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Source: *Journal of the North American Benthological Society*, Vol. 5, No. 3 (Sep., 1986), pp. 221-229

Published by: The University of Chicago Press on behalf of the Society for Freshwater Science

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Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds

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Abstract. Nutrient-releasing artificial substrata were deployed in streams draining clearcut and forested watersheds to evaluate resources potentially limiting to populations of benthic algae. Nitrogen, phosphorus, and calcium were released singly and in combination in the two streams that differed primarily in light availability. Periphyton were harvested after one- and two-month exposure periods and analyzed for chlorophyll. The two-month substrata were additionally analyzed for algal community structure. Algal periphyton in the clearcut stream accumulated more chlorophyll and biovolume than in the forested stream across all nutrient treatments. Algal community structure was significantly different between streams but not between nutrient treatments. Algal physiognomies were also significantly different between streams with filamentous green algae dominating the clearcut stream and erect diatoms dominating the forested stream. Light appears to limit algal accumulation in the forested stream and there is evidence that some populations in the clearcut stream may be nutrient limited. Adequate light also resulted in a more architecturally diverse community.

Key words: *periphyton, algae, benthos, nutrients, micro-architecture, streams, productivity.*

In low order streams of forested watersheds most energy that enters the system is allochthonous, derived from surrounding terrestrial vegetation (e.g., Vannote et al. 1980). The primary producers in such systems are largely benthic algae whose productivity appears to be light limited (Gregory 1980, Keithan and Lowe 1985, Sumner and Fisher 1979, Whitton 1975). In investigations where light is made available to such streams, often through clearcutting, increases in algal biomass and changes in community structure have been reported (Hansmann and Phinney 1973, Murphy and Hall 1981, Webster et al. 1983). The cause of this shift in the algal community is difficult to identify, however, because of the multitude of parameters that co-vary with increased light following clearcutting, such as significant shifts in water chemistry and in water temperature. For example, Shortreed and Stockner (1983) found that increased light intensities following watershed logging led to a shift in algal community structure, but because of phosphorus limitation increase in algal biomass was not consistently significant.

The objectives of this study were to examine effects of specific nutrient additions on the accumulation and structure of the benthic algae community in streams draining a clearcut and a forested watershed in the southern Appalachian Mountains. Specifically, we wanted to answer the questions: 1. Does light limit algal accumulation in the forested stream system? 2. Are some populations of algae shade-adapted and limited by nutrients rather than by light? 3. What factors limit algal accumulation in the stream in the clearcut watershed? 4. Are certain algal morphologies or physiognomic forms favored in specific light and nutrient regimes?

Methods

Study site

This study was conducted at Coweeta Hydrologic Laboratory, Macon Co., North Carolina, located in the Nantahala Mountains, in the Blue Ridge Province of the southern Appalachian Mountains. The 2185-ha laboratory is operated by the U.S.D.A. Forest Service.

Two streams were selected for study. Big

Hurricane Branch drains watershed 7 (WS 7), a 58.7-ha experimental watershed which was grazed lightly by cattle from 1941 to 1952 and cable logged during the winter of 1976-1977. Regrowth is dominated by hardwood sprouts, herbs, vines, and seedlings. Big Hurricane Branch is a second-order stream, has a southern aspect, and is not heavily shaded by the regrowing terrestrial vegetation. Many stream sections receive full sun. Natural stream substrata vary from sections of steep exposed bedrock to short reaches of low-gradient sand and gravel with infrequent small pools containing sediment. Dissolved nutrient levels in Big Hurricane Branch prior to logging were low (nitrate-N = 2 $\mu\text{g/L}$, ammonium-N = 4 $\mu\text{g/L}$, phosphate-P = 2 $\mu\text{g/L}$, calcium = 0.85 mg/L) (Swank and Douglas 1977). Small increases in dissolved N and Ca followed logging but present concentrations are near pre-logging levels (Webster et al. 1983). Mean discharge based on 26 years of records before logging was 17.7 L/s. While water temperatures in Big Hurricane Branch were initially elevated by clearcutting (Swift 1983), temperature differences between Big Hurricane Branch and the reference stream were slight at the time of this study. Hugh White Creek drains watershed 14 (WS 14), a 61.1-ha reference watershed. WS 14 was selectively logged sometime before 1930 and, except for the chestnut blight, has been undisturbed for 60 years. The vegetation on WS 14 is oak hickory forest with extensive undergrowth of *Rhododendron*, especially near the stream. Hugh White Creek is a second-order stream, has a northwestern aspect and is heavily shaded. Incident light on Hugh White Creek is approximately 1% that of Big Hurricane Branch. The stream substrata are similar to those of Big Hurricane Branch. Dissolved nutrient levels in Hugh White Creek are low (nitrate-N = 4 $\mu\text{g/L}$, ammonium-N = 4 $\mu\text{g/L}$, phosphate-P = 2 $\mu\text{g/L}$, calcium = 0.46 mg/L) (Webster et al. 1983). Mean discharge is 19.5 L/s, based on 40 years of records. Further characteristics of these streams were reported by Swank and Douglas (1977).

