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Phosphorus–Limited Growth Dynamics of Lotic Periphytic Diatom Communities: Areal Biomass and Cellular Growth Rate Responses[1,2]

Max L. Bothwell

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Bothwell, M. L. 1989. Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. Can. J. Fish. Aquat. Sci. 46: 1293–1301.

Three long-term phosphate enrichment experiments were conducted at the Experimental Troughs Apparatus (EXTRA), South Thompson River, British Columbia to determine the relationship between external orthophosphate (PO_4^{3-}) concentration and peak areal biomass (PB) of periphytic diatom communities. Levels of PO_4^{3-} which saturated PB were two orders of magnitude greater than those required to saturate specific growth rates in thin film periphyton communities of similar taxonomic composition. With PO_4^{3-} additions between 0.1 to 1.0 μg $P \cdot L^{-1}$, PB responded in a hyperbolic fashion, initially increasing rapidly, then showing signs of saturation. PB continued to increase in a slow, linear manner above 1.0 μg $P \cdot L^{-1}$. Maximum PB (PB_{max}) was calculated to occur at ca. 28 μg $P \cdot L^{-1}$. At higher PO_4^{3-} concentrations (>30–50 μg $P \cdot L^{-1}$) PB was no longer P limited. Below the saturation point, PB was approximated by a log–linear function of PO_4^{3-}.

Trois expériences d'enrichissement à long terme par le phosphate ont été effectuées dans des bacs expérimentaux de la station EXTRA (Experimental Troughs Apparatus) dans la rivière Thompson Sud, en Colombie-Britannique, afin de déterminer la relation entre la concentration d'orthophosphate d'origine extérieure (PO_4^{3-}) et la biomasse aréale maximale (BM) de communautés de diatomées périphytiques. Les concentrations de PO_4^{3-}, qui ont saturé la BM, étaient de deux ordres de grandeur supérieure à celles nécessaires pour saturer des taux de croissance spécifiques du mince mucilage des communautés du périphyton, dont la composition taxonomique est semblable. Avec des apports entre 0,1 et 1,0 μg $P \cdot L^{-1}$ de PO_4^{3-}, la biomasse a donné une réaction hyperbolique, en augmentant rapidement d'abord, puis en montrant des signes de saturation. La biomasse a continué de s'accroître lentement de façon linéaire lorsque l'apport était supérieur à 1,0 μg $P \cdot L^{-1}$. Selon les calculs, la biomasse doit atteindre une valeur maximale (BM_{max}) aux environs de 28 μg $P \cdot L^{-1}$. Aux concentrations plus élevées de PO_4^{3-} (30–50 μg $P \cdot L^{-1}$), BM n'était plus limitée en fonction de P. Au-dessous du point de saturation, on a obtenu une valeur approximative de biomasse maximale par une fonction log-linéaire de PO_4^{3-}.

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A discrepancy exists in the literature between phosphate concentrations which result in high periphyton biomass in rivers and those which saturate cellular growth rates of many of these species. Excessive periphyton biomass is reported to occur when phosphate levels are >10 μg $P \cdot L^{-1}$ (MacKenthun 1968; Wong and Clark 1976; Horner and Welch 1981; Horner et al. 1983). Additions of phosphate at these levels are often used to stimulate algal production during lotic enrichment experiments (Stockner and Shortreed 1978; Peterson et al. 1983, 1985; Perrin et al. 1987). In contrast, detailed comparisons of the growth of periphyton communities in three rivers in British Columbia indicated that ambient soluble reactive phosphorus (SRP) levels of 3–4 μg $P \cdot L^{-1}$ were sufficient to saturate periphytic diatom growth rates (Bothwell 1985). Direct enrichment trials with PO_4^{3-} have now shown that concentrations of only 0.3–0.6 μg $P \cdot L^{-1}$ will saturate specific growth rates of periphytic diatoms in the South Thompson River, British Columbia (Bothwell 1988).

There is a simple explanation for the disparity between these findings. While growth rates of individual cells and thin periphyton films saturate at low P concentrations, growth of the community as a whole does not. As algal accumulations become more dense, cells within the mat may become P limited while those closer to the surface of the periphyton matrix remain P replete. Hence, higher concentrations of P in the overlying water should augment growth rates of cells deeper in the matrix by increasing the supply rate of the limiting nutrient.

Using microelectrodes, Jorgensen and Revsbech (1985) have demonstrated the presence of a diffusive boundary layer which limits the rate of transport of metabolites in periphyton communities. Enhancement of nutrient flux by mixing has been shown to be important to the metabolism (Whitford and Schumacher 1961, 1964; Rodgers and Harvey 1976), growth, and accumulation (Whitford 1960; McIntire 1966; Reisen and Spencer 1970; Stevenson 1984; Horner and Welch 1981) of lotic algae. Some investigators have specifically shown the significance of diffusive transport of phosphate ions in lotic (Schumacher and Whitford 1965; Sperling and Grunewald 1969; Lock and John 1979) and lentic (Riber and Wetzel 1987) periphyton communities. Recently, Perrin et al. (1987) used this diffusion mechanism to explain why lotic periphyton accrual in a river on Vancouver Island, British Columbia, continued to increase in spite of the fact that growth saturation concentrations of P had been surpassed.

[1]This is the third paper in a series from EXTRA.
[2]NHRI Contribution No. 88055.

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Despite the above mentioned studies, the relationship between nutrient levels which limit cellular growth rates and those that control areal biomass of the same communities has never been quantitatively established, even under one given set of physical conditions. This paper describes the results of three phosphate enrichment experiments at Environment Canada's Experimental Troughs Apparatus (EXTRA) in 1984–85 which were undertaken to determine the relationship between external P concentration and the peak areal biomass (PB) of lotic periphytic diatom communities under uniform physical conditions. The establishment of this relationship is important for the management of lotic eutrophication problems because algal standing crop is of immediate concern to aquatic resource managers.

