

NUTRIENT AND LIGHT LIMITATION OF ALGAE IN TWO NORTHERN CALIFORNIA STREAMS¹

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ABSTRACT

Nutrient-diffusing substrates were used to investigate nutrient limitation of attached algal assemblages in a shaded stream and an unshaded stream in northern California. Water from both streams contained low levels of nitrogen ($<14 \mu\text{g}\cdot\text{L}^{-1}$) and very low N:P ratios (<2). After 31 days of colonization and growth, attached algal biomass on nitrate-diffusing substrates was significantly greater than on control substrates in the unshaded stream. Nitrate-diffusing substrates also supported larger numbers of grazing insects in the unshaded stream. The prostrate diatoms *Achnanthes lanceolata* Bréb. and *Cocconeis placentula* Ehr. displayed the most consistent positive responses to nitrate enrichment. Nutrient enrichment did not increase the accrual of algal biomass in the shaded stream, but algal biomass was significantly greater at sites located under openings in the tree canopy, implicating light as a limiting factor in this stream. Several *Navicula* and *Nitzschia* species, and one unidentified *Gomphonema* species, were positively associated with higher light levels in the shaded stream. Shade appears to be the primary factor limiting algal growth in small northern California streams, but when its effect is reduced by logging, the inherently low levels of nitrogen in these streams can become limiting.

Key index words: algae; assemblage structure; diatoms; grazers; nutrients; shade; streams

Shade and nutrients are prominent among the variables which limit algal growth in streams. Streamside vegetation often restricts the amount of light striking the surface of small streams, especially in forested ecosystems, and can prevent primary production from exceeding community respiration (Fisher and Likens 1973, Vannote et al. 1980). However, when canopy development over streams is negligible as a result of logging or stream geomorphology, primary production may provide a substantial contribution to community metabolism (Minshall 1978). Under such unshaded conditions, low ambient nutrient levels can assume limiting roles in unpolluted streams (Stockner and Shortreed 1978).

Compared to lentic ecology, research into the effects of light and nutrient variation on primary production has been limited in stream ecology. For ex-

ample, only a few experiments have directly examined the effect of varied light levels on stream algal assemblages. Gregory (1980) stimulated primary production in a shaded Oregon stream by augmenting light levels, and Triska et al. (1983) reported decreased accumulation of periphyton biomass in experimentally shaded channels in a northern California stream. Other studies compared the species composition of algal assemblages in streams for logged and unlogged watersheds, attributing differences in assemblage structure to light effects (Hansmann and Phinney 1973, Shortreed and Stockner 1983, Lowe et al. 1986). Nutrient limitation in streams has been investigated more effectively through the use of specific nutrient amendments. Nitrate and phosphate have been applied experimentally in a variety of streams, stimulating algal growth in most instances (Stockner and Shortreed 1978, Elwood et al. 1981, Peterson et al. 1983, Triska et al. 1983, Pringle and Bowers 1984, Grimm and Fisher 1986, Lowe et al. 1986).

In this study, we investigated the effect of nutrient enrichment and shade on attached algae in two northern California headwater streams. Low nitrogen concentrations in the streams suggested that algal growth was nitrogen-limited. We tested this hypothesis by introducing nutrient-diffusing clay substrates into the streams, and simultaneously investigated the extent of light limitation by varying the amount of shade experienced by algae growing on the substrates.

MATERIALS AND METHODS

Study streams. Barnwell Creek and Fox Creek are unpolluted tributaries of the South Fork of the Eel River in Mendocino County, California, USA. Both streams are contained within the Nature Conservancy's Northern California Coast Range Preserve (39°45' N, 123°40' W), and are separated by only one km at their mouths. Barnwell Creek is a second-order stream whose watershed was clearcut in the early 1950's. As a consequence of logging, canopy development is minimal. Occasional patches of shade over Barnwell are provided by regenerating redwood (*Sequoia sempervirens* (D. Don) Endl.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), big leaf maple (*Acer macrophyllum* Pursh), *Ceanothus* spp., and madrone (*Arbutus menziesii* Pursh). Local variation in shade is also produced by logging debris and the stream bank, but much of Barnwell Creek is exposed to at least 6 h of direct sunlight during July and August. Fox Creek is also a second-order stream, but in contrast to Barnwell Creek, is heavily shaded. Old-growth Douglas fir, California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.), and big leaf maple form the bulk of streamside vegetation. Water temperature ranged from 15–21° C in Barnwell Creek and 14–19° C in Fox Creek during the course of this study. Discharge is similar in both streams, and approximated $6 \text{ L}\cdot\text{s}^{-1}$ at the study's end. Because this study took place during

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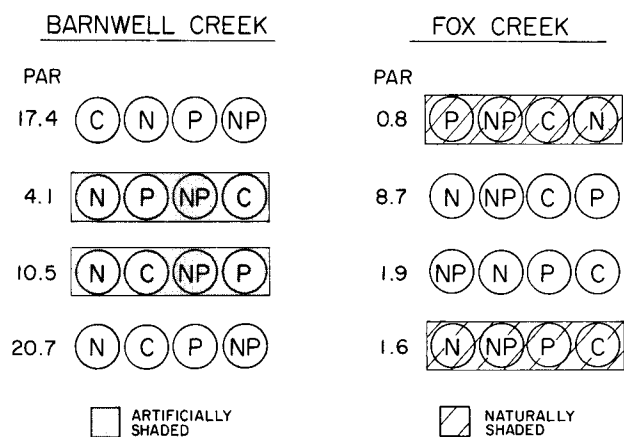


