM rates which is likely due to the ability of algae to regulate chl *a* content. This implies that rates from AFDM would be more accurate for parameterizing models, especially models that account for variable chl *a* content. Our mesocosm design proved to be an effective way to conduct experiments to estimate model parameters, as our results are generally similar to those in the literature. Finally, model parameters derived from these experiments can be used in water quality models intended to predict diatom dominated-periphyton community responses to nutrient additions in streams.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

ACKNOWLEDGMENTS

Travis S. Schmidt coordinated this project including funding, experimental design and execution and wrote the manuscript, data release, and model archive. Christopher P. Konrad aided in the experimental design, modeled the data, and wrote the manuscript. Janet L. Miller coordinated the experimental design and execution, curation of data, and aided manuscript development. Stephen D. Whitlock was central to coordination efforts with EPA, helped fund and design the study as well as development of the manuscript. Craig A. Stricker provided essential quantification services, data curation, and aided manuscript development. Holly Rogers, Erin Jefferey, and Gaby Ruso helped execute the experiment. The authors would like to acknowledge Lester Yuan and Jacques Oliver for reviewing the manuscript. Funding for this project was provided by a cooperative agreement with the U.S. Environmental Protection Agency. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Disclaimers: “The views expressed in this article are those of the authors and do not necessarily represent the views or policies of the U.S. Environmental Protection Agency.” “This manuscript is distributed solely for purposes of scientific peer review. Its content is deliberative and provisional, so it must not be disclosed or released by reviewers. Because the manuscript has not yet been approved for publication by the U.S. Geological Survey (USGS), it does not represent any official USGS finding or policy.”

LITERATURE CITED

Amos HM, Miniat CF, Lynch J, Compton J, Templer PH, Sprague LA, Shaw D, Burns D, Rea A, Whitall D, Myles L, Gay D, Nilles M, Walker J, Rose AK, Bales J, Deacon J and Pouyat R, 2018 What Goes Up Must Come Down: Integrating Air and Water Quality Monitoring for Nutrients. Environ Sci Technol 10.1021/acs.est.8b03504.

APHA, 1998 Methods for the examination of water and wastewater,

Arar EL and Collins GC, 1997 In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. In, Editor (Editor)^(Editors). U.S. Environmental Protection Agency Report EPA Method 445.0, Cincinnati, Ohio.

Auer MT and Canale RP, 1982 Ecological Studies and Mathematical Modeling of Cladophora in Lake Huron: 3. The Dependence of Growth Rates on Internal Phosphorus Pool Size. Journal of Great Lakes Research 8:93–99.

Baron JS, Driscoll CT, Stoddard JL and Richer EE, 2011 Empirical Critical Loads of Atmospheric Nitrogen Deposition for Nutrient Enrichment and Acidification of Sensitive US Lakes. BioScience 61:602–613.

Bicknell BR, Imhoff JC, Kittle JLJ, Jobes TH and Donigian ASJ, 2005 HSPF Version 12.2 User’s Manual. In, Editor (Editor)^(Editors). AQUA TERRA Consultants, Mountain View, California.

Biggs BJF, 2000 Eutrophication of streams and rivers: dissolved nutrient-chlorophyll relationships for benthic algae. Journal of the North American Benthological Society 19:17–31.

Borchardt MA, 1994 Effects of Flowing Water on Nitrogen- and Phosphorus-Limited Photosynthesis and Optimum N:P Ratios by Spirogyra Fluviatilis (Charophyceae). Journal of Phycology 30:418–430.

Borchardt MA, 1996 Nutrients. San Diego, Academic Press,

Bothwell ML, 1988 Growth Rate Responses of Lotic Periphytic Diatoms to Experimental Phosphorus Enrichment: The Influence of Temperature and Light. Canadian Journal of Fisheries and Aquatic Sciences 45:261–270.

Bothwell ML, 1989 Phosphorus–Limited Growth Dynamics of Lotic Periphytic Diatom Communities: Areal Biomass and Cellular Growth Rate Responses. Canadian Journal of Fisheries and Aquatic Sciences 46:1293–1301.

Bowie GL, Mills WB, Porcella DB, Campbell CL and Pagenkopf JRR, G.L., 1985 Rates, Constants, and Kinetics Formulations in Surface Water Quality Modeling. In, Editor (Editor)^(Editors). Tetra Tech Envionmental, Lafayette, CA.