Materials and Methods

Periphyton biomass experiments were run at EXTRA on the South Thompson River near Little Shuswap Lake, British Columbia. Details of the construction and operation of this research facility are given elsewhere (Bothwell 1988). Multiple, parallel Plexiglas troughs (each 2 m long by 19 cm wide) were fed fresh river water at 50 $L \cdot min^{-1}$ resulting in a water depth and velocity of approximately 1 cm and 50 $cm \cdot s^{-1}$, respectively. The bottoms of the troughs were lined with open-cell styrofoam-DB (Snow Foam Inc., El Monte, CA) to serve as a colonization substratum. Stock phosphate (K_2HPO_4) solutions were continuously metered into the enriched troughs using precision piston pumps (RH type, Fluid Metering Inc. NY). The troughs were shielded from UV-B radiation by UV-opaque Plexiglas covers (UF1 type).

Three experiments were conducted: trial 1, 15 October–13 December 1984; trial 2, 29 January–2 April 1985; and trial 3, 4 October–21 November 1985. In the first two experiments five troughs were used; a control (ambient river water) and P additions of 0.1, 0.2, 1.0, and 5.0 $\mu g\ P \cdot L^{-1}$ of PO_4^{3-}. In the third trial, eleven troughs were used to determine the effect of much higher levels of P enrichment on periphyton biomass: a control and additions of 0.1, 0.2, 0.5, 1.0, 2.0, 5.0, 10, 25, 50, and 100 $\mu g\ P \cdot L^{-1}$ were employed. Each experiment began with fresh styrofoam substratum, commencement of water flow and nutrient addition.

Biomass Measurements

Algal biomass was measured during each experiment at weekly intervals by removing quadruplicate (5.0-cm^2) cores of the substratum with the adhering periphyton community. The cores were immediately extracted in 90% acetone using a Polytron grinder (cv = 10.9% for quadruplicate cores, Bothwell 1983). Extracts from each trough were combined for a single fluorometric chlorophyll *a* determination (Holm-Hansen et al. 1965) on each sampling date. In the latter stages of trial 3, small isolated tufts of filamentous green algae began to appear in troughs heavily enriched with P. These algae were excluded from all sampling for biomass and cell physiological measurements.

During the first two trials samples for particulate organic carbon (POC) were collected when algal biomass neared its maximum level. Periphyton from each trough were homogenized for 10 s in a Waring blender with filtered river water and the resulting suspension was screened through a 550-μm Nitex net. Quadruplicate, 50-mL subsamples were filtered through preignited Whatman GF/F filters and analyzed for POC with a Hewlett-Packard CHN analyzer (model 185B). Triplicate 25-mL subsamples were filtered on GF/F filters for acetone extraction and chlorophyll determination. Chlorophyll *a* and POC values were used to compute carbon:chlorophyll *a* ratios of the communities as a function of the P treatment as algal density approached its peak. The average carbon:chlorophyll *a* conversion values observed in trials 1 and 2 for each level of P enrichment were used to convert chlorophyll *a* values to POC estimates of biomass in trial 3.

The relationship between P concentration and areal algal biomass was assessed in each treatment. For each treatment of every experiment, PB was estimated by averaging the highest three chlorophyll *a* values observed. The highest PB value in each experiment as a function of P addition was termed the maximum peak biomass, PB_{max}. For each trial, PB values were normalized to PB_{max}. Statistical comparisons of biomass response curves were performed by testing differences in the slopes (*t*-test) of the data linearized by log-transformation of the independent variable, i.e. P addition. The response of PB to P enrichment was compared when biomass was expressed as chlorophyll *a* and as POC.

Growth Rate Measurements

Concurrent with long-term biomass accumulation trials 1 and 2, other troughs at EXTRA were used in shorter duration experiments to measure periphyton specific growth rates in response to P enrichment (Bothwell 1988). Specific growth rates (μ) expressed as divisions $\cdot d^{-1}$ were computed for the control and all treatment levels using procedures detailed by Bothwell (1988). Maximum growth rates with respect to phosphorus ($\mu_{max\text{-}P}$) were calculated from Eadie-Hofstee transformations of μ versus P addition (Dowd and Riggs 1965) and used to determine relative specific growth rates, $\mu:\mu_{max\text{-}P}$.

Alkaline Phosphatase

Periphyton alkaline phosphatase activity (APA) was measured near the end of the short-term growth rate experiments during 1984–85. Periphyton harvested from the troughs were resuspended in filtered river water, briefly agitated in a Waring blender and screened through a 550-μm mesh Nitex net. APA determinations were made on triplicate 8-mL subsamples using the fluorometric method of Pettersson (1980) as modified by Bothwell (1988). Chlorophyll values were used to normalize particulate APA and results expressed as the rate of appearance of the hydrolysis product 4-methylumbelliferyl (MU). APA levels indicated the relative degree of P limitation of the periphyton.

Algal Taxonomy

Periphyton samples collected midway through trials 1 and 2 were fixed in Lugol's solution and used for algal enumeration. Quantitative cell counts were made at 500× magnification in Utermöhl chambers. Only cells containing cytoplasm were enumerated. A minimum of 100 individuals of the dominant species and at least 300 cells in total were counted.

Water Chemistry and Physical Measurements

Triplicate samples for water chemistry were normally taken from the control trough at weekly intervals. All samples were filtered immediately through prewashed 0.45-μm Sartorius membrane filters. Those for SRP were preserved with chloro-

TABLE 1. Summary of the physical conditions and water nutrient chemistry during three long-term periphyton biomass experiments at EXTRA during 1984–85. Values are the means observed in each experimental period.

