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Responses of benthic algae to pulses in current and nutrients during simulations of subscouring spates

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Abstract. We tested the hypothesis that modest increases in discharge and nutrients, like those occurring during spates, could have a positive effect on benthic algae in streams. Patterns in orthophosphate (PO₄-P), total phosphate (TP), nitrate (NO₃-N), and total Kjeldahl nitrogen (TKN) concentrations in stream waters showed that nutrient concentrations could increase during and after spates. In-stream nutrient concentrations were correlated to indicators of spates in an agricultural basin more than in a forested catchment. Nutrient and current concentrations were manipulated in experimental stream channels to simulate a subscouring spate, i.e., a spate during which organisms are not removed from substrates. Increasing PO₄-P and NO₃-N concentrations in the water for 12 h had little immediate effect on algal biomass but did increase phosphorus concentrations in periphyton. This increase in periphyton-P did not stimulate algal growth. Doubling current from 10 to 20 cm/s for 24 h had no effect on benthic algal biomass during the 24-h manipulation. Increasing current increased periphyton-N in high nutrient conditions but decreased periphyton-N concentrations and algal growth rates in low nutrient conditions. Changes in periphyton chemistry provided valuable information for development of hypotheses to explain responses of algae to environmental manipulations. Our results suggest that subscouring spates will probably inhibit algal growth in nutrient-poor streams, but could stimulate algal growth in nutrient-rich streams.

Key words: periphyton, benthic algae, diatoms, nutrients, nitrogen, phosphorus, intracellular, current, spates.

Although spates can have a devastating impact on benthic algal communities in streams, they may have some positive effects (Resh et al. 1988). Algal scouring commonly occurs with increases in discharge and current velocity during spates (Douglas 1958, Siegfried and Knight 1977, Tett et al. 1978, Wehr 1981, Fisher et al. 1982, Power and Stewart 1987). However, some increases in discharge and current during spates are not sufficient to scour algae from substrata (Grimm and Fisher 1989, Stevenson 1990). Since increases in current velocity can stimulate algal metabolism (e.g., Whitford and Schumacher 1961, Pfeifer and McDiffett 1975, Vilenkin and Pertsov 1983), similar increases in current during subscouring spates (defined as those that do not remove algae from substrata) may have a positive effect on benthic algae.

Increases in nutrient concentrations in stream waters during spates may be a second way in which spates have positive effects on benthic algae in streams. Algal accumulation can be limited by nutrient concentrations in streams

(Grimm and Fisher 1986, Lowe et al. 1986). The relationship between nutrient concentrations and discharge during spates is variable within and between streams, but can be positive (see review in Meyer et al. 1988).

We hypothesize that subscouring increases in current velocity and increases in nutrient concentrations can occur during spates and can stimulate algal growth rates. We tested this hypothesis by monitoring nutrient concentrations in two streams to determine whether changes occurred during spates in our study area. In addition, we manipulated current velocity and nutrient concentrations in experimental stream channels to simulate a subscouring spate. We then assessed the effects of manipulations on algal abundances, on nitrogen and phosphorus concentrations of the periphyton, and on algal growth rates.

Methods

Study site

The study was conducted in Wilson Creek and Hart's Run, two streams in Bernheim Forest Nature Preserve, a private wildlife sanctuary 50

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km south of Louisville, Kentucky. Hart's Run is a small 3rd-order stream with 7.5-km² catchment which is 97% forested; remaining fields are open or used to grow crops for wildlife, but are without fertilizers. Hart's Run at baseflow has a 40 L/s discharge and an average channel width of 6 m. Wilson Creek is larger than Hart's Run with a baseflow of 70 L/s and an average channel width of 10 m, but it is still a 3rd-order stream; drains a 14.8-km² catchment which is 70% forested. The nonforested lands in the Wilson Creek catchment are used as pastures, for crops with fertilizers added, and for residential use. Current velocities in both these streams vary from <5 cm/s in pools to >30 cm/s in riffles. The upper reaches of both streams drain predominately Devonian oil shale, with the lower reaches cutting through dolomitic limestone. Siltstone cobble is the dominant substrate in both streams.

Nutrient and discharge patterns in streams

Water samples were collected from Hart's Run (33 samples on 14 dates) and Wilson Creek (44 samples on 19 dates) from 11 November 1988 through 24 May 1989 to relate water chemistry to spates. Filtered and unfiltered samples were collected on all but a few sampling dates. Filtered samples were taken with a 60-mL polyurethane syringe and passed through Gelman GN-6 filters (0.45- μ m pore size, 25 mm diameter) in the field. All samples were placed in acid-washed 125-mL polyurethane bottles and immediately packed in ice. In the laboratory, the samples were frozen until analyzed (<60 d later).