Caquet T, Lagadic L, Jonot O, Baturo W, Kilanda M, Simon P, Le Bras S, Echaubard M and Ramade F, 1996 Outdoor experimental ponds (mesocosms) designed for long-term ecotoxicological studies in aquatic environment. Ecotoxicology and Environmental Safety 34:125–133. [PubMed: 8812177]

Carpenter SR, 1996 Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680.

Cerco CF and Cole TM, 1994 Three-Dimensional Eutrophication Model of Chesapeake Bay Volume 1: Main Report (No. WES/TR/EL-94–4). Army Engineer Waterways Experiment Station Vicksburg MS Environmental Lab. In, Editor (Editor)^(Editors). Army Engineer Waterways Experiment Station Vicksburg, MS.

Cerucci M, Jaligama GK and Ambrose RB, 2010 Comparison of the Monod and Droop Methods for Dynamic Water Quality Simulations. Journal of Environmental Engineering 136:1009–1019.

Chapra SC, Pelletier GJ and Tao H, 2008 QUAL2K: A Modeling Framework for Simulating River and Stream Water Quality: Documentation and Users Manual In, Editor (Editor)^(Editors). Civil and Environmental Engineering Dept, Tufts University Medford, MA.

Charles DF, Tuccillo AP and Belton TJ, 2019 Use of diatoms for developing nutrient criteria for rivers and streams: A Biological Condition Gradient approach. Ecological Indicators 96:258–269.

Chyan W, Zhang DY, Lippard SJ and Radford RJ, 2014 Reaction-based fluorescent sensor for investigating mobile Zn2+ in mitochondria of healthy versus cancerous prostate cells. Proc Natl Acad Sci U S A 111:143–148. [PubMed: 24335702]

Cottingham KL, Lennon JT and Brown BL, 2005 Knowing when to draw the line: designing more informative ecological experiments. Frontiers in Ecology and the Environment 3:145–152.

Crayton WM and Sommerfeld MR, 1979 Composition and abundance of phytoplankton in tributaries of the lower Colorado river, Grand Canyon region. Hydrobiologia 66:81–93.

Dodds WK, Smith VH and Lohman K, 2002 Nitrogen and phosphorus relationships to benthic algal biomass in temperate streams. Canadian Journal of Fisheries and Aquatic Sciences 59:865–874.

Droop MR, 1974 The nutrient status of algal cells in continuous culture. Journal of the Marine Biological Association of the United Kingdom 54:825–855.

Echenique-Subiabre I, Dalle C, Duval C, Heath MW, Coute A, Wood SA, Humbert JF and Quiblier C, 2016 Application of a spectrofluorimetric tool (bbe BenthoTorch) for monitoring potentially toxic benthic cyanobacteria in rivers. Water Res 101:341–350. [PubMed: 27286469]

EPA, 2014 Expert Workshop: Nutrient Enrichment Indicators in Streams. In: U.S. EPA Expert Workshop. U.S. Environmental Protection Agency.

EPA, 2016 National rivers and streams assessment. In, Editor (Editor)^(Editors). Office of Water and Office of Research and Development, Washington, D.C., p. 116.

Fisher SG, Gray LJ, Grimm NB and Busch DE, 1982 Temporal Succession in a Desert Stream Ecosystem Following Flash Flooding. Ecological Monographs 52:93–110.

Francoeur SN, 2001 Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. Journal of the North American Benthological Society 20:358–368.

Gerloff GC and Fitzgerald GP, 1976 The nutrition of Great Lakes Cladophora, U S. Environmental Protection Agency, Office of Research and Development, Environmental Research Laboratory,

Haag D and Matschonat G, 2001 Limitations of controlled experimental systems as models for natural systems: a conceptual assessment of experimental practices in biogeochemistry and soil science. Science of The Total Environment 277:199–216. [PubMed: 11589400]

Hill WR and Fanta SE, 2008 Phosphorus and light colimit periphyton growth at subsaturating irradiances. Freshwater Biology 53:215–225.

Hill WR, Fanta SE and Roberts BJ, 2009 Quantifying phosphorus and light effects in stream algae. Limnology and Oceanography 54:368–380.

Hill WR, Roberts BJ, Francoeur SN and Fanta SE, 2011. Resource synergy in stream periphyton communities. Journal of Ecology 10.1111/j.1365-2745.2010.01785.x:no-no.