Trial	Dates	Temp (°C)	PAR ($E \cdot m^{-2} \cdot d^{-1}$)	$NO_3^- + NO_2^-$ ($\mu g\ P \cdot L^{-1}$)	NH_4^+ ($\mu g\ P \cdot L^{-1}$)	SRP ($\mu g\ P \cdot L^{-1}$)	SiO_2 ($mg \cdot L^{-1}$)
1	15 Oct.–13 Dec. 1984	6.5	6.1	57.6	NA	2.1	5.6
2	29 Jan.–2 Apr. 1985	1.5	13.7	75.5	4.5	1.3	5.9
3	4 Oct.–21 Nov. 1985	8.4	7.4	29.3	4.4	2.4	5.3

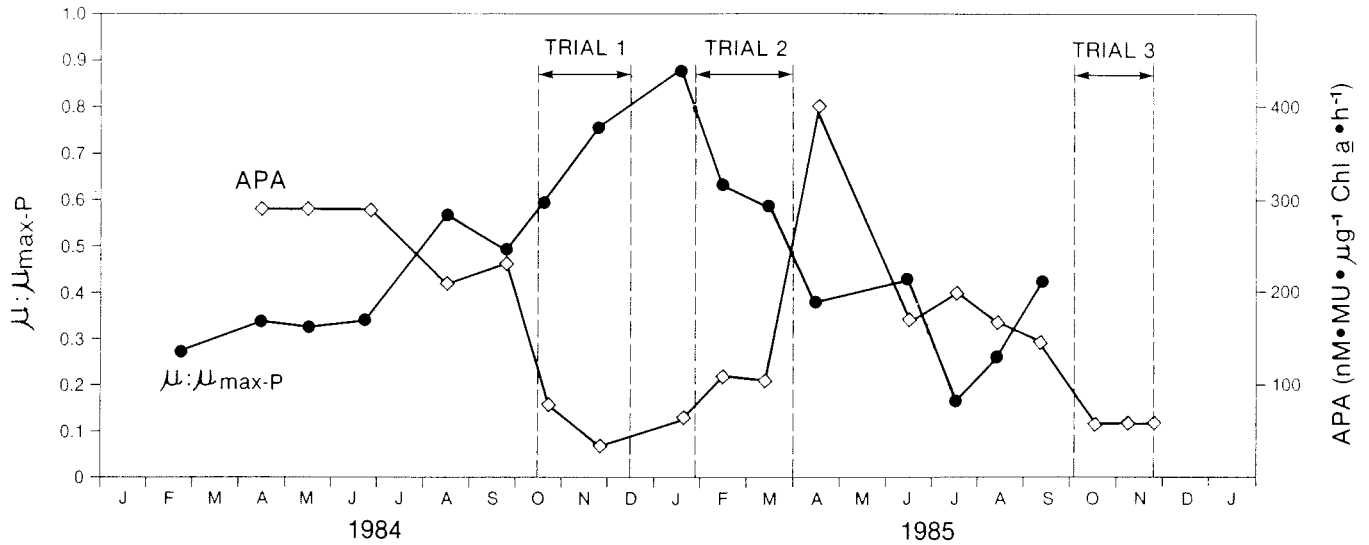

FIG. 1. Seasonal changes in relative specific growth rates ($\mu:\mu_{max\text{-}P}$) and alkaline phosphatase activity (APA) of periphyton communities in the control trough at EXTRA during 1984–85. Time periods for the three long-term biomass accumulation trials are depicted by broken lines.

form. Samples for soluble reactive silicate, ammonium and nitrate + nitrite were refrigerated until analysis. All analyses were conducted by the Pacific and Yukon Regional Water Quality Branch Laboratory, Department of Environment, North Vancouver, using procedures outlined in their manual (Environment Canada 1979). Orthophosphorus concentrations added to the enriched troughs were computed from known dilutions of the standard K_2HPO_4 solutions. Higher augmented P concentrations were authenticated by SRP measurements.

Water temperature was measured daily at 0900–1000 h with a mercury thermometer. Hourly integrals of photosynthetically active radiation (PAR) were recorded during experiments using a LiCor (Lincoln, Nebraska) integrating light meter (LI-550B) and a quantum sensor (LI-190SB). Mean temperature and mean daily PAR (Einsteins per square meter per day) were calculated for each trial period.

Results

Growth Conditions

SRP levels in the South Thompson River are low throughout the year (ca. 1–3 $\mu g\ P \cdot L^{-1}$, Table 1). Nitrate + nitrite levels during the trials reported here usually exceeded 50 $\mu g\ N \cdot L^{-1}$, except in trial 3 when low values in early October brought the average down to 29.3 $\mu g\ N \cdot L^{-1}$ (Table 1). Silicate concentrations in the South Thompson are always high, 5–6 mg $SiO_2 \cdot L^{-1}$ (Table 1) and are not a factor limiting diatom growth (Eppley 1977).

In the October–December period of 1984 and 1985 (i.e. trials 1 and 3) diatom community APA of ~50–75 nmoles $MU \cdot \mu g^{-1}$ chlorophyll $a \cdot h^{-1}$ and $\mu:\mu_{max\text{-}P}$ of ~0.6–0.8 (trial 1 only; Fig. 1) both indicated that the periphyton were only moderately P limited. In trial 2 (February–March) P deficiency was increasing during the course of the experiment. APA was 75–100 nmoles $MU \cdot \mu g^{-1}$ chlorophyll $a \cdot h^{-1}$ for the first 3–4 wk of the experiment then increased rapidly to >200 before the end of the trial. Correspondingly, $\mu:\mu_{max\text{-}P}$ declined from 0.8 to 0.5 (Fig. 1). Results of these experiments corroborate findings of Bothwell (1985, 1988) that P is the nutrient controlling algal growth rates in the South Thompson River and that the relative degree of P limitation varies seasonally.

The mean temperature during trial 2, 1.5°C, was much lower than temperatures in trials 1 and 3 of 6.5 and 8.4°C, respectively (Table 1). Because water temperature is the most important physical factor controlling the growth rates of algae at EXTRA (Bothwell 1988), slower algal growth rates during trial 2 would be expected compared with the other two trials.

Light levels also varied between experiments with average values of 6.1, 13.7, and 7.4 $E \cdot m^{-2} \cdot d^{-1}$ (Table 1). However, the magnitude of these seasonal changes does not significantly influence growth rates of periphytic diatoms at EXTRA (Bothwell 1988).

Algal Taxonomy

As in previous experiments at EXTRA, diatoms dominated at all times of the year. *Tabellaria fenestrata* and *Diatoma tenue*

TABLE 2. A Summary of the dominant algal taxa at EXTRA during trials in 1984–85.