Using standard procedures (U.S. EPA 1983), filtered samples were analyzed colorimetrically for orthophosphate (PO₄-P) by the ascorbic acid, two-reagent method and for nitrate-nitrogen (NO₃-N) by manual cadmium reduction; unfiltered samples were analyzed colorimetrically for total phosphorus (TP) as above and potentiometrically for total Kjeldahl nitrogen (TKN) by ion selective electrode using the micro Kjeldahl digestion technique. TKN by definition is only ammonia-nitrogen plus all organically bound nitrogen (U.S. EPA 1983), and does not include nitrate or any other oxidized forms.

Relationships between stream water chemistry (PO₄-P, NO₃-N, TP, and TKN) and indicators of spates were assessed using correlation

analysis. Continuous records for discharge in Hart's Run and Wilson Creek were not available. Therefore, we used mean daily discharge of Beargrass Creek, Middle Fork, which is the closest 3rd-order stream with a gaging station (U.S. Geological Survey, Water Resources Division, unpublished data). Beargrass Creek is 50 km from the study area. Rainfall was recorded 4 km from our site (at Bernheim Forest Nature Preserve, Clermont, Kentucky, unpublished data). We used four permutations of the rainfall data as indicators of spates: 1) rainfall the day of sampling (d_0), 2) rainfall the day before sampling (d_{-1}), 3) rainfall during a 2-d period including d_0 and d_{-1} , and 4) rainfall during a 4-d period including d_0 and the three previous days.

Nutrient-current experiment

Nutrient concentrations and current were manipulated in experimental streams at the University of Louisville's facility by Wilson Creek. Stream water was drawn by a 1-hp pump through PVC pipe into 24 vinyl gutters (3.05 m long, 0.1 m wide) which were used as flow-through stream channels.

Algae were allowed to colonize 84 unglazed ceramic tiles (each 28.45 cm²) in 10 cm/s currents for 9 wk in three artificial stream channels. Approximately every 10 d, when spates occurred in Wilson Creek, loosely attached benthic matter (algae, silt, etc.) was washed from tiles by hosing pumped water over the tiles to simulate the spates in streams. Communities on tiles were not disturbed 10 d prior to the experiment. Comparisons (Stevenson, unpublished data) show that this method of precolonization produces algal communities like those that can be found in the same abiotic conditions in the natural stream.

At noon of 5 December 1989, three or four pre-colonized tiles were placed in each of 24 channels. Then current and nutrient concentrations were manipulated to produce four treatments: a control, increased (spate-like) current velocity only, increased nutrient concentrations only, and a current-plus-nutrient (CN) treatment. Different numbers of tiles were used in channels because we did not have enough pre-colonized tiles with the same initial algal abundances for all channels. Spates were simulated in 12 of the 24 channels by doubling current velocity from approximately 10 cm/s to

20 cm/s. In six channels of each flow regime, nutrients were increased to 30 $\mu\text{g PO}_4\text{-P/L}$ and to 600 $\mu\text{g NO}_3\text{-N/L}$ by dripping a nutrient solution into the upstream end of channels. Drip rates were measured each hour to ensure accurate delivery of nutrients. The nutrient concentrations produced in this treatment were the same as concentrations observed in Wilson Creek after a rain during the previous spring. After 12 h (at midnight) nutrient addition was terminated. Spate-like conditions were maintained by continuing increased discharge and currents for 12 h after nutrient enrichment was terminated. After 24 h all currents were reset to 10 cm/s. Terminating nutrient enrichment before resetting currents to prespate levels simulated a pattern that occurs in streams. Solute concentrations are typically higher when discharge increases during spates than at the same discharge when flows are decreasing (McDiffett et al. 1989).

Benthic algal samples were collected immediately after decreasing currents to base flow and ending the simulated spate (day 0) and also 3 d and 6 d later. Periphyton from one tile from each channel was scraped into a graduated plastic bottle. Tiles were then replaced in channels to maintain a consistent flow pattern over other tiles. In the field, periphyton samples were homogenized by vigorous shaking and were diluted to 100 mL. A 10.0-mL aliquot was taken from each sample for periphyton chemistry analysis, packed in ice, transported to the laboratory, and refrigerated until analyzed. The remaining sample was preserved with M^3 , which is a solution of formaldehyde and glacial acetic acid (APHA 1985), and used for algal identification and enumeration and ash-free dry mass (AFDM) determination.

Nutrient chemistry and community biomass analyses

Periphyton nutrient concentrations were determined by drying periphyton samples in porcelain crucibles in a drying oven at 105°C. Dried samples were homogenized, and separate portions were then weighed (dry mass, DM) and analyzed as above for TP, $\text{NO}_3\text{-N}$, and TKN.