Johnson CA, Stricker CA, Gulbransen CA and Emmons MP, 2018 Determination of δ13C, δ15N, or δ34S by isotope-ratio-monitoring mass spectrometry using an elemental analyzer In: Techniques and Methods, Editor (Editor)^(Editors). Report 5-D4, Reston, VA, p. 29.

Jøsrgensen EG, 1969 The Adaptation of Plankton Algae IV. Light Adaptation in Different Algal Species. Physiologia Plantarum 22:1307–1315. [PubMed: 20925681]

Kilham P, 1971 A hypothesis concerning silica and the freshwater planktonic diatoms. Limnology and Oceanography 16:10–18.

Laboratory E, 1995 CE-QUAL-R1: A Numerical One-Dimensional Model of Reservoir Water Quality; User's Manual. In, Editor (Editor)^(Editors). U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Lamberti GA and Steinman AD, 1993 Research in Artificial Streams: Applications, Uses, and Abuses. Journal of the North American Benthological Society 12:313–384.

Liber K, Kaushik NK, Solomon KR and Carey JH, 1992 Experimental designs for aquatic mesocosm studies: A comparison of the "anova" and "regression" design for assessing the impact of tetrachlorophenol on zooplankton populations in limnocorrals. Environmental Toxicology and Chemistry 11:61–77.

Martin JL, Ambrose RB and Wool TA, 2006 WASP7 Benthic Algae-Model Theory and User's Guide: Supplement to Water Analysis Simulation Program (WASP) User Documentation.. In, Editor (Editor)^(Editors). U.S. Enviornmental Protection Agency, Washington, D.C.

McIntire CD, 1993 Historical and other perspectives of laboratory stream research In: Research in Artificial Streams: Applications, Uses, and Abuses, Lamberti GA and Steinman AD (Lamberti GA and Steinman AD(Lamberti GA and Steinmans AD). North American Benthological Society, pp. 318–323.

Mebane CA, Schmidt TS and Balistrieri LS, 2017 Larval aquatic insect responses to cadmium and zinc in experimental streams. Environ Toxicol Chem 36:749–762. [PubMed: 27541712]

Medley CN and Clements WH, 1998 Responses of diatom communities to heavy metals in streams: the influence of longitudinal variation. Ecological Applications 631–644:3.

Mulholland PJ, Steinman AD, Palumbo AV, Elwood JW and Kirschtel DB, 1991 Role of Nutrient Cycling and Herbivory in Regulating Periphyton Communities in Laboratory Streams. Ecology 72:966–982.

Odum EP, 1984 The mesocosm. BioScience 34:558–562.

Pan Y, Stevenson RJ, Hill BH, Herlihy AT and Collins GB, 1996 Using Diatoms as Indicators of Ecological Conditions in Lotic Systems: A Regional Assessment. Journal of the North American Benthological Society 15:481–495.

Potapova M and Carlisle DM, 2011 Development and application of indices to assess the condition of benthic algal communities in U.S. streams and rivers. Open File Report 2011–1126 In: Open-File Report, Editor (Editor)^(Editors). U.S. Geological Survey Report 2011–1126, Reston. VA, p. 44.

Potapova MG and Charles DF, 2002 Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. Journal of Biogeography 29:167–187.

Potapova MG, Charles DF, Ponader KC and Winter DM, 2004 Quantifying species indicator values for trophic diatom indices: a comparison of approaches. Hydrobiologia 517:25–41.

Rier ST and Stevenson RJ, 2006 Response of Periphytic Algae to Gradients in Nitrogen and Phosphorus in Streamside Mesocosms. Hydrobiologia 561:131–147.

Rogers HA, Schmidt TS, Dabney BL, Hladik ML, Mahler BJ and Van Metre PC, 2016 Bifenthrin Causes Trophic Cascade and Altered Insect Emergence in Mesocosms: Implications for Small Streams. Environ Sci Technol 50:11974–11983. [PubMed: 27731978]

Rosemarin AS, 1982 Phosphorus Nutrition of Two Potentially Competing Filamentous Algae, Cladophora Glomerata (L.) Kütz. and Stigeoclonium Tenue (Agardh) Kütz. from Lake Ontario. Journal of Great Lakes Research 8:66–72.

Schindler DW, 1998 Whole-Ecosystem Experiments: Replication Versus Realism: The Need for Ecosystem-Scale Experiments. Ecosystems 1:323–334.