FIG. 1. Experimental layout of substrates in Barnwell Creek and Fox Creek. C = control, P = phosphate, N = nitrate, NP = nitrate + phosphate. PAR = photosynthetically active radiation, $E \cdot m^{-2} \cdot day^{-1}$, measured 16 August 1986.

the middle of California's dry season, discharge was not influenced by rain. Sandstone cobbles provide most of the substrate for attached algae in Barnwell and Fox Creeks. Diatoms dominate epilithic algal assemblages, but colonies of the cyanobacteria *Nostoc* and *Tolypothrix* are common in both streams (Hill 1987).

Experimental design. Nutrient-diffusing substrates similar to those of Fairchild et al. (1985) were used to test the hypothesis that the growth of epilithic algae in the two streams was nutrient limited. Clay saucers (outside diam = 11.6 cm, height = 3.6 cm) were filled with approximately 200 mL of a 2% agar solution made with (a) distilled water (control), (b) 0.1 M KH_2PO_4 , (c) 0.1 M $NaNO_3$, or (d) 0.1 M KH_2PO_4 + 0.1 M $NaNO_3$. The open top of each saucer was cemented with silicon aquarium sealant to an impermeable plexiglass plate, restricting the net movement of phosphate and nitrate ions to diffusion through the clay walls of the saucer. Fairchild et al. (1985) demonstrated that diffusion of nitrate and phosphate ions out of clay pots is a negative logarithm function over time and that fairly large quantities of these ions continue to diffuse after 23 days.

A complete set of substrates containing the four different agar solutions were placed at each of four sites in Barnwell Creek and at each of four sites in Fox Creek on 18 July 1985. All sites were riffle-run sections of the streams. The four substrates at each site were placed immediately adjacent to each other in a line perpendicular to the current. Sites on each stream were separated by approximately 100 m, and were located within 500 m of the mouth of each stream. Two of the four sites at Barnwell Creek were randomly chosen to be shaded with gray nylon screening that reduced light approximately 40%. The other two sites were exposed to ambient sunlight. Two of the four sites at shaded Fox Creek were chosen because they were located under relatively open areas in the tree canopy. The other two sites at Fox Creek were more extensively shaded by the canopy. The combination of light and nutrient conditions resulted in a split-plot design for both streams (Fig. 1).

Algal sampling and analysis. After 31 days, attached algae were sampled from the sloping side of each clay substrate. A neoprene ring (2 cm inside diam) was pressed onto the substrate side and partially filled with water immediately after each substrate was removed from the stream. Attached algae within the ring were dislodged with a stiff brush, and the resulting algal slurry was collected with a syringe. Samples from four locations (90° apart) on the side of each clay substrate were combined into a single sample representing each substrate. This single sample was subdivided volumetrically with a syringe into three equal aliquots. One aliquot was filtered onto a Whatman GFF filter for mea-

TABLE 1. Nutrient concentrations and photosynthetically active radiation (PAR) for Barnwell Creek and Fox Creek.

Stream	Date	N ^a	P ^b	N:P ^c	PAR ^d
Fox Creek	7/17/85	13.59	24.47	1.22	—
	8/21/85	10.22	25.40	0.88	2.5 ± 0.6
Barnwell Creek	7/17/85	11.91	41.81	0.63	—
	8/21/85	0.28	41.81	0.01	8.2 ± 1.8

^a $NO_3-N + NO_2-N + NH_4-N$, $\mu g \cdot L^{-1}$.

^b Soluble reactive phosphorus, $\mu g \cdot L^{-1}$.

^c Molar ratio.

^d $E \cdot m^{-2} \cdot day^{-1}$, $\bar{X} \pm SE$.

surement of ash-free dry matter (AFDM). The filter was dried to constant weight at 60° C, placed in a muffle furnace (500° C) for four hours, and weighed again. AFDM of the aliquot was calculated from the difference in filter weight before and after incineration. The second aliquot was diluted with sufficient 100% acetone to achieve a 90% acetone solution. After extraction for 24 h at 6° C, chlorophyll *a* in the solution was measured fluorometrically by the method of Holm-Hansen et al. (1965). The third aliquot was preserved in Lugol's solution and later filtered onto a Millipore AA membrane filter (pore size = $\sim 0.8 \mu m$). The filter was cleared with immersion oil and mounted on a microscope slide with Permount (Wetzel and Likens 1979). Algal cells containing chloroplasts were identified and counted on the filter at 1000 \times (oil immersion) with a phase contrast microscope. At least two complete transects were scanned, and a minimum of 300 cells was counted on each filter. Algae that could not be identified to the species level were given numerical designations (i.e. "*Navicula* sp. 1"). Algal cell densities (cells per cm^2 of clay substrate surface) were converted to biovolume densities (μm^3 per cm^2 of clay substrate surface) by multiplying the cell density of each taxon by its estimated cell volume. Cell volume for each taxon was estimated by inserting average cell dimensions (measured on at least 20 individuals) into the volume formula which best approximated the shape of the cell.