Samples preserved for algal community enumeration were homogenized with a biohomogenizer (Model M133/1281-0, Biospec Products, Inc., Bartlesville, Oklahoma) and dyed with a

lactophenol/cotton blue dye. An aliquot was mounted in syrup (Stevenson 1984), and density estimates were made for live algal cells (intact cells with chloroplasts or cotton-blue-stained cytoplasm). More than 400 cells were typically counted in one 180- μm wide transect across the coverslip (22 \times 22 mm). Biovolumes were estimated using geometric formulas (Stevenson et al. 1985) after measuring the dimensions of 10 cells of each taxon. The preserved sample remaining after slide preparation was concentrated and used to determine AFDM (APHA 1985).

Data analyses

Three parameters were measured to assess algal community standing crop: cell abundances (cells/cm²), biovolume ($\mu\text{m}^3/\text{cm}^2$), and AFDM (mg/cm²). Three measures provide a better assessment of algal standing crop than one because each may be biased by differing cell sizes, vacuole proportions in cells, or proportions of bacteria and detritus in samples (Stevenson and Lowe 1986). Relative abundances (%) and cell abundances of each algal taxon were also calculated. Periphyton-P, periphyton-TKN, periphyton- NO_3 , and periphyton-TN were calculated by multiplying the concentration of the nutrient per unit DM by the ratio between DM/AFDM. Total-nitrogen (TN) was determined by adding TKN and $\text{NO}_3\text{-N}$. The atomic N:P ratios for water and periphyton chemistry were also calculated.

Immediate effects of current and nutrient manipulations were determined by analyzing day-0 data with two-way analyses of variance (Wilkinson 1989). The model included nutrient and current factors with a nutrient-by-current interactive term ($n = 24$).

Long-term effects (over a 6-d period) of treatments on algal growth were assessed primarily with regression analyses. Specific algal growth rates were determined from changes in natural-log transformed cell abundances in each treatment. Simple linear regression was used to determine growth rates (r_i) for the i^{th} species with the following model:

$$\ln(N_i) = a_i + r_i D$$

where N_i and r_i are the cell abundance and growth rate of the i^{th} species, respectively, a_i is a constant, and D is the number of days of com-

munity development after the simulated spate. Differences in growth rates among treatments were assessed by comparing r_i (i.e., slopes of regression lines) with 95% confidence intervals (Zar 1974). Simple linear regression was also used to determine changes (slope = β_i) in periphyton chemistries (not natural-log transformed) during community development after the simulated spate.

Channel- and time-specific growth rates were calculated to study the relationship between growth rates, periphyton nutrients, and periphyton AFDM, because AFDM did vary among channels within treatments. These growth rates were calculated as above, as per capita changes in cell abundances, biovolume, and AFDM per day, except only data from one channel and one 3-d period were used for each calculation. All standing crop data were natural-log transformed before calculation. Algal growth rates in a specific channel and during a specific 3-d period were related to average periphyton-P, periphyton-TKN, periphyton-NO₃, and periphyton AFDM during the 3-d periods by simple linear regression.

Results

Nutrient patterns in streams

Nutrient concentrations were significantly correlated with indicators of spates more frequently in Wilson Creek than Hart's Run (Table 1). Concentrations of NO₃-N and PO₄-P in Wilson Creek and Hart's Run were positively correlated ($p < 0.05$) to mean daily discharge in Beargrass Creek. In Wilson Creek, concentrations of NO₃-N, PO₄-P, and TP were positively correlated to the previous day's rainfall and to the total rainfall occurring during the 2-d and 4-d periods ($p < 0.05$). Hart's Run PO₄-P concentrations were positively related to rainfall on the sampling date ($p < 0.01$); NO₃-N and TKN were positively related ($p < 0.05$) to rainfall during the 4-d and 2-d rainfall periods, respectively. Comparison of correlation coefficients shows indicators of spates accounted for more variation in NO₃-N and PO₄-P than in TKN and TP.

Nutrient concentrations in Wilson Creek seven days before the experiment were 110 μg NO₃-N/L and 3.5 μg PO₄-P/L. They varied between 95–200 μg NO₃-N/L and 2.4–5.0 μg PO₄-P/L during the experiment.

Immediate effects of spates

Algal standing crop was not immediately affected by doubling current or by nutrient addition (Fig. 1). The average abundance of diatoms for all treatments was 3.0×10^6 cells/cm² (1 SE = $\pm 0.253 \times 10^6$, $n = 24$) on day 0. Abundances were not significantly different ($p > 0.05$) among treatments on day 0. The high means in controls were due to unusually high abundances of *Achnanthes minutissima* in three of the six replicate samples. No difference among treatments were observed on day 0 for AFDM or biovolume assessments of standing crop ($p > 0.05$).

Species composition was also not immediately affected by the spate manipulations (Fig. 2). Diatoms composed more than 90% of the algae observed. *Achnanthes minutissima* was the most abundant alga in the benthic algal assemblages on day 0. *Synedra ulna*, *Cymbella affinis*, and *Nitzschia acicularis* were less abundant but composed significant proportions of the biovolumes of these assemblages. Only the abundances of *S. ulna* were significantly ($p < 0.05$, $n = 24$) greater in nutrient treatments than in controls just after the spate manipulations. No significant differences were observed in abundances of any other taxon on day 0.