Schmidt TS, Rogers HA, Miller JL, Mebane CA and Balistrieri LS, 2018 Understanding the captivity effect on invertebrate communities transplanted into an experimental stream laboratory. Environ Toxicol Chem 37:2820–2834. [PubMed: 30035388]

Sickman JO, Melack JM and Clow DW, 2003 Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California. Limnology and Oceanography 48:1885–1892.

Smith AJ and Tran CP, 2010 A weight-of-evidence approach to define nutrient criteria protective of aquatic life in large rivers. Journal of the North American Benthological Society 29:875–891.

Spivak AC, Vanni MJ and Mette EM, 2011 Moving on up: can results from simple aquatic mesocosm experiments be applied across broad spatial scales? Freshwater Biology 56:279–291.

Stevenson RJ, Hill BH, Herlihy AT, Yuan LL and Norton SB, 2008 Algae–P relationships, thresholds, and frequency distributions guide nutrient criterion development. Journal of the North American Benthological Society 27:783–799.

Stevenson RJ, Rier ST, Riseng CM, Schultz RE and Wiley MJ, 2006 Comparing Effects of Nutrients on Algal Biomass in Streams in Two Regions with Different Disturbance Regimes and with Applications for Developing Nutrient Criteria. Hydrobiologia 561:149–165.

Suplee MW, Watson V, Teply M and McKee H, 2009 How Green is Too Green? Public Opinion of What Constitutes Undesirable Algae Levels in Streams. Journal of the American Water Resources Association 45:123–140.

Watson V and Berlind P, 1990 Control Of Algal Standing Crop By P And N In The Clark Fork River. In: lark Fork Symposium Session 2: Biotic Response. University of Montana, Missula, MT.

Welch HE and Bergmann MA, 1989 Seasonal Development of Ice Algae and its Prediction from Environmental Factors near Resolute, N.W.T., Canada. Canadian Journal of Fisheries and Aquatic Sciences 46:1793–1804.

Wong SL and Clark B, 1976 Field Determination of the Critical Nutrient Concentrations for Cladophora in Streams. Journal of the Fisheries Research Board of Canada 33:85–92.

Zheng L, Gerritsen J, Beckman J, Ludwig J and Wilkes S, 2008 Land Use, Geology, Enrichment, and Stream Biota in the Eastern Ridge and Valley Ecoregion: Implications for Nutrient Criteria Development1. JAWRA Journal of the American Water Resources Association 44:1521–1536.

Research Impact Statement

Parameter estimates for water quality models predictive of periphyton growth rates and accrual in streams were derived from a diatom-dominated community in a nutrient addition mescocosm experiment.