Treatment ($\mu g\ P \cdot L^{-1}$)	Dominant algal species[a]	
	Trial 1	Trial 2
0.0 control	*Tabellaria fenestrata* (48.7%) *Fragilaria vaucheriae* (20.5%) *Diatoma tenue* (15.4%)	*Diatoma tenue* (34.6%) *Tabellaria fenestrata* (31.7%) *Fragilaria vaucheriae* (17.9%)
0.1	*Tabellaria fenestrata* (45.3%) *Tabellaria flocculosa* (22.8%) *Fragilaria vaucheriae* (12.3%)	*Diatoma tenue* (38.4%) *Fragilaria vaucheriae* (24.8%) *Tabellaria fenestrata* (13.9%)
0.2	*Tabellaria fenestrata* (46.7%) *Synedra ulna* v. *oxyrychus* (19.6%) *Fragilaria construens* v *venter* (13%)	*Diatoma tenue* (54.4%) *Fragilaria vaucheriae* (16.8%)
1.0	*Fragilaria vaucheriae* (51.4%) *Tabellaria fenestrata* (16.6%) *Diatoma tenue* (15.9%)	*Diatoma tenue* (47.4%) *Fragilaria vaucheriae* (20.9%) *Fragilaria crotonensis* (14.6%)
5.0	*Fragilaria vaucheriae* (67.6%)	*Fragilaria vaucheriae* (50.5%) *Diatoma tenue* (17.4%) *Hannaea arcus* (14.7%)

[a]Species contributing >10% of total cell numbers.

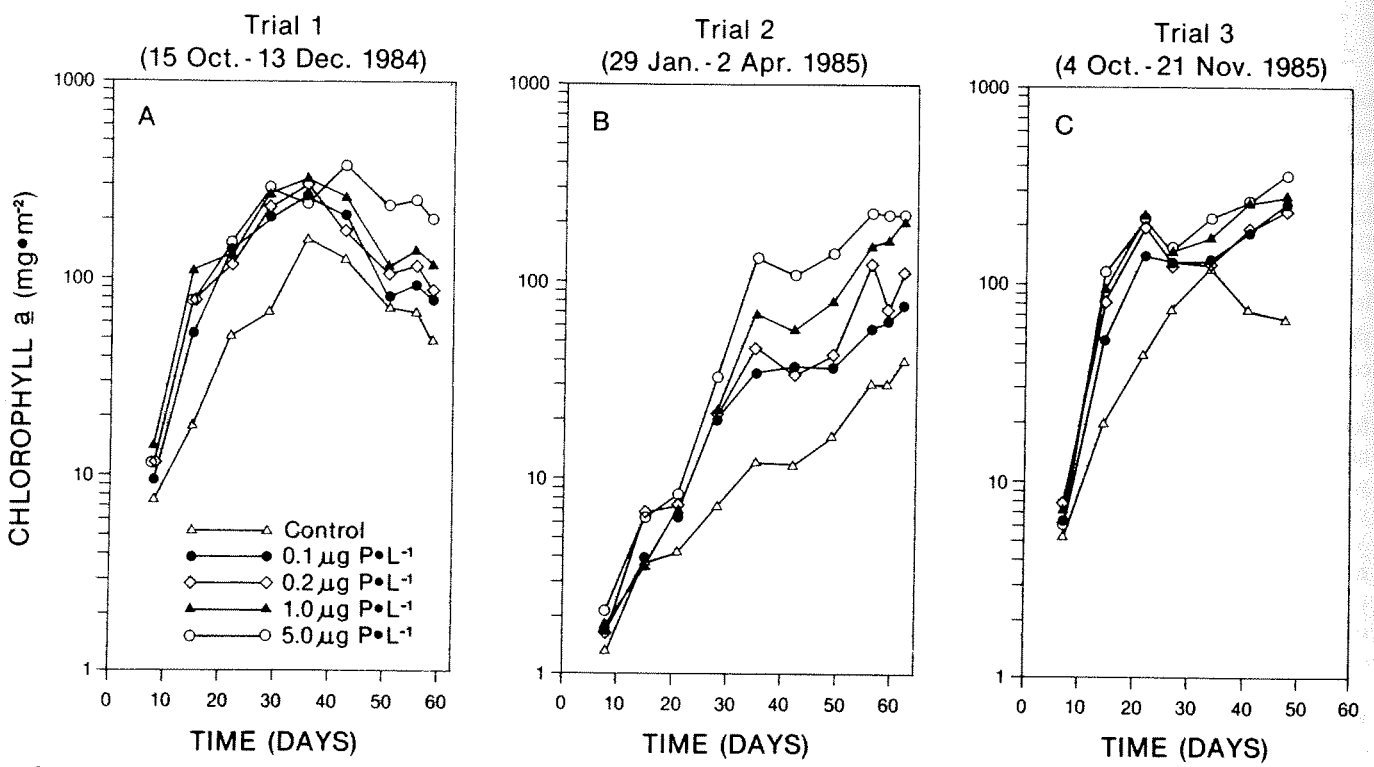

FIG. 2. Algal biomass (chlorophyll *a*) during long-term accumulation trial 1 (2A), trial 2 (2B), and trial 3 (2C). Chlorophyll levels in the control and with phosphate additions of 0.1, 0.2, 1.0, and 5.0 $\mu g\ P \cdot L^{-1}$ are shown. Chlorophyll levels with 10, 25, 50 and 100 $\mu g\ P \cdot L^{-1}$ of phosphate during trial 3 are not shown.

were most important in the control and lower P treatments. These two dominant species were displaced by *Fragilaria vaucheriae* at the highest P enrichments (Table 2). Small tufts of the filamentous green algae, *Stigeoclonium* sp. were observed in trial 3 at higher P enrichment levels.

Time-Course Biomass Curves

The three experiments were run for periods ranging from 47–62 d. Although the shape of the time–course biomass curves differed in each trial, they shared some similar features (Fig. 2). In each case an exponential increase in biomass occurred in the first 2–4 wk. This was followed by a period of varying length in which the rate of increase slowed. If an experiment was of sufficient duration (for the experimental treatment), a plateau followed by a decline was observed. In the first experiment, biomass leveled off at 30–40 d and then declined (Fig. 2A). In trial 2 the rate of increase slowed after about 40 d. Biomass in the control and lower treatment levels however, was still increasing at the termination of trial 2 (Fig. 2B). In the third experiment, there was a sharp decline in the rate of biomass increase after ~20 d. At day 33 a maximum biomass was reached in the control (Fig. 2C).