Nutrient concentrations in the periphyton were differentially affected by changes in current velocity and in nutrient concentrations in the water (Fig. 3). Phosphorus concentrations in periphyton on day 0 increased ($p < 0.0002$) from 5.6 to 7.4 mg PO₄-P/g AFDM as a result of nutrient enrichment. Current and nutrient treatments decreased TKN concentrations in the periphyton ($p < 0.001$). A positive interactive effect of the CN treatment on TKN in the periphyton was also indicated ($p < 0.001$). Nitrate-N in periphyton was not immediately (on day 0) affected by simulated spate conditions.

Long-term effects of spates

The pulse in current velocity had a negative effect on benthic algal growth rates during the 6-d period after the simulated spate (Fig. 1). Algal community growth rates as measured by biovolume and AFDM were significantly greater ($p < 0.05$) in control than current treatments (Fig. 4). Growth rates of cell abundances were low in control treatment because of the high

TABLE 1. R values from Pearson correlation matrices. Nutrient concentrations from two streams, Hart's Run and Wilson Creek, were correlated to periods of rainfall as indicators of discharge; day 0 is sample day, day -1 is previous day, 2-d is sample day + previous day, and 4-d is sample day + 3 previous days. Discharge is mean daily discharge from Beargrass Creek Middle Fork in Louisville, Kentucky.

	Nutrient	Rainfall		Total rainfall		Discharge
		day 0	day (-1)	2-day	4-day	
Hart's	PO ₄ -P	0.506***	-0.083	0.203	-0.082	0.425*
	TP	-0.062	0.195	0.120	0.107	-0.072
	NO ₃ -N	0.254	0.227	0.328	0.382*	0.695***
	TKN	0.285	0.272	0.384*	0.239	0.206
Wilson	PO ₄ -P	-0.007	0.797***	0.781***	0.593***	0.599***
	TP	0.159	0.371*	0.419**	0.370*	0.250
	NO ₃ -N	-0.026	0.754***	0.734***	0.661***	0.643***
	TKN	0.225	-0.070	0.068	-0.035	0.193

* 0.05 ≥ *p* > 0.01.

** 0.01 ≥ *p* > 0.005.

*** *p* ≤ 0.005.

abundances of one small algal taxon, *A. minutissima*, in three of the six replicate samples.

Nutrient enrichment had no long-term effect on algal community growth rates. Algal standing crop increased from days 0 to 6 (*p* < 0.05) in control, nutrient-enriched, and the CN treatments (Fig. 1). These increases in algal standing crop were generally evident as significantly (*p* < 0.05) positive growth rates (Fig. 4). While increases in cell abundances and AFDM standing crop were highest in nutrient and CN treatments, they were not significantly higher than in control treatments.

The simulation of small spates had little long-term effect on species composition (Fig. 2). In general, the species with the fastest growth rates in control conditions also had the fastest growth rates in nutrient and CN treatments (Fig. 5). No relationship existed between the species with the fastest growth rates in control conditions and in the current treatment. Low growth rates and relatively high variation compared with mean growth rates probably limited our ability to compare species growth rates in the current treatment.

Phosphorus and total nitrogen concentrations in the periphyton decreased during the post-spate period (Fig. 3). Periphyton-P increased (*t*-test, *p* < 0.005) from 5.7 mg P/g AFDM to 8.2 mg P/g AFDM from day 0 to day 3, but decreased (*t*-test, *p* < 0.005) to 5.2 mg P/g AFDM by day 6 in control conditions. Phosphorus decreased steadily from day 0 to day 6 in the nutrient treatment ($\beta = -0.270 \pm 0.119$ SE, *n* =

16) and in the CN treatment ($\beta = -0.299 \pm 0.150$ SE, *n* = 18). Phosphorus concentrations in periphyton did not change significantly ($\beta = -0.110 \pm 0.137$ SE, *n* = 16) in the current treatment.

Total N (sum of TKN and NO₃-N) patterns in periphyton were complicated by different changes in TKN and in NO₃-N during the study. Total Kjeldahl nitrogen decreased in all treatments from day 0 to day 6, but NO₃-N patterns varied among treatments. Periphyton-TKN decreased from as high as 34.2 mg TKN/g AFDM in control conditions on day 0 to about 7.5 mg TKN/g AFDM in control ($\beta = -4.491 \pm 0.137$ SE, *n* = 16), nutrient ($\beta = -1.834 \pm 0.800$ SE, *n* = 16), and CN treatments ($\beta = -3.338 \pm 0.629$ SE, *n* = 18) on day 6. Periphyton-TKN concentrations did not change significantly during the 6-d period ($\beta = -0.807 \pm 1.106$ SE, *n* = 16). Nitrate-N concentration increased in nutrient ($\beta = 0.440 \pm 0.122$ SE, *n* = 16) and CN treatments ($\beta = 0.378 \pm 0.187$, *n* = 18), but decreased from day 0 to day 6 in the current treatment ($\beta = -0.085 \pm 0.018$ SE, *n* = 16). Nitrate-N in periphyton did not change from day 0 to day 6 in the control treatment. In general NO₃-N (range: 0.5–4 mg NO₃-N/g AFDM) was a small proportion of TN. Overall, TN decreased significantly (*p* < 0.05) during the study in control, nutrient, and CN treatments, but did not change significantly in the current treatment.