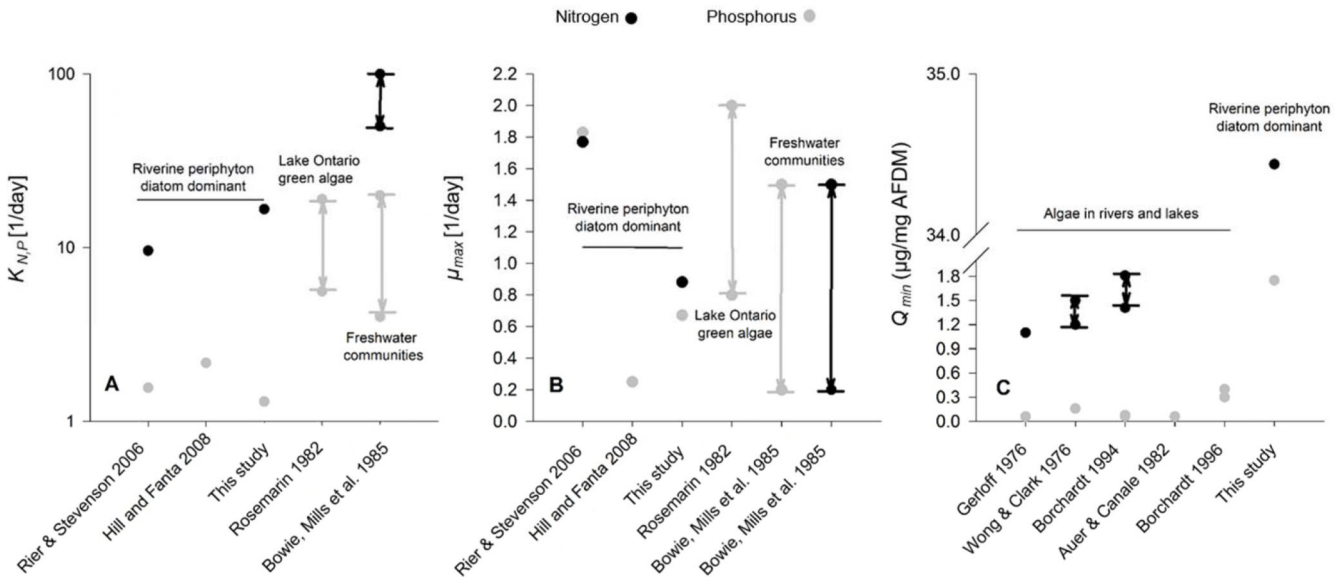

Figure 1.

Comparison of the (a) half saturation constants ($K_{N,P}$), (b) growth rates (μ_{max}), and (c) minimum intra-cellular quota (Q_s) for algae and diatom communities.

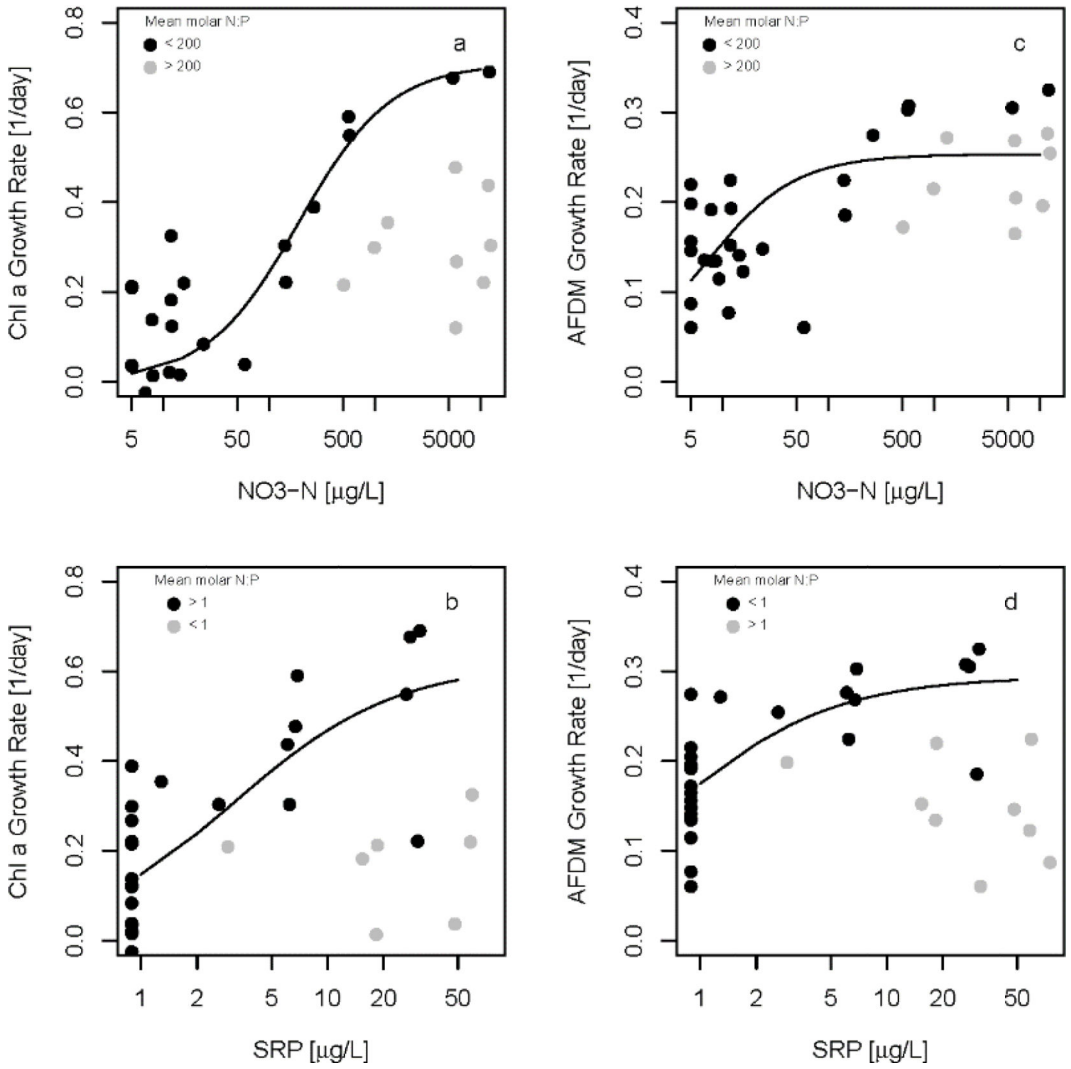

Figure 2.