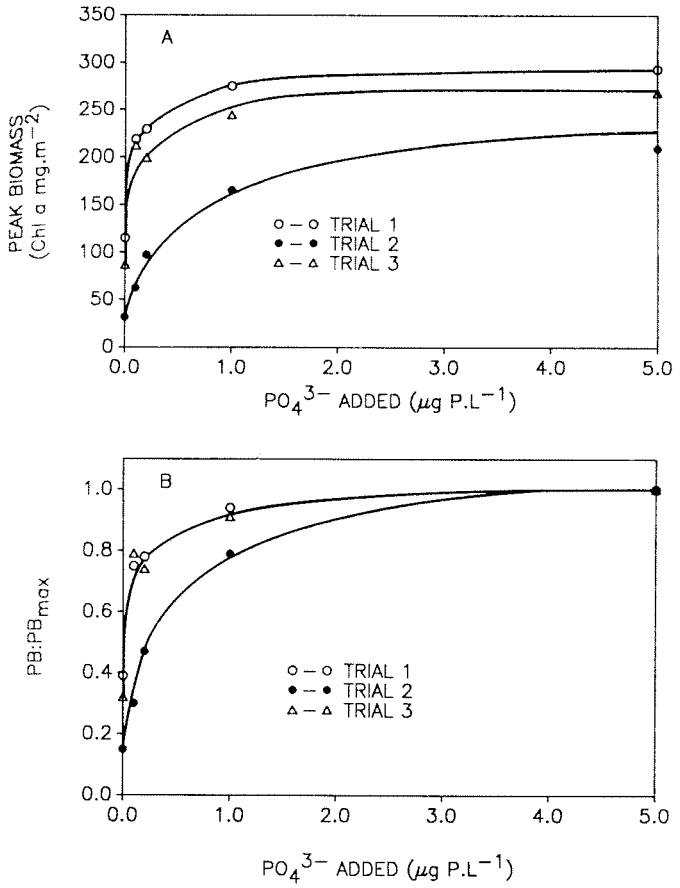

FIG. 3. (A) Peak biomass (chlorophyll *a*) as a function of phosphate treatment during trial 1 (open circle), trial 2 (solid dot) and trial 3 (open triangle). (B) Relative peak biomass (PB:PB_{max}) as a function of phosphate treatment during trials 1, 2, and 3. PB_{max} was assumed to be the biomass at 5 μg P·L^{-1}. PB:PB_{max} curves for trials 1 and 3 are nearly identical and are represented by the same line. All curves in A and B are drawn by eye.

The failure to see a biomass plateau and decline in all of the treatments within the duration of the last two experiments was due to the effects of slower growth rates and slower colonization on biomass accumulation. Even though colonization rate was not directly measured, an approximation of relative seeding rates among the trials can be made by comparing chlorophyll *a* levels after 1 wk (Bothwell 1983; Bothwell and Jasper 1983). Chlorophyll *a* values averaged for all troughs on day 8 were: 10, 1.6, and 6 mg·m^{-2} in trials 1, 2, and 3, respectively (Fig. 2). This suggests widely varying settlement rates between the experiments with the largest difference being between trials 1 and 2. The impact of low settlement rate on accumulation in trial 2 was compounded by the effects of low temperature on growth rate. With an average temperature of only 1.5°C, $\mu_{max\text{-}P}$ (0.18 divisions·d^{-1}) in trial 2 was only about half the value found during trial 1 ($\mu_{max\text{-}P}$ = 0.34 divisions·d^{-1}; Bothwell 1988). The combined influence of these two factors reduced the biomass accumulation rate to such an extent that the 62-d duration of trial 2 was not long enough to allow chlorophyll *a* to reach levels at which sloughing would have become significant. Toward the end of trial 3, chlorophyll *a* values in the enriched troughs were similar to those at which sloughing occurred in trial 1 and declines would probably have occurred if the experiment had not been terminated due to adverse weather.

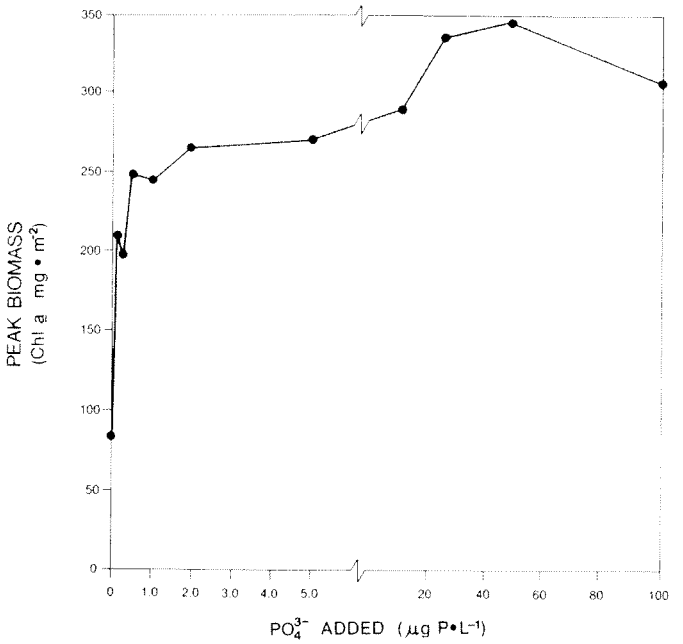

FIG. 4. Peak biomass in trial 3 as a function of added phosphate up to 100 μg P·L^{-1}. The abscissa scale is broken at 6 μg P·L^{-1} to accommodate the wide range in phosphate values.