Grazing insects. Grazing insects that colonized the experimental substrates in Barnwell Creek were identified and counted with an underwater viewer just before the substrates were removed for algal sampling. Grazing insects were not counted on the Fox Creek substrates.

Nutrient analysis. Dissolved nitrogen and phosphorus concentrations were measured in both streams at the beginning and end of the study. Water samples were filtered through combusted Whatman GFF filters at streamside, frozen on dry ice, and stored frozen in a freezer. After thawing, ammonia and reactive phosphorus concentrations in the samples were determined by the methods of Strickland and Parsons (1972). Nitrate in the samples was reduced to nitrite with hydrazine sulfate (Kamphake et al. 1967), and nitrite concentration was then measured following the procedure of Strickland and Parsons (1972). Dissolved nitrogen concentrations were fairly low in both streams, and N:P ratios were less than two (Table 1).

Light measurement. Light was measured at all experimental sites the end of the study (Fig. 1). Synoptic light measurements were made with light meters containing ozalid paper (Friend 1961). Ten sheets of ozalid paper were stapled together and placed in darkened petri dishes which had clear circular apertures approximately one cm in diameter. These dishes were placed on dry rocks immediately adjacent to the stream, and were left exposed to ambient light for 24 or 48 h. An integrated measure of irradiance was obtained by counting the number of paper layers exposed by light. The ozalid paper was calibrated for photosynthetic active radiation (PAR) with a LI-COR quantum sensor.

Light was also measured every 100 m in the lower one km of each stream at the end of the study with ozalid light meters. At

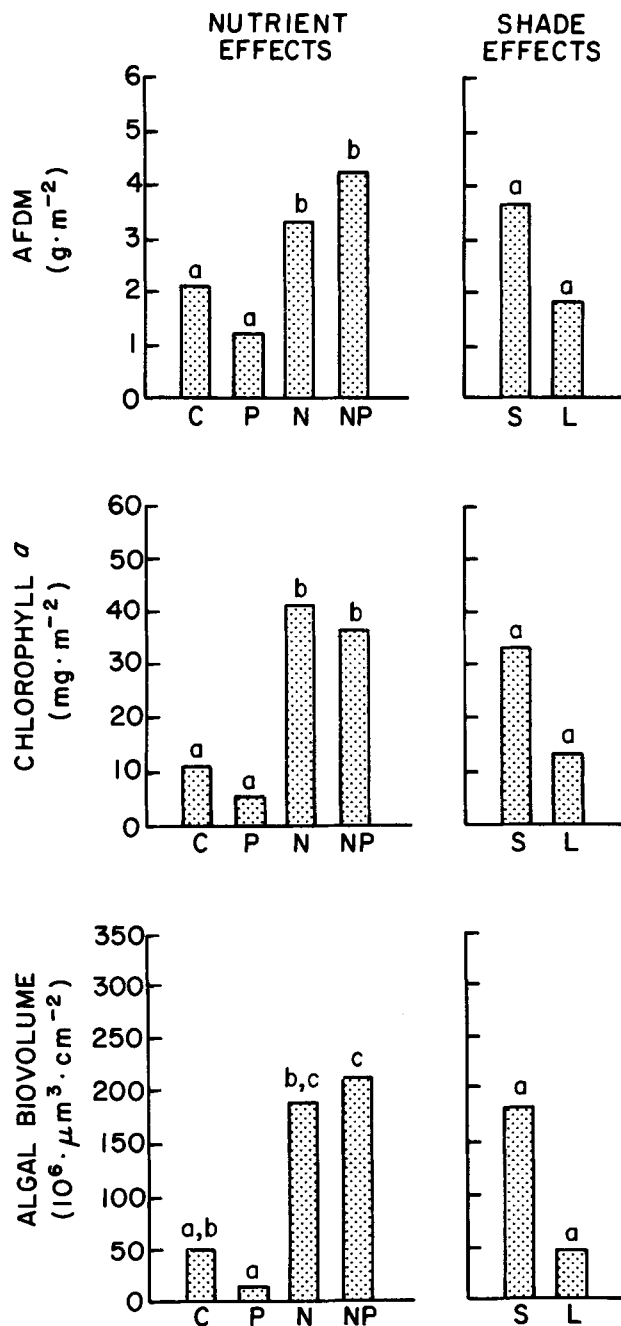


FIG. 2. Biomass of algae on experimental substrates after 31 days in Barnwell Creek. Bars represent mean treatment values. C = control, P = phosphate, N = nitrate, NP = nitrate + phosphate, S = shaded, L = less shaded. Bars with the same superscript letters represent means that are not significantly different (Fisher's protected least significant difference procedure, $P < 0.05$).

the time of measurement, Barnwell Creek received over three times the PAR that Fox Creek received (Table 1). The difference between the streams was statistically significant (Mann-Whitney $t = 12.5$, $P < 0.05$).