Relation between stream-mean dissolved nutrient concentration and stream specific growth rate (*r*) estimated from biomass on days 3 to 10 as an exponential function of time since day 3. Specific growth rates calculated from the Monod equation (line) fit to streams passing a molar N:P ratio filter (black points). Specific growth rates for streams not passing the filter (gray points) were excluded from model fit and generally plot below the best-fit lines indicating secondary nutrient limitation.

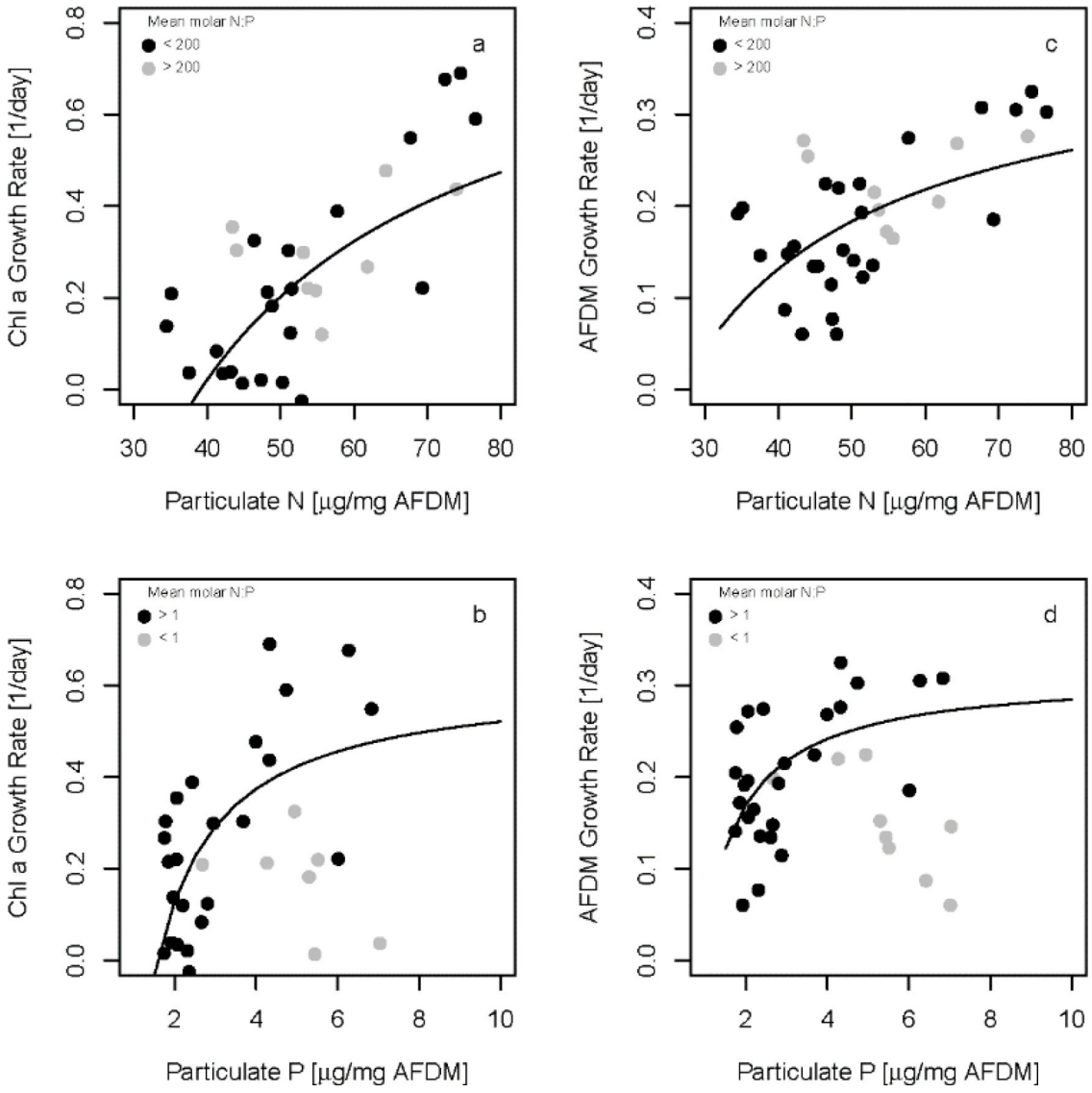

Figure 3.