Nutrient releasing substrata were constructed from clay flower pots with outer diameter 8.8 cm, height 8.0 cm, and internal volume approximately 250 ml when sealed using a plastic petri dish and silicon adhesive (Fairchild and Lowe 1984). Pots were filled with 250 ml of 2%

agar solution containing 0.5-M concentrations of three nutrients, calcium as CaCl_2 , phosphate as KH_2PO_4 , and nitrate as NaNO_3 , in eight combinations (Ca+N+P, Ca+P, Ca alone, Ca+N, N alone, P+N, P alone, no nutrients). In addition, NaCl and KCl were added when necessary to standardize Na and K concentrations at 0.5 M in all nutrient combinations. To complete the substrata a 000 Neoprene® stopper sealed the small aperture of each pot.

On 20 April 1983, six replicates of each treatment were deployed in each stream in shallow riffles 30-40 m upstream from the gauging stations. Substrata were glued to metal bars in groups of three with 5 cm between pots. A linear arrangement of substrata was devised such that an upstream substratum would not leach nutrients toward a substratum immediately downstream that did not already have a supply of those nutrients in question. For example, a typical arrangement in a series of three substrata might be N, N+P, N+P+Ca. The metal bars, each bearing three pots, were arranged linearly in each stream approximately 1 m apart and anchored with galvanized gutter nails.

Substrata were collected after one and two months of exposure and gently cleaned with a toothbrush and squirt bottle. The resulting suspension was brought to a constant volume of either 150 or 200 ml. A 5-ml subsample was preserved in 0.5% formalin solution for later algal cell enumeration. MgCO_3 was added to the remaining suspension, which was filtered (Gelman A/E glass fiber filter) and frozen. Samples were spectrophotometrically analyzed for chlorophylls *a*, *b*, and phaeophytin (APHA 1980).

A portion of each 5-ml subsample from the 2-mo exposure substrata was analyzed for algal density and community structure using a Palmer-Maloney nannoplankton counting chamber and a Bausch and Lomb research microscope. The volume of subsample analyzed varied depending on cell densities. The community was analyzed at 400 \times magnification. When required, specific identifications of non-diatom algae were made with 1000 \times magnification of wet mounts. Certain diatom taxa required acid cleaning and mounting in Hyrax® for species identification. Species densities were calculated using the following formula:

$$\text{cells/cm}^2 \text{ of species } x = n(V/v)S^{-1}$$

TABLE 1. Photosynthetic pigment concentrations on flower pots in Coweeta streams. Pots were placed in the stream on 20 April 1983. Values are means \pm 95% CI.