The N:P ratio in periphyton decreased rapidly during the study while N:P ratios in the water column remained relatively constant. The

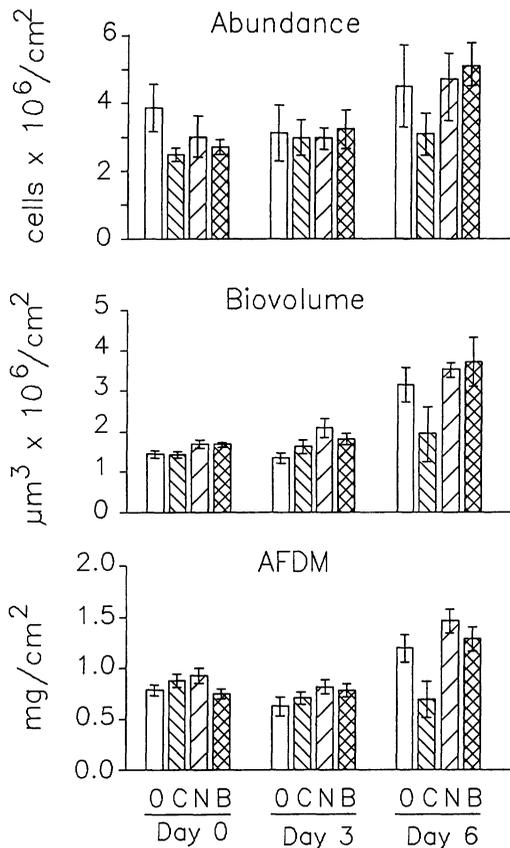


FIG. 1. Algal biomass (mean \pm 1 SE) in experimental streams on days 0, 3, and 6. O—control treatment, C—current treatment, N—nutrient treatment, and B—current-plus-nutrient treatment.

atomic N:P ratio in periphyton decreased from 13.4:1 to 3.1:1 from days 0 to 6 of the study. The atomic N:P ratio ($\text{NO}_3\text{-N}:\text{PO}_4\text{-P}$) in the water column was 78:1 on day 0; it had been 42:1 two weeks before the study and was 37:1 on day 2 of the study.

Three-day growth rates of algal communities, as measured by biovolume and AFDM, were inversely related ($p < 0.01$) to AFDM standing crop and complexly related to N in the periphyton (Table 2). Whereas AFDM growth of periphyton was positively related ($p < 0.05$) to periphyton TKN, AFDM growth and biovolume growth were negatively related to periphyton $\text{NO}_3\text{-N}$. Growth rates were not related to periphyton-P by any of the parameters of algal standing crop. Higher variability in cell abundances than in AFDM and biovolume measures

of standing crop prevented regression coefficients for cell abundances from being statistically significant, even though the magnitude of regression coefficients of all measures of standing crop were similar.

Discussion

Nutrient concentrations in the water of streams may increase, decrease, or remain unchanged as discharge increases during spates (Lewis and Grant 1979, Meyer and Likens 1979, Mulholland et al. 1981, Lesack et al. 1984, Benson 1985, Biggs and Close 1989, McDiffett et al. 1989). Land use in catchments probably affects the change in nutrient concentration during spates. We found that nutrient concentrations increased after spates and that persistence of nutrient pulses was positively related to the proportion of land used for agriculture and rural residential development. In Hart's Run, a low nutrient stream with a forested catchment, few correlations occurred between dissolved nutrients in this stream and rainfall or discharge in a nearby stream. Since most variation in nutrients was correlated with rainfall and discharge on the day of sampling in Hart's Run, we hypothesize that nutrient pulses persisted for much less time in Hart's Run than in Wilson Creek, where nutrients were highly correlated with the rainfall that had occurred during 2-4-d periods.

Pulses in nutrients during spates were expected to have positive effects on nutrient availability and growth rates of benthic algae. Phytoplankton rapidly sequesters nutrients when they are made available (Rhee 1973, 1978, López-Figueroa and Rüdiger 1991). Pulses in $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ concentrations that lasted 12 h increased periphyton-P in our study, had no effect on periphyton- NO_3 , and decreased periphyton-TKN.