Intra-cellular (particulate) nutrient concentration (µg/ mg ash-free dry mass) and specific growth rates for experimental streams. Specific growth rates calculated from the Droop equation (line) fit to streams passing a molar N:P ratio filter (black points) to reduce secondary nutrient limitation. Specific growth rates for streams not passing the filter (gray points) were excluded from model fit and generally plot below the best-fit lines indicate secondary nutrient limitation. Mean molar N:P is based on the dissolved nutrient concentrations in the stream.

Table 1.

Experimental stream mean nutrient concentrations and specific growth rate estimates from an exponential growth model. Means of aqueous nutrients are the average (n = 4 in most cases) concentrations observed in experimental streams over the duration of the experiment and the result of treatments. Other means are for periphyton (particulate) content and are also the average (n = 4 in most cases) of values observed over the course of experiment.

Stream	Mean NO_3-N [μg/L]	Mean SRP [μg/L]	Mean N [μg/mg AFDM]	Mean P [μg/mg AFDM]	Mean C [μg/mg AFDM	Mean chl *a* [μg/mg AFDM]	chl *a* r^1 [1/day]	SE^2 [1/ day]	AFDM r^1 [1/day]	SE^2 [1/ day]
A5	7.8	0.9	34.4	2.0	197.1	1.6	0.138	0.037	0.191	0.025
B6	8.6	0.9	45.3	2.6	300.1	1.9	−0.103	0.043	0.134	0.01
C6	5.0	0.9	42.1	2.1	214.2	1.6	0.034	0.062	0.156	0.019
D9	6.7	0.9	52.9	2.4	309.4	2.0	−0.025	0.009	0.135	0.01
A4	5.0	2.9	35.1	2.7	201.8	1.2	0.209	0.164	0.198	0.055
D7	5.0	31.8	48.0	7.0	331.2	1.1	−0.053	0.035	0.06	0.012
C9	5.0	75.0	40.8	6.4	303.4	1.4	−0.073	0.035	0.087	0.014
D8	14.3	0.9	50.3	1.7	240.9	2.4	0.015	0.022	0.141	0.001
D2	9.3	0.9	47.2	2.9	309.5	1.8	−0.068	0.033	0.115	0.002
B5	7.9	18.3	44.8	5.4	277.2	2.6	0.013	0.034	0.134	0.016
C3	5.0	48.2	37.5	7.0	195.4	2.2	0.037	0.041	0.146	0.01
C4	23.8	0.9	41.3	2.7	232.3	3.1	0.083	0.046	0.148	0.01
D5	11.4	0.9	47.4	2.3	280.3	2.8	0.021	0.079	0.077	0.005
A6	5.0	18.5	48.2	4.3	287.5	2.5	0.213	0.069	0.22	0.024
A2	11.8	59.5	46.4	4.9	251.1	1.6	0.325	0.089	0.224	0.019
C2	58.5	0.9	43.2	1.9	183.8	2.1	0.039	0.084	0.06	0.005
D6	12.0	0.9	51.4	2.8	244.5	2.5	0.123	0.041	0.193	0.011
A8	11.8	15.4	48.8	5.3	298.3	2.4	0.182	0.149	0.152	0.013
B3	15.6	58.3	51.5	5.5	293.1	1.0	0.219	0.062	0.123	0.004
C8	504.9	0.9	54.8	1.9	244.8	2.7	0.215	0.036	0.172	0.018
C5	263.2	0.9	57.7	2.4	329.2	5.1	0.389	0.009	0.274	0.009
B8	140.0	6.3	51.1	3.7	252.8	6.4	0.303	0.049	0.224	0.012
B9	143.3	30.4	69.3	6.0	246.2	5.6	0.221	0.056	0.185	0.008
A3	1315.3	1.3	43.4	2.1	215.3	2.0	0.354	0.129	0.272	0.036
D3	983.3	0.9	53.1	3.0	232.9	4.0	0.299	0.012	0.215	0.006
D1	561.8	6.9	76.6	4.7	234.6	7.2	0.59	0.03	0.303	0.007
A9	573.3	26.5	67.7	6.8	223.1	8.3	0.549	0.012	0.308	0.005
C7	5768.9	0.9	55.6	2.2	266.6	3.0	0.12	0.004	0.165	0.015
B7	5895.5	0.9	61.8	1.8	253.1	4.2	0.267	0.044	0.205	0.007
B1	5751.3	6.7	64.4	4.0	164.5	8.4	0.477	0.019	0.268	0.007
B2	5439.2	27.8	72.4	6.3	170.5	5.0	0.677	0.014	0.305	0.007
A7	10591.9	0.9	53.7	2.0	294.3	2.4	0.221	0.073	0.196	0.025
D4	12390.4	2.6	44.0	1.8	311.2	4.5	0.303	0.049	0.254	0.008
C1	11734.8	6.1	74.0	4.3	209.5	7.1	0.437	0.01	0.276	0.001