RESULTS

Barnwell Creek. Periphyton on the experimental substrates in Barnwell Creek responded significantly

TABLE 2. F values from the split-plot analysis of variance of shade and nutrient effects on algae attached to experimental substrates in Barnwell Creek. Analysis of variance performed on log transformed data.

Factor (df)	AFDM	Chl <i>a</i>	Biovolume
Shade (1,2)	0.495	1.323	0.433
Nutrients (3,6)	17.281**	15.873**	5.168*
Nutrients \times shade (3,6)	1.545	0.640	0.200

* $P < 0.05$.

** $P < 0.01$.

to nitrate enrichment (Fig. 2, Table 2). Periphyton AFDM was 1.5 and 2 times greater on nitrate and nitrate + phosphate substrates than on the control substrates, whereas chlorophyll *a* and algal biovolume, parameters that reflect only the algal component of periphyton, were approximately four times greater on nitrate and nitrate + phosphate substrates. Phosphate enrichment did not increase the algal growth, as no significant difference existed between control and phosphate substrates or between nitrate and nitrate + phosphate substrates. Although shading with nylon screen appeared to increase periphyton growth several-fold, the increase was not statistically significant (Fig. 2, Table 2).

Diatoms dominated the algal assemblages growing on the experimental substrates in Barnwell Creek, comprising more than 98% of total algal biovolume. The 15 most abundant species made up over 90% of both biovolume and numbers and are listed in Table 3. The mean biovolumes of most of these species were greatest on nitrate-diffusing substrates, but large variability between sites resulted in insignificant F values for all but two. Only *Achnanthes lanceolata* and *Cocconeis placentula* responded to nutrient diffusion in a statistically significant fashion. These small diatoms were 17 times (*A. lanceolata*) and 2.5 times (*C. placentula*) more abundant on nitrate and nitrate + phosphate substrates than on the control substrates. Phosphate enrichment did not significantly increase the growth of any algal species. Shading did not produce statistically significant effects on the abundances of individual species on the substrates.

Nitrate enrichment influenced the distribution of grazing insects on the experimental substrates in Barnwell Creek. Three to four times the numbers of caddisfly larvae (*Glossosoma* and *Lepidostoma*) and mayfly nymphs (*Ameletus*, *Cinygma*, and small baetids) were counted on the nitrate and nitrate + phosphate substrates than were counted on control or phosphate substrates at the end of the experiment (Fig. 3). The nitrate enrichment effect on total grazer numbers was statistically significant ($P < 0.05$, Friedman's test).

Fox Creek. Differences in light between sites substantially influenced algal biomass in Fox Creek (Fig. 4, Table 4). Chlorophyll *a* and algal biovolume were three and eight times greater at sites under gaps in the tree canopy. Mean AFDM was also greater at

TABLE 3. Mean biovolumes ($10^6 \cdot \mu\text{m}^3 \cdot \text{cm}^{-2}$) of diatoms on nutrient-diffusing substrates in Barnwell Creek. C = control. P = phosphate. N = nitrate. NP = nitrate + phosphate. Analysis of variance performed on $\log(x + 1)$ transformed data. Means with the same superscript letters are not significantly different as determined by 5% Fisher's least significant differences. Superscript letters only appear for species that had overall statistically significant responses to nutrient treatments (ANOVA $F > 4.757$).

Species	C	P	N	NP	$F_{3,6}$
<i>Achnanthes lanceolata</i> Bréb.	0.72 ^a	0.83 ^a	14.47 ^b	14.00 ^b	10.268***
<i>A. minutissima</i> Kütz.	4.47	3.13	33.81	20.96	0.515
<i>Cocconeis placentula</i> Ehr.	2.09 ^a	2.78 ^a	5.97 ^b	8.21 ^b	7.092*
<i>Diatoma vulgare</i> Bory	3.10	0.39	1.07	2.56	2.523
<i>Epithemia turgida</i> (Ehr.) Kütz.	4.95	0.88	1.82	1.47	0.343
<i>Melosira varians</i> Ag.	14.06	0.58	56.95	85.23	0.805
<i>Navicula cryptocephala</i> Kütz.	0.15	0.08	4.68	6.31	0.507
<i>Navicula</i> sp. 1	0.94	0.63	17.87	15.48	3.919
<i>Nitzschia frustulum</i> var. <i>perpusilla</i> (Rabh.) Grun.	0.31	0.21	2.45	3.82	1.062
<i>N. linearis</i> W. Sm.	1.22	0.08	9.19	16.11	3.348
<i>N. palea</i> (Kütz.) W. Sm.	2.19	0.31	2.56	9.30	2.085
<i>Nitzschia</i> sp. 1	0.48	0.40	8.30	5.48	2.937
<i>Rhoicosphenia curvata</i> (Kütz.) Grun. ex. Rabh.	0.16	0.22	3.70	4.09	0.046
<i>Rhopalodia gibba</i> (Ehr.) O. Mull.	8.19	0.83	1.68	0.75	3.552
<i>Synedra ulna</i> (Nitz.) Ehr.	1.58	0.40	8.19	5.71	0.265

* $P < 0.05$.

*** $P < 0.001$.

better illuminated sites but not in a statistically significant fashion.