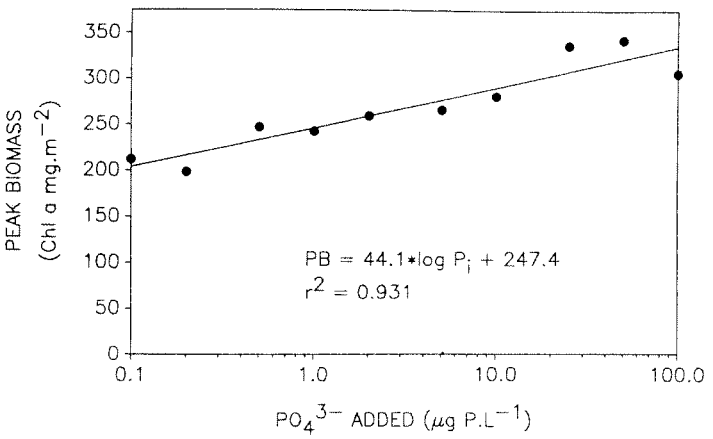

FIG. 5. Semi-log plot of peak biomass in trial 3 as a function of added phosphate up to 100 μg P·L^{-1}. Data are the same as in Fig. 4, but here are plotted against the log of the phosphate concentration. The line is the linear regression of the data fitted by least squares.

Biomass Versus Phosphorus

Peak biomass plotted as a function of phosphate addition always showed saturation kinetics. Curves with different maxima were obtained in each trial (Fig. 3A). Curvilinear kinetics suggest that PB is proportional to community growth rate.

Even with declining biomass in trial 1, higher PO_4^{3-} levels consistently supported greater areal biomass (Figs. 2A and 3A). The peaking and subsequent decline of biomass under conditions of constant nutrient loading (but with areal biomass still responding proportionally to enrichment) (Fig. 2A), indicates that higher supply concentrations of P are required to sustain a given level of algal biomass than are needed to initially create it.

To focus on relative periphyton biomass response to P additions, biomass data in each trial were normalized to the value for biomass at 5 μg P·L^{-1}. The normalized plots for PB were

TABLE 3. Carbon:chlorophyll (weight/weight) at different levels of P enrichment during two periphyton biomass trials at EXTRA.

Treatment ($\mu g\ P \cdot L^{-1}$)	Carbon:chlorophyll *a*		
	Trial 1	Trial 2	Average
0.0 control	63	73	68.0
0.1	62	45	53.5
0.2	49	40	44.5
1.0	44	30	37.0
5.0	36	33	34.5

nearly identical for trials 1 and 3 (Fig. 3B). However, low temperatures in trial 2 slowed growth rates to such an extent that the $PB:PB_{max}$ curve for that trial differed significantly ($P<0.05$) from the other two.

The most important feature of the biomass response curves was that while they achieve about 70% of their maximum value at very low P levels they do not show complete saturation at such low concentrations. Areal biomass, measured as chlorophyll *a*, continued to increase between 1 and 5 $\mu g\ P \cdot L^{-1}$ in all trials. In trial 3, when P enrichments greater than 5 $\mu g\ P \cdot L^{-1}$ were used, algal biomass continued to respond to P additions up to ca. 25–50 $\mu g\ P \cdot L^{-1}$ (Fig. 4). This is two orders of magnitude greater than concentrations known to saturate the specific growth rates of periphytic diatoms in this river (Bothwell 1988). Over the range of P addition from 0.1 to 100 $\mu g\ P \cdot L^{-1}$ the biomass data were well fitted ($r^2=0.931$) by the log–linear equation:

$$PB = 44.1 \log P_i + 247.4$$

where PB is chlorophyll *a* (milligrams per square metre) and P_i is the bulk water orthophosphate concentration in micrograms P per litre. (Fig. 5).

Carbon–to–Chlorophyll Ratio

Carbon:chlorophyll *a* in the controls during trials 1 and 2 were 63 and 73, respectively (Table 3). These values are close to those reported in the literature for algae grown under moderate P limitation (Perry 1976; Goldman 1980; Hunter and Laws 1981) and are consistent with the relative specific growth rates in the river during those time periods, i.e. $\mu:\mu_{max\text{-}P}=0.5-0.8$ (Fig. 1). Carbon:chlorophyll *a* ratio declined with P addition. Many workers have demonstrated a close negative correlation between carbon:chlorophyll *a* and cell division rate under both N and P limited growth (Caperon and Meyer 1972; Laws and Bannister 1980; Hunter and Laws 1981). At 5 $\mu g\ P \cdot L^{-1}$ enrichment carbon:chlorophyll *a* values decreased to 33–36 (Table 3) approaching levels found in algae grown under nearly P replete conditions (Perry 1972; Goldman 1980). The greatest change in carbon:chlorophyll *a* occurred with low increments in P, i.e. 0.1 to 1.0 $\mu g\ P \cdot L^{-1}$.

Because algal carbon:chlorophyll *a* declines with P enrichment, chlorophyll *a* is a potentially biased measure of biomass in enrichment experiments. Shifts in carbon:chlorophyll *a* could create the erroneous impression that algal biomass was responding to nutrient additions when perhaps only the chlorophyll *a* content of the cells had increased. To assess the magnitude of this bias, normalized data for specific growth rate (μ) and peak biomass based on both chlorophyll *a* and organic carbon were compared for trial 3 where the actual PB_{max} value was attained. The graphic comparison in Fig. 6 of $\mu:\mu_{max}$ and $PB:PB_{max}$

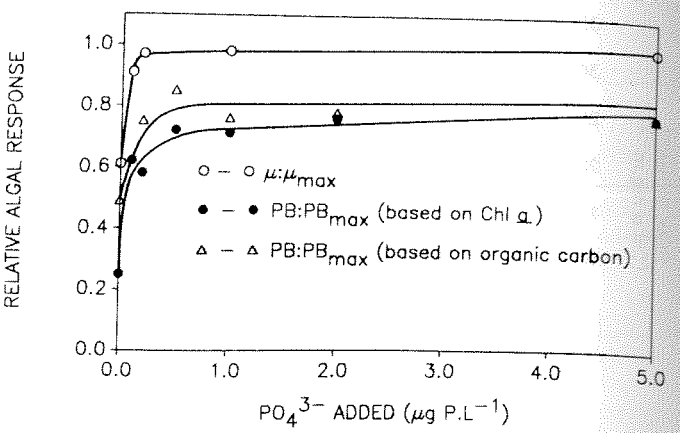

FIG. 6. Relative algal responses to phosphate addition. Relative specific growth rate ($\mu:\mu_{max}$) is compared with relative peak biomass ($PB:PB_{max}$) based on both chlorophyll *a* and POC. Specific growth rate data are the average values obtained during short-term experiments (Bothwell 1988) run simultaneously with the long-term accumulation trials. The peak biomass data are the values from long-term trial 3 and are normalized to biomass at 50 $\mu g\ P \cdot L^{-1}$. All curves are drawn by eye.