Decreases in periphyton-TKN without decreases in AFDM indicated differentially greater loss of periphyton-TKN than periphyton-carbon or periphyton-P. One hypothesis to explain N loss is that increases in periphyton-P stimulated algal or bacterial growth and N-rich cells drifted from the periphyton. In that way loss of N-rich cells would decrease periphyton-TKN, but algal standing crop could have stayed equal in current and control treatments. Alternatively, increased P may have caused the loss of pe-

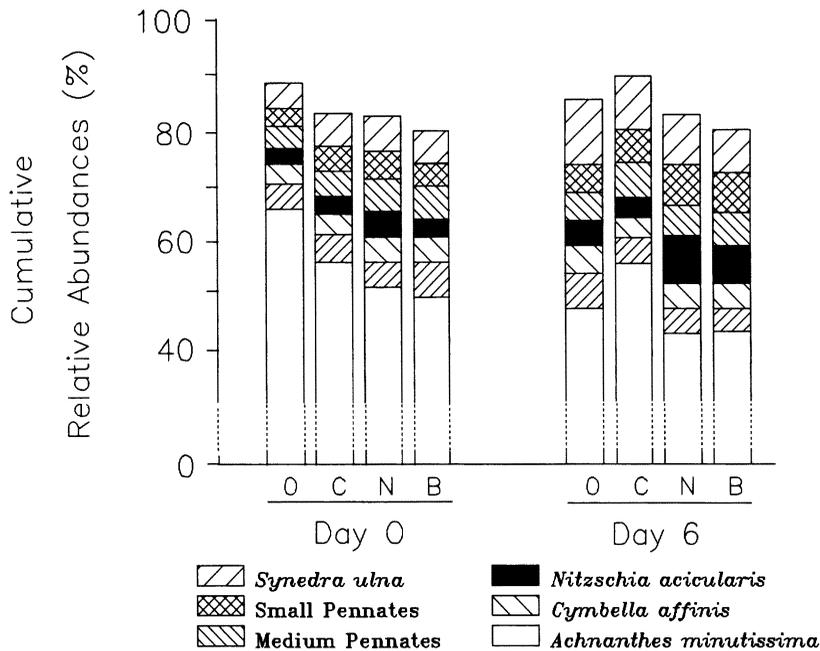


FIG. 2. Relative abundances of the most common diatoms in the experimental streams on days 0 and 6. Treatment codes as in Figure 1.

riphyton-TKN by stimulating a biochemical pathway that affected the form and stability of intracellular or extracellular pools of ammonia and/or organic N (both measured as TKN). Nitrogen metabolism in algal cells starts with active transport of NO_3 , NO_2 , or NH_3 into cells. Nitrate is first reduced to NO_2 and then to NH_3 . Ammonia can be assimilated to produce amino acids. Algae are known to leak (excrete) NO_3 , NO_2 , NH_3 , and amino acids (e.g., López-Figueroa and Rüdiger 1991, Marsot et al. 1991) and excrete exoenzymes. Therefore, the decrease in periphyton-TKN may have been caused by efflux of TKN from cells and from the periphyton.

Current velocity was predicted to have a positive effect on periphyton nutrients, but it negatively affected periphyton-TKN. Increasing current velocity from 10 cm/s to 20 cm/s for 24 h did have a positive effect on periphyton-TKN in high nutrient conditions, since periphyton-TKN was greater in the CN treatment than in the nutrient-alone treatment. Increasing current had no immediate effect on periphyton-P or periphyton- NO_3 in either nutrient regime. Again, decreases in periphyton-TKN without decreases in periphyton AFDM require loss of N from the substrata. Previous studies have

shown only that current velocity increased nutrient uptake or algal metabolism (e.g., Whitford and Schumacher 1961, Lock and John 1979). The positive effect of current has been attributed to a decrease in the thickness of a nutrient-poor layer of water that develops around cells, which increases molecular exchange between free-flowing stream waters and water near the cell membrane (Whitford 1960). This model assumes that extracellular nutrient concentrations near the cell membrane are lower than in well-mixed water farther from the cell.

The effect of current on periphyton-TKN was related to nutrient concentrations in the water. While current negatively affected periphyton-TKN in ambient nutrient conditions, current positively affected periphyton-TKN in enriched nutrient conditions. The latter positive effect of current was evident in higher periphyton-TKN in the CN treatment than in the nutrient treatment.

We hypothesize that the negative effect of current on periphyton TKN in low nutrient conditions was due to extracellular periphyton-N being rinsed from periphyton. The diverse metabolisms of algae and bacteria indicate exoenzymes, nucleotides, free amino