In contrast to the stimulatory effect of additional light, nutrient enrichment had little positive effect on biomass accrual. Mean AFDM and algal biovolume were actually greatest on control substrates, and the 32% more chlorophyll *a* on nitrate + phosphate substrates was small compared to the increase in biomass caused by openings in the tree canopy. Substrates that diffused only nitrate or only phosphate accumulated consistently smaller quantities of biomass and were largely responsible for the highly significant *F* value generated by the analysis of variance of algal biovolume.

Only diatoms colonized the substrates in Fox Creek. The 15 most abundant species comprised greater than 90% of both biovolume and numbers. Five of these species (*Gomphonema* sp. 1, *Navicula radiosa*, *Navicula* sp. 1, *Nitzschia palea*, and *Nitzschia frustulum* var. *perpusilla*) were significantly more abundant at the sites with greater light (Table 5). The mean biovolumes of the other 10 species also were larger for the open canopy sites, but because of the extremely low power of the statistical analysis (only 2 degrees of freedom for the shade effects error term), no other *F* values were significant.

Five diatom species displayed statistically significant responses to the nutrient treatments in Fox Creek (Table 6). The responses of four of these diatoms (*Navicula* sp. 1, *Nitzschia palea*, *Nitzschia* sp. 1, and *Epithemia* sp. 1) were characterized by low abundances on nitrate and phosphate substrates. Only the diminutive *Nitzschia frustulum* var. *perpusilla* appeared to increase as a result of nutrient enrichment, responding positively to both nitrate and phosphate.

DISCUSSION

Ratios of nitrogen to phosphorus in Barnwell and Fox Creeks were far lower than any ratios proposed

to delineate the boundary between nitrogen and phosphorus deficiency (Redfield 1958, Thut and Haydu 1971, Rhee and Gotham 1980, Schanz and Juon 1983), indicating considerable potential for nitrogen limitation of algal growth. This potential was realized in Barnwell Creek during the period of our experiment, demonstrated by nitrate-stimulated accumulation of algal biomass. Phosphorus in Barnwell Creek appeared to be more than adequate for algal growth; there was no evidence of even secondary limitation of photosynthesis by phosphorus on nitrate-diffusing substrates.

The failure of nitrate enrichment to stimulate algal growth in Fox Creek implied the presence of another factor limiting primary production in this stream. Micronutrient deficiency or some other unmeasured variable could have constrained photosynthetic rates, but in forested ecosystems such as the Fox Creek watershed, shade from overhanging trees is thought to be the principal factor limiting primary production in small streams (Minshall 1978, Vannote et al. 1980). Light-limited primary production appeared likely in heavily shaded Fox Creek, where variation in canopy cover significantly affected the amount of algal biomass growing on experimental substrates. In several other studies of small streams in forested portions of the northwestern U.S., inherently low nitrogen concentrations appeared to limit algal growth only when light levels were greater than those normally found under a well-developed canopy (Gregory 1980, Triska et al. 1983).

In contrast to the shaded conditions at Fox Creek, light was at least saturating at Barnwell Creek. Mean algal biomass was actually several times greater at artificially shaded sites than at unshaded ones. Although the difference was not statistically significant in the analysis of variance, the greater mean biomass from shaded sites suggested the possibility of photoinhibition. Photoinhibition of photosynthesis is a

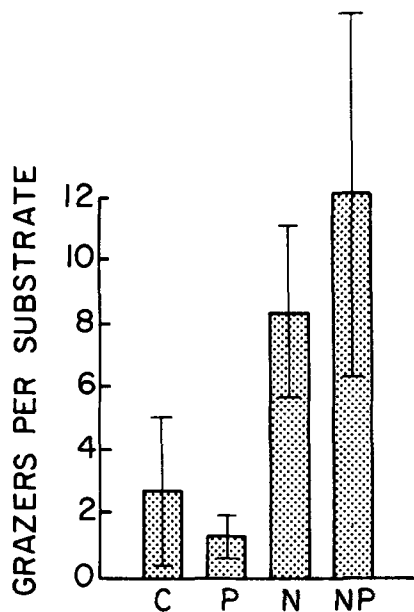


FIG. 3. Numbers of grazing insects on experimental substrates in Barnwell Creek. Bars represent mean treatment values ± 1 SE. C = control, P = phosphate, N = nitrate, NP = nitrate + phosphate.

common phenomenon in the surface waters of lakes and oceans (Goldman and Horne 1983, Kirk 1983), but has not been investigated in streams. Some level of photoinhibition in Barnwell Creek does not seem unlikely, given the relatively large amount of direct sunlight impinging upon this clear-water stream during summer.

The diminished algal biomass on substrates containing only NaNO_3 or K_2HPO_4 in Fox Creek was puzzling. Fairchild et al. (1985) reported the relative inhibition of algal growth on clay substrates containing 0.5 M K_2HPO_4 compared to substrates containing 0.05 M K_2HPO_4 , but the 0.5 M substrates supported many times the algal biomass than did control substrates in their experiment. No inhibitory effect of NaNO_3 has been reported in previous experiments which employed 0.5 M concentrations in clay substrates (Grimm and Fisher 1986, Lowe et al. 1986), and the 0.1 M NaNO_3 used in this study was obviously not inhibitory in Barnwell Creek. More importantly, algal biomass on control substrates was not significantly greater than that on nitrate + phosphate substrates in Fox Creek, arguing against a consistent toxic effect of diffusing K_2HPO_4 or NaNO_3 in this stream. It is possible that the smaller amounts of algal biomass found on substrates containing only nitrate or phosphate resulted from chance variation, although the probability of this type 1 error was low (<1%).