(using the biomass at 50 $\mu g\ P \cdot L^{-1}$ as PB_{max}) demonstrates that algal biomass based on carbon as well as on chlorophyll *a* requires higher levels of P to achieve saturation than specific cellular growth rates.

Discussion

This study clearly shows that added PO_4^{3-} causes increases in areal biomass of taxonomically similar communities of periphytic algae despite the fact that the concentration of PO_4^{3-} required to saturate specific growth rates has been exceeded. In all trials PB continued to increase with P additions of from 1 to 5 $\mu g\ P \cdot L^{-1}$. When higher enrichments were used, PB continued to increase with PO_4^{3-} additions up to 25-50 $\mu g\ P \cdot L^{-1}$. This sharply contrasts with the fact that extracellular PO_4^{3-} levels of 0.3–0.6 $\mu g\ P \cdot L^{-1}$ always saturate specific growth rates of periphytic diatoms in the South Thompson River (Bothwell 1988). These apparently conflicting findings corroborate the thesis that denser algal accumulations require higher concentrations of P to saturate and maintain growth of the whole community.

A shift from cellular controlled to community controlled growth rates of the periphyton mat should be reflected in a PB versus P curve. Close examination of the relative peak biomass curve in trial 3, reveals the presence of three phases in PB response (Fig. 7). Phase I, between 0 and ~1.0 $\mu g\ P \cdot L^{-1}$ of added PO_4^{3-}, is characterized by a rapid initial increase in PB which approaches saturation at ~0.5 $\mu g\ P \cdot L^{-1}$. The shape of the PB response curve during phase I is similar to a Monod cellular growth rate curve.

Phase II, from ~2.0 to ~30 $\mu g\ P \cdot L^{-1}$, is characterized by a slow linear increase in $PB:PB_{max}$ with higher P concentrations (Fig. 7). In this interval, relative peak biomass is closely predicted by the equation:

$$PB:PB_{max} = 0.0097\ P_i + 0.73,$$

where P_i is the bulk water PO_4^{3-} concentration in micrograms P per litre. From the regression equation, PB will equal PB_{max} at about 28.0 $\mu g\ P \cdot L^{-1}$. A linear increase in PB at intermediate P levels would be expected if the mechanism controlling areal

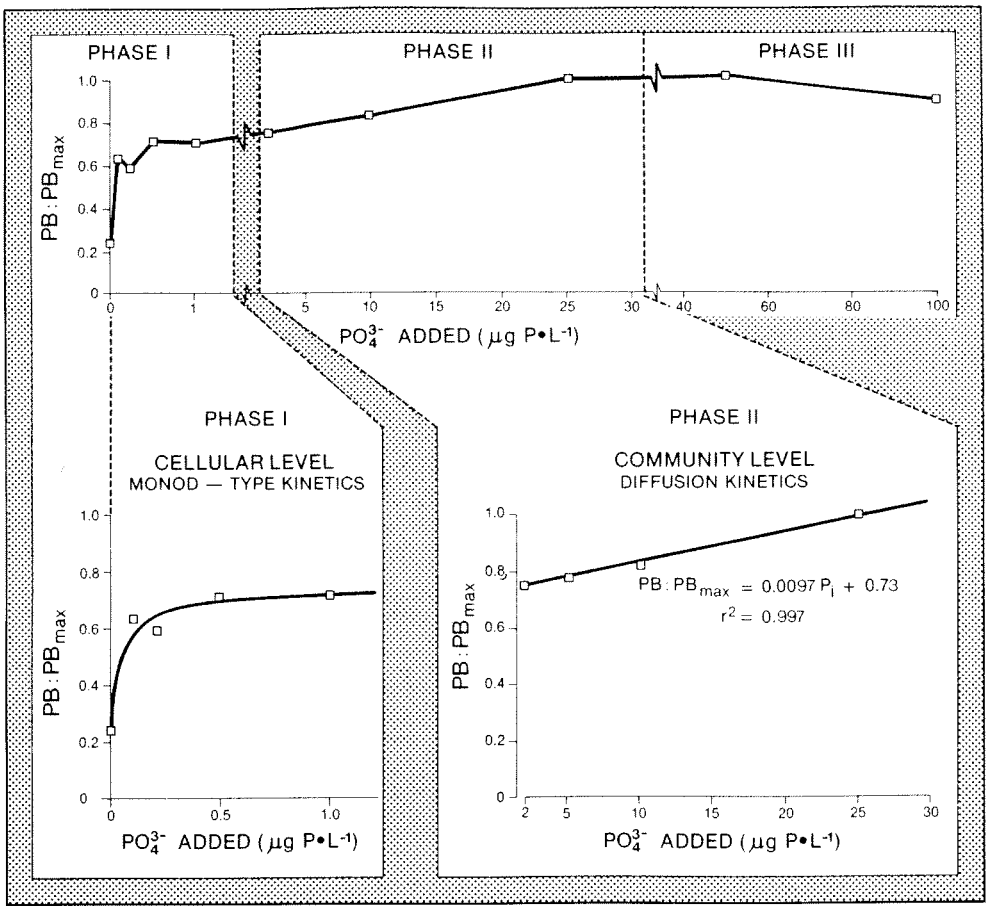

FIG. 7. Relative peak biomass in trial 3 as a function of added phosphate up to 100 μg P·L^{-1}. The data are normalized to the chlorophyll *a* value obtained at 50 μg P·L^{-1} and show three phases in areal biomass response. Phase I: a rapid initial response showing saturation at 0.5–1.0 μg P·L^{-1} and suggesting control by cellular growth rate kinetics. Phase II: a linear response at higher levels of phosphate addition (2–28 μg P·L^{-1}) indicating diffusion-limited kinetics. Phase III: complete saturation of areal biomass at phosphate levels >30–50 μg P·L^{-1}. Beyond this point some other factor(s) limits algal biomass.

biomass is physical diffusion of the limiting nutrient into the periphyton matrix.