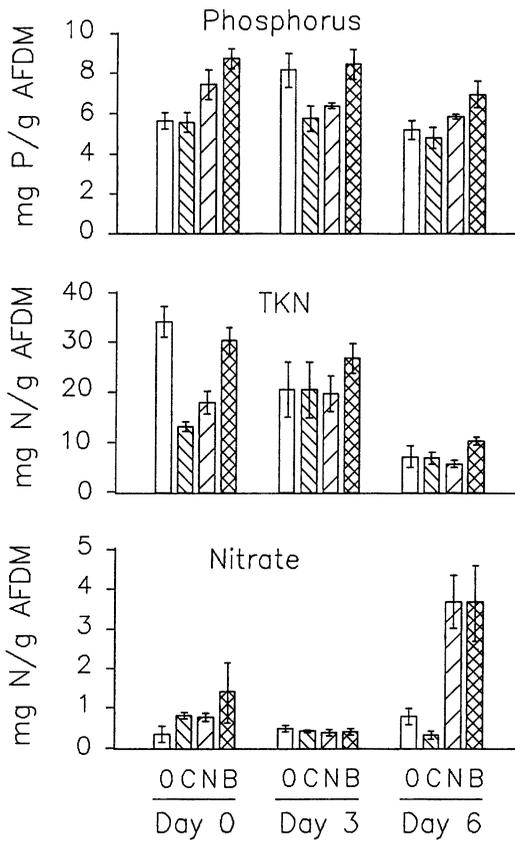


FIG. 3. Periphyton chemistries (means \pm 1 SE, mg nutrient/g AFDM of periphyton) in experiment streams on days 0, 3, and 6. Treatment codes as in Figure 1.

acids, and proteins accumulate in the polysaccharide matrix surrounding the detritus, bacteria, algae, fungi, and microinvertebrates that compose the periphyton (Admiraal and Peletier 1979, Francko 1989, Sinsabaugh and Linkins 1990, Marsot et al. 1991). These substances could accumulate from cell leakage, excretion, or adsorption from the water column.

According to a model that includes N-efflux and N-uptake by periphyton, the mixing of stream waters with interstitial waters of the periphyton matrix would negatively affect periphyton-TKN if loss of extracellular N and of N effluxed from intracellular sources were greater than N uptake. Periphyton-TKN could be sustained if N uptake was greater than loss of extracellular and effluxed N. Since algal uptake of inorganic N is positively related to extracellular concentrations of inorganic N, in-

creasing NO_3 concentrations in stream water from 100–200 $\mu\text{g NO}_3\text{-N/L}$ to 600 $\mu\text{g NO}_3\text{-N/L}$ must have been sufficient to shift the N flux between cells and surrounding medium from a net N loss to a net gain. Thus effects of currents on benthic algae may vary with nutrient concentrations in stream water and in the periphyton.

Several factors indicated that N-metabolism was limited by development of periphyton and/or the extracellular matrix of the periphyton. Periphyton-TKN concentrations decreased, but periphyton- NO_3 increased. The magnitude of these changes was so great that they probably involved intracellular N. Water column nutrients did not decrease during the study. Algal growth was negatively related to AFDM in this study and another (Stevenson 1990). Algal growth rates were not related to periphyton-P, but were positively related to periphyton-TKN. Periphyton-TN (Total Nitrogen) decreased during the study to an N:P ratio that was less than the N:P ratio reported for algal cells known to be N-limited (Redfield 1958, Rhee 1978). The small proportion of the cell contents that was composed of periphyton-TN ($\approx 1\%$) was characteristic of N-deficient cells (see review by Syrett 1962).

Periphyton has been shown to decrease ion exchange rates between the periphyton and the

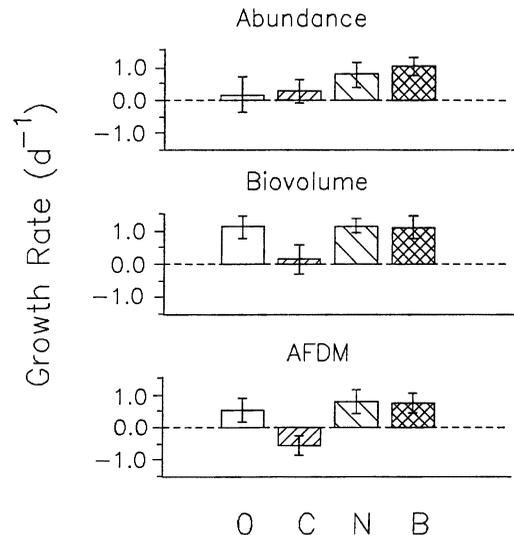


FIG. 4. Growth rates (means \pm 1 SE) of algal standing crop from day 0 to day 6 in the four experimental treatments. Treatment codes as in Figure 1.