The prostrate growth forms of *Achnanthes lanceolata*, *Cocconeis placentula*, and *Nitzschia frustulum* var. *perpusilla* may predispose these diatoms for nutrient limitation within established periphyton communities. *A. lanceolata*, *C. placentula*, and *N. frustulum* var. *perpusilla* are found close to the base of the substrate

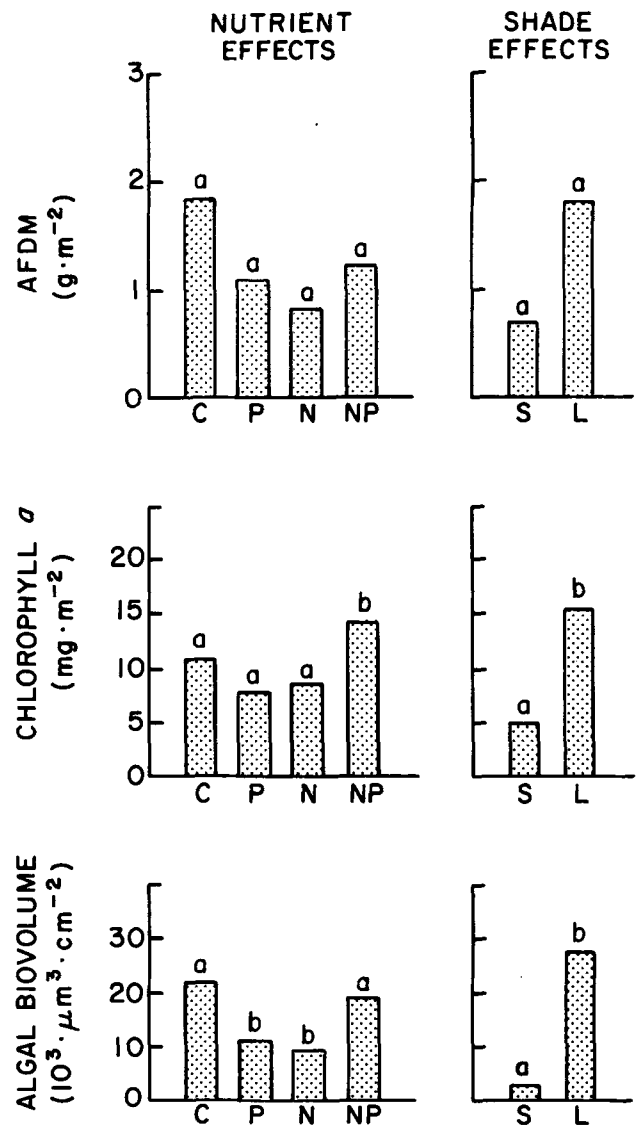


FIG. 4. Biomass of algae on experimental substrates after 31 days in Fox Creek. Bars represent mean treatment values. C = control, P = phosphate, N = nitrate, NP = nitrate + phosphate, S = shaded, L = less shaded. Bars with the same superscript letters represent means that are not significantly different (Fisher's protected least significant difference procedure, $P < 0.05$).

and are often overlain by other algal species (Korte and Blinn 1983, Steinman and McIntire 1986, Hill 1987). Nutrients supplied by stream water must diffuse through overlying species before reaching adnate species and could be substantially depleted through uptake by the overlying species. Diffusion of nutrients from the substrate reverses this process and may elicit stronger responses from adnate species than from overlying species when nutrients limit growth. *Achnanthes* and *Cocconeis* species responded positively to nitrate enrichment in other studies that have employed nutrient-diffusing substrates (Fairchild et al. 1985, Lowe et al. 1986). The tiny diatom *Nitzschia frustulum* var. *perpusilla*, which responded positively to both nitrate and phosphate diffusion

TABLE 4. *F* values from the split-plot analysis of variance of shade and nutrient effects on algae attached to experimental substrates in Fox Creek. Analysis of variance performed on log transformed data.

Factor (df)	AFDM	Chl <i>a</i>	Biovolume
Shade (1,2)	5.027	29.833*	48.974*
Nutrients (3,6)	3.469	9.814**	11.162**
Nutrients × shade (3,6)	1.545	0.640	0.200

* *P* < 0.05.

** *P* < 0.01.

from substrates in Fox Creek, has not previously been reported to be nutrient-limited in streams.