Stream	Mean NO_3-N [µg/L]	Mean SRP [µg/L]	Mean N [µg/mg AFDM]	Mean P [µg/mg AFDM]	Mean C [µg/mg AFDM	Mean chl *a* [µg/mg AFDM]	chl *a* r^1 [1/day]	SE^2 [1/ day]	AFDM r^1 [1/day]	SE^2 [1/ day]
B4	11995.1	31.3	74.5	4.3	248.6	7.4	0.69	0.003	0.325	0.008

[1]Growth rate

[2]Standard Error.

Table 2.

Coefficients, standard errors (SE), and coefficients of determination (R^2) for Monod and Droop Models.

				Monod Model (equation 1)					Droop Model (equation 2)				
Response	**Time Scale**[1]	**Nutrient**	**Filter**	μ_{max} [1/day]	**SE [1/day]**	K_s [µg/L]	**SE [µg/L]**	R^2	$\widehat{\mu}_{max}$ [1/day]	**SE [1/day]**	Q_s [µg/gm]	**SE [µg/mg]**	R^2
chl *a*	Stream	N	NP<200	0.709	0.078	189.58	71.359	0.782	0.926	0.171	39.074	2.268	0.45
chl *a*	Incremental	N	NP<200	0.974	0.179	272.77	149.88	0.378	1.204	0.143	40.156	1.299	0.495
chl *a*	Max growth	N	NP<200	0.881	0.135	16.64	8.462	0.354	1.602	0.491	41.644	5.397	0.253
chl *a*	Stream	P	NP>1	0.617	0.092	3.177	1.309	0.596	0.619	0.11	1.581	0.197	0.35
chl *a*	Incremental	P	NP>1	0.312	0.085	2.727	3.117	0.087	0.342	0.102	1.593	0.463	0.049
chl *a*	Max growth	P	NP>1	0.672	0.112	1.304	0.999	0.237	0.71	0.192	1.16	0.587	0.071
AFDM	Stream	N	NP<200	0.253	0.024	6.262	2.168	0.364	0.391	0.063	26.557	3.574	0.335
AFDM	Incremental	N	NP<200	0.346	0.047	6.724	3.035	0.09	0.637	0.079	30.543	2.114	0.362
AFDM	Max growth	N	NP<200	0.424	0.053	0.952	1.224	0.024	0.647	0.203	24.501	10.52	0.187
AFDM	Stream	P	NP>1	0.294	0.022	0.682	0.182	0.515	0.313	0.037	0.916	0.195	0.288
AFDM	Incremental	P	NP>1	0.26	0.034	0.279	0.255	0.022	0.277	0.051	0.567	0.439	0.016
AFDM	Max growth	P	NP>1	0.441	0.043	0.296	0.213	0.108	0.424	0.079	0.282	0.541	0.01

[1]Models were fit using three different data time scales: Stream is based on stream mean concentration of nutrients for days 3 through 10 and specific growth rates estimated from the exponential growth model; Incremental is based on specific growth rates calculated for each sample interval (day 3–5, day 5–7, day 7–10) and mean nutrient concentrations at the beginning and end of the interval; Max growth is based on mean nutrient concentration for day 3 and 5 and growth from days 3 and 5, a time period associated with fast growth rates.