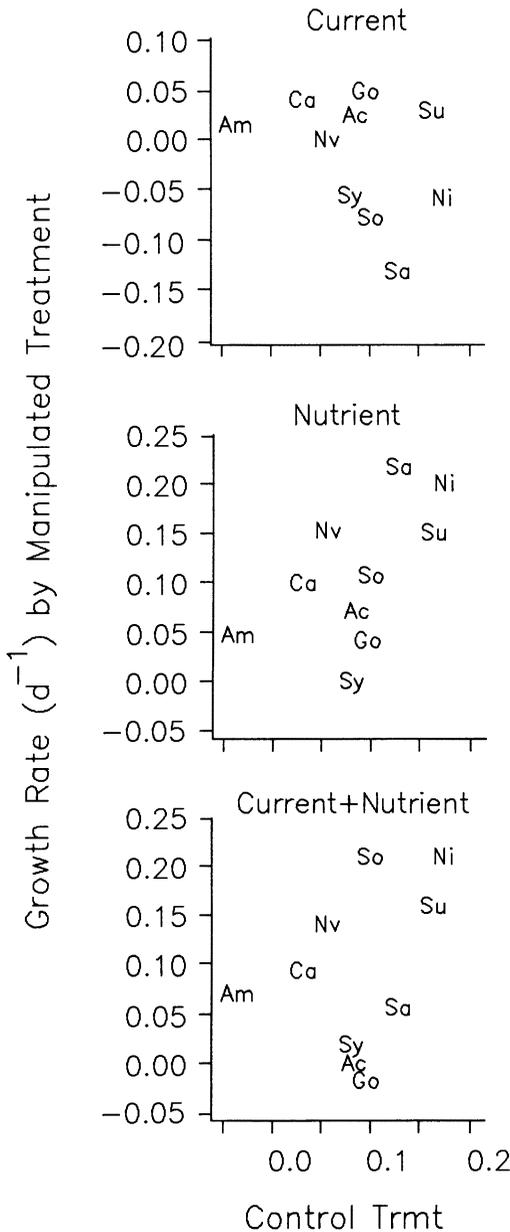


FIG. 5. Growth rates of diatoms in control treatments (plotted along x-axes) compared with their growth rates in three experimental treatments (plotted along the three different y-axes). Letter codes mark the growth rate of a taxon: Ac—*Achnanthes* spp., Am—*Achnanthes minutissima*, Ca—*Cymbella affinis*, Go—*Gomphonema* spp., Ni—*Nitzschia acicularis*, Nv—*Navicula cryptocephala* var. *veneta*, Sa—*Surirella angusta*, So—*Surirella ovata*, Su—*Synedra ulna*, Sy—*Synedra acus*.

water column in a number of studies (e.g., Rose and Cushing 1970, Ribber and Wetzel 1987, Moeller et al. 1988, Bothwell 1989, Burkholder et al. 1990). However, a decrease in NO_3 and NH_3 availability with increasing periphyton standing crop (AFDM, biovolume, density) could not directly explain the observed changes in N pools. Decreases in inorganic N exchange between water column and periphyton could cause most of the above effects, but could not directly explain the increase in periphyton- NO_3 . The increase in periphyton- NO_3 and decrease in periphyton-TKN concentrations indicates that NO_3 is either: (1) not being reduced to NH_3 , or (2) not being metabolized to a retainable intracellular form which would be measured as periphyton-TKN. These processes may be limited by availability of light, carbohydrates, CO_2 , or micronutrients (see review by Syrett 1962).

Periphyton nutrient concentrations have been used in studies of nutrient uptake by benthic algae (see Davis et al. 1990), but have not been used to assess nutrient status of cells. Assay of periphyton nutrient concentrations should be a valuable complement to water-column nutrient concentrations for assessment of nutrient availability to benthic algae. First, many benthic algae can absorb and store phosphorus in greater concentrations than immediately needed for division (Stevenson and Stoermer 1982). So if extracellular nutrient concentrations were to decrease for a short time, growth could be maintained on intracellular stores (Rhee 1973, Droop 1974). In addition, the periphyton and surrounding matrix interfere with nutrient exchange between cells in the periphyton and the water column. Of course all periphyton-N and periphyton-P were not in algal cells, but careful use of periphyton-nutrient concentrations as an indicator may help assessment of the nutrient availability to benthic algae.

Changes in water chemistry and current velocity during spates are complex and variable within and among streams. Pulses in current and nutrients did not increase nutrient availability and growth rates of benthic algae as expected. Periphyton-P increased during short exposures to high phosphate concentrations in our simulations of subscouring spates and could therefore stimulate algal growth if P were limiting. However, without nutrient enrichment, periphyton N-content and algal growth rates decreased after a 24-h increase in current.

TABLE 2. A matrix of regression coefficients describing the change in 3-d growth rates as a function of periphyton (Peri) chemistry (mg/g AFDM) and AFDM (mg/cm²) during sampling intervals.

Standing crop parameter	Peri-P	Peri-TKN	Peri-NO ₃	Peri-AFDM
Cell abundance	-0.0059	0.00558	-0.0702	-0.246
Biovolume	-0.0137	0.00490	-0.1023**	-0.476**
AFDM	-0.0141	0.00628*	-0.0929**	-0.414**

* $0.05 \geq p > 0.01$.

** $p \leq 0.01$.

Therefore, subscouring spates may have positive or negative effects on benthic algae in streams depending upon nutrient concentrations in stream water during the spate.

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