Individual diatom species vary in growth form and specific nutrient requirements, so not all of the 27 species that colonized the clay substrates in Barnwell Creek would be expected to respond equally to nitrogen enrichment. However, it was surprising that only *Achnanthes lanceolata* and *Cocconeis placentula* exhibited statistically significant increases with nitrogen enrichment. These two species together comprised less than 15% of total algal biovolume on nitrate-diffusing substrates, and obviously could not account for the four times greater algal biovolume on these substrates. At least part of the explanation for the inconsistent response of the other 25 diatoms lay in the variability between sites in Barnwell Creek, independent of the shade treatments. *Melosira varians*, for example, represented greater than 35% of the algal biovolume on the nitrate-diffusing substrates at one experimentally shaded site but comprised less than 3% on nitrate-diffusing substrates at the other shaded site. The diatoms available for colonization may have varied greatly from site to site, and the development of particular assemblages at each site may have been strongly dependent on the species available for initial colonization at that site, many of which could have been nitrogen-limited.

TABLE 5. Mean biovolume ($10^6 \mu\text{m}^3 \cdot \text{cm}^{-2}$) of diatoms on substrates at shaded (S) and less shaded (L) sites in Fox Creek. Analysis of variance performed on $\log(x + 1)$ transformed data.

Species	S	L	<i>F</i> _{1,2}
<i>Achnanthes lanceolata</i>	0.75	7.31	8.538
<i>A. minutissima</i>	0.18	3.10	16.282
<i>Cocconeis placentula</i>	0.46	1.46	0.976
<i>Epithemia turgida</i>	0.04	0.11	0.132
<i>Epithemia</i> sp. 1	0.04	0.15	0.085
<i>Gomphonema clevei</i> Fricke	0.06	0.45	0.065
<i>Gomphonema</i> sp. 1	0.03	1.00	153.111***
<i>Navicula radiosa</i> Kütz.	0.06	0.45	0.065
<i>Navicula</i> sp. 1	0.62	3.96	30.648*
<i>Nitzschia frustulum</i> var. <i>perpusilla</i>	0.01	0.27	109.508***
<i>N. linearis</i>	0.26	1.22	11.046
<i>N. palea</i>	0.22	3.81	28.843**
<i>Nitzschia</i> sp. 1	0.03	1.04	10.549
<i>Rhoicosphenia curvata</i>	0.22	1.46	3.541
<i>Synedra ulna</i>	0.07	0.86	0.279

* *P* < 0.05.

** *P* < 0.01.

*** *P* < 0.001.

TABLE 6. Mean biovolumes ($10^6 \mu\text{m}^3 \cdot \text{cm}^{-2}$) of diatoms on nutrient-diffusing substrates in Fox Creek. Abbreviations and statistical analysis are the same as for Table 3.

Species	C	P	N	NP	<i>F</i> _{5,6}
<i>Achnanthes lanceolata</i>	3.66	3.54	3.40	5.52	4.128
<i>A. minutissima</i>	3.03	1.08	0.88	1.57	0.448
<i>Cocconeis placentula</i>	0.34	0.44	1.99	1.06	1.543
<i>Epithemia turgida</i>	0.12	0.07	0.06	0.06	0.268
<i>Epithemia</i> sp. 1	0.19 ^a	0.01 ^b	0.08 ^a	0.11 ^a	13.041**
<i>Gomphonema clevei</i>	0.07	0.26	0.22	0.34	2.066
<i>Gomphonema</i> sp. 1	0.82	0.02	0.34	0.89	0.903
<i>Navicula radiosa</i>	0.59	0.60	0.09	0.23	0.765
<i>Navicula</i> sp. 1	3.23 ^{ac}	1.81 ^a	0.51 ^b	3.62 ^c	17.819**
<i>Nitzschia frustulum</i> var. <i>perpusilla</i>	0.07 ^a	0.18 ^b	0.13 ^b	0.19 ^b	36.856***
<i>N. linearis</i>	0.88	0.60	0.31	1.18	0.966
<i>N. palea</i>	5.42 ^a	0.97 ^b	0.46 ^b	1.20 ^b	7.252*
<i>Nitzschia</i> sp. 1	0.69 ^a	0.36 ^{ab}	0.20 ^b	0.90 ^a	6.131*
<i>Rhoicosphenia curvata</i>	0.74	0.73	0.65	1.25	2.122
<i>Synedra ulna</i>	0.78	0.33	0.06	0.69	0.622

* *P* < 0.05.

** *P* < 0.01.

*** *P* < 0.001.

In spite of the widely accepted generalization that light limits algal growth in many flowing-water ecosystems, only a few experiments have been published which explored the effect of light on benthic diatom assemblage structure. Hudon and Bourget (1983) found that a number of *Navicula* and *Nitzschia* species were more abundant at depths which received more light in the St. Lawrence River, and Lowe et al. (1986) observed greater quantities of *Navicula*, *Nitzschia*, and *Gomphonema* species in an unshaded stream than in a shaded one. Assemblages on substrates located at less shaded sites in Fox Creek were also significantly richer in several *Navicula* and *Nitzschia* species, as well as an unidentified *Gomphonema* species. These diatoms may have inherently higher requirements for light, and their increased abundance could be a direct result of light enrichment. Conversely, the abundances of some of the diatoms may have been mediated by interactions with the rest of the periphyton community. Many *Navicula* and *Nitzschia* species are positively associated with organic or fine-particled substrates (Belanger et al. 1985), and some of those in Fox Creek may have responded directly to the greater substrate conditioning caused by the increased overall growth of the periphyton at less shaded sites.