Beyond a high level of P (i.e. >30–50 μg P·L^{-1}), during phase III, biomass no longer responds to further nutrient increase (Fig. 7). The lack of continued biomass response may result from the onset of secondary nutrient limitation or more likely from limitations on biomass accrual set by either physical instability of the periphyton community or by light limitation within the mat (Jasper and Bothwell 1986).

A shift in the mechanism controlling the amount of accrued biomass is indirectly supported by the observation that the transition from phase I to phase II occurs at a concentration of phosphate which is close to those known to saturate growth rates of these same diatom communities at the cellular level. During late fall–early winter (the time period of trial 3) addition of 0.2 μg P·L^{-1} phosphate is sufficient to saturate specific growth rate (see Bothwell 1988, Fig. 6B). The plateau for accrued biomass (chlorophyll *a*) in phase I is reached at a slightly higher PO_4^{3-} level, i.e. ~0.5 μg P·L^{-1} (Fig. 7). As previously discussed, this minor discrepancy may be explained by the shift in carbon:chlorophyll *a*. Even without this consideration, however, the coincidence of specific growth rate saturation and a change from a Monod to a linear model response in PB is striking.

A sharp decline in the rate of increase in periphyton areal biomass with P addition was reported earlier by Horner et al. (1983). Working with the attached filamentous green algae *Mougeotia* sp. they found that the slope of biomass response was steep with P additions up to ca. 25 μg P·L^{-1} but that above this concentration continued biomass response was less marked (Horner et al. 1983). Their findings are qualitatively similar to the ones reported here; the primary difference being the level of P at which biomass response begins to sharply decline. Green algae, especially large-celled filamentous forms, have higher extracellular nutrient requirements for maximal growth than do most diatoms. Two species, *Stigeoclonium tenue* and *Cladophora glomerata*, have been shown to have specific growth rates which are saturated by P concentrations in the range of 25–40 μg P·L^{-1} (Rosemarin 1983). Although other species such as *Pithophora oedogonia* may have even higher P requirements (Spencer and Lembi 1981), the 25 μg P·L^{-1} concentration at which Horner et al. (1983) found a sharp decline in the rate of biomass increase in *Mougeotia* is in the range of growth saturation values reported by Rosemarin (1983). In view of the findings at EXTRA, the inflection point at ca. 25 μg P·L^{-1} reported by Horner et al. (1983) may also represent a shift in mechanism controlling biomass, i.e. a change from cellular to whole mat growth kinetics. Such a shift would be consistent with their own

observation that at higher P enrichments, and hence higher biomass levels, increasing current velocity usually had a more stimulating effect than at lower P levels (Horner et al. 1983).

The transition point from phase I to phase II kinetics is set primarily by the biological determinant of species growth rate saturation. On the other hand, the slope of the line during phase II should be largely a function of parameters controlling physical diffusion. Factors facilitating diffusion such as higher current velocity, turbulence or a more porous periphyton matrix structure should in theory result in a steeper slope in phase II.

Implications for Lotic Eutrophication

The actual response of algal periphyton biomass to nutrient enrichment in nature will be modified by a number of different biological and physical factors. In many situations algae are cropped efficiently by grazers (Elwood and Nelson 1972; Sumner and McIntire 1982; Lamberti and Resh 1983; McAuliffe 1984; Jacoby 1985, 1987). In some cases grazing may be so effective that the relationship between algal standing crop and response to increases in the limiting nutrient concentration is masked, at least temporarily (Manuel and Minshall 1980; Elwood et al. 1981). Although no attempt was made to exclude grazers in the present experiments, herbivores usually did not occur in large numbers and were probably not an important determinant in algal biomass. Physical factors are also involved in determining periphytic biomass. Current velocity and substratum stability (rock size) are particularly important in lotic systems. At EXTRA, the use of a completely nonmobile substratum would mimic the most stable substrata found in nature. Because of substratum stability and low grazing pressure, the relationship reported here between areal biomass and P concentration, probably approximates an upper limit for diatom-dominated, P limited, temperate streams provided that other factors are the same, e.g. water velocity, light, and levels of other nutrients.

The growth of lotic periphyton communities into a more nutrient-limited condition as biomass accumulates is certainly very common and is one of the reasons for the discrepancy between the low levels of nutrients known to saturate growth rates of many algal species and the much higher levels usually reported to cause more dense accumulations of periphyton in nature. Even though higher standing crops result when P in the water is elevated above concentrations which saturate cellular level growth kinetics, it is important to note that large increases in areal biomass still occur with very low increments in phosphate. In trial 3, PB nearly tripled with addition of just 0.1–0.2 $\mu g\ P \cdot L^{-1}$, i.e. an amount of P below the detection limit of standard chemical methods for orthophosphate. Under the conditions of experiment 3, diatom PB at 1.0 $\mu g\ P \cdot L^{-1}$ was ca. 70% of the maximum biomass which could be attained with P enrichment alone.

The fact that diatom $PB:PB_{max}$ of 0.7 can be attained at PO_4^{3-} of ~1.0 $\mu g\ P \cdot L^{-1}$ has obvious implications for riverine eutrophication. It shows that high accumulations of periphytic algae in lotic conditions can occur with very small increments of P concentration. Downstream biological removal of P from river water will determine the areal extent of algal proliferation. This is, of course, a major consideration in many cases of river enrichment resulting from point source nutrient loading. However, the data from the present experiments at EXTRA indicate that once P concentrations have already exceeded a certain low level in diatom dominated rivers, algal biomass at any specific location relative to a point source may only change moderately with reductions in existing loading levels. Because the physical characteristics of a particular river reach impacted by nutrient loading differ in a variety of ways from controlled experimental facilities, an assessment of the relative sensitivity of a river to nutrient reduction will be needed to determine the efficacy of reducing algal proliferations by nutrient control measures.

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