Site	Date	Chlorophyll <i>a</i> (mg/pot)	Chlorophyll <i>b</i> (mg/pot)	Phaeophytin (mg/pot)	<i>n</i>
Big Hurricane	21 May 1983	0.022 \pm 0.005	0.007 \pm 0.003	0.011 \pm 0.004	24
	17 June 1983	0.052 \pm 0.009	0.044 \pm 0.014	0.009 \pm 0.005	18
Hugh White	21 May 1983	0.003 \pm 0.001	0.002 \pm 0.001	0.007 \pm 0.002	24
	17 June 1983	0.004 \pm 0.002	0.001 \pm 0.001	0.003 \pm 0.002	13

where n = number of cells of species x counted in volume v , V = the total sample volume and S = the surface area of the substratum = 138 cm². Density data were converted to species biovolume/cm² by measuring five random cells of each species, determining the biovolume/cell and multiplying cells/cm² \times biovolume/cell. Biovolume data were log transformed and subjected to a 2-way analysis of variance using a conventional statistical package (SAS 1985). Student-Newman-Keuls multiple range tests were used to evaluate factors of significant variation (Zar 1974). Finally, samples were pooled within watersheds and tested (t -test) for differences in distribution of species and algal physiognomies between watersheds.

Results

Twenty-three of the 96 substrata placed into the two streams were lost in a storm before the

2-mo pick up, however; at least one and in many instances two or three replicates were collected for each treatment.

Pigment concentrations did not differ significantly between the various nutrient combinations in the clearcut or reference stream by analysis of variance. Therefore, pigment data were pooled within each watershed. Chlorophylls *a* and *b* were substantially greater in the clearcut stream than in the reference stream (Table 1), and there was relatively little phaeophytin. The trends observed in pigment data were also found in the biovolume data (Fig. 1). Although differences among nutrient treatments were not significant in either watershed (analysis of variance, $\alpha=0.05$), a trend toward increased algal biovolume with nutrient addition was observed in the clearcut stream. No trends of algal response to nutrient addition were evident in the reference stream. In fact,

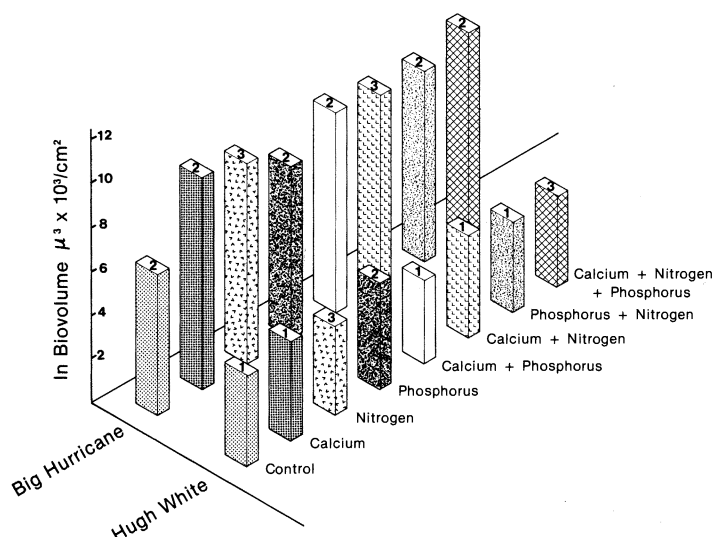


FIG. 1. Periphyton biovolume on substrata in Big Hurricane Branch (clearcut) and Hugh White Creek (reference) following two months of exposure. The number of replicates in each treatment is shown on the top of each bar.

TABLE 2. Distribution of Coweeta periphyton by watershed following two months of substrata exposure. Significant differences in distribution of species biovolume (*t*-test, $\alpha=0.05$).

Significantly More Abundant in Big Hurricane Branch (clearcut stream)	Significantly More Abundant in Hugh White Creek (reference stream)	No Significant Difference in Distribution
BACILLARIOPHYTA	BACILLARIOPHYTA	BACILLARIOPHYTA
<i>Achnanthes lanceolata</i> Bréb.*	<i>Achnanthes detha</i> Hohn & Hellerman*	<i>Achnanthes deflexa</i> v. <i>alpestris</i> Lowe & Kociol.
<i>A. minutissima</i> Kütz.	<i>Eunotia exigua</i> (Bréb.) Grun.*	<i>A. lanceolata</i> v. <i>atibia</i> Grun
<i>Cymbella minuta</i> Hilse ex Rabh.*	<i>E. rhomboides</i