The design of the experiments provided relatively little statistical power to detect treatment effects. Shade treatments were replicated only twice in each stream, causing the appropriate error term in the split-plot analysis of variance to have only 2 degrees of freedom. The critical *F* value for shade effects at the *P* < 0.05 level was 18.51, a value difficult to obtain in field experiments. It is noteworthy that shade effects were strong enough in Fox Creek to achieve statistical significance in the analyses of chlorophyll *a* and algal biovolume, despite the minimal

replication. Greater replication of shade treatments probably would have resulted in a greater number of significant *F* values in the analysis of shade effects on the densities of individual Fox Creek diatom species, five of which had *F* values exceeding 3.50 (Table 5). Greater replication would have also increased the power of the statistical analysis to detect nutrient treatment effects on the densities of individual species, although the 6 degrees of freedom associated with the appropriate error term allowed for a critical *F* value at the *P* < 0.05 level of 4.76, a value considerably easier to achieve than the 18.51 value for shade treatment effects. Nonetheless, greater replication of nutrient treatments at each site in Barnwell Creek probably would have increased the number of individual species with responses to nitrate enrichment that were statistically significant.

Physical-chemical limitation of primary production probably affects higher trophic levels as well. Epilithic algae are heavily grazed by aquatic insects in Barnwell Creek, and the growth of at least two of the important grazers (the mayfly *Ameletus* and the caddisfly *Neophylax*) appears limited by insufficient food (Hill 1987, Hill and Knight 1987). Although the clay substrates used in this study may not provide a representative surface to observe natural grazer-algae interactions, the fact that 3–4 times more grazing insects were found on substrates diffusing nitrate was consistent with the hypothesis that grazer populations were indirectly limited by low nitrogen concentrations. Grazers were not counted on the substrates in Fox Creek, so it is unknown if sites experiencing greater light supported more primary consumers than did more shaded sites. However, natural densities of caddisfly larvae (*Glossosoma* and *Neophylax*) significantly deplete periphyton biomass in Fox Creek (Hill, unpubl. data), suggesting the possibility of competition and food-limitation at this trophic level.

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WATER COLUMN PRODUCTIVITY ATTRIBUTABLE TO DISPLACED BENTHIC DIATOMS IN WELL-MIXED SHALLOW ESTUARIES¹

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ABSTRACT

We attempted to determine the extent to which benthic diatoms contribute to water column primary productivity in shallow-water estuaries and to elucidate the primary mechanisms responsible for suspending the diatoms. A preliminary study conducted in Mugu Lagoon, California indicated that productivity of ocean water entering the lagoon during flood tides was often several orders of magnitude less than that of the same water mass about 3 h later. Benthic pennate diatoms displaced from the sediments into the water column accounted for the increase. A more detailed study was conducted in Barataria Estuary, Louisiana where, for one month, daily measurements were made of benthic and water column productivity and several other environmental variables. During the month, the relationship between water column and benthic primary productivity varied from strongly negative to weakly negative to positive. K-systems analysis indicated that factors comprised of wave height, meteorological tides, astronomical tides, and benthic productivity and standing crop accounted for the full range of variation in water column productivity. Benthic pennate diatoms represented an average of 74% of the diatom taxa in water column samples. We conclude that the primary productivity of well-mixed shallow estuarine waters is often greatly augmented by displaced benthic algae.

Key index words: Barataria Estuary; benthic diatoms; chlorophyll *a*; discriminant analysis; K-systems analysis; Mugu Lagoon; phytoplankton; primary productivity; suspended algal cells; tidal currents

Entrainment of benthic diatoms into the water column of shallow estuarine systems is well documented (Williams 1962, Pamatmat 1968, Cadée and Hegeman 1974, Holland et al. 1974, Gallagher 1975, Karentz and McIntire 1977, Roman and Tenore 1978, Baillie and Welsh 1980, Colijn and Dijkema 1981, Davis and McIntire 1983, Varela and Penas 1985). The main mechanisms responsible for suspending benthic algae differ. For intertidal flats heavy rainfall during periods of subaerial exposure has been noted (Williams 1962, Colijn and Dijkema 1981). For areas covered by shallow water, waves generated by strong winds may disrupt the coherent sediment layer normally stabilized by a film of microflora (Pamatmat 1968, Cadée and Hegeman 1974, Holland et al. 1974, Colijn and Dijkema 1981). Other investigators (Gallagher 1975, Baillie and Welsh 1980, Davis and McIntire 1983, Shaffer and Cahoon 1987) found tidal currents to be the primary mechanism for suspending benthic microflora. In addition, displacement of benthic microflora can occur when supersaturation bubbles (caused by high productivity) increase the buoyancy of the benthic microfloral mats (Phifer 1929).

Despite the large number of studies documenting the entrainment of benthic algae into estuarine waters, it appears that only two attempts (Baillie and Welsh 1980, Lukatelich and McComb 1986) were made to determine the quantitative importance of this phenomenon. These studies found that chlorophyll content and number of benthic diatoms in the water column of shallow estuaries were related to tidal currents (Baillie and Welsh 1980) and wind-induced currents (Lukatelich and McComb 1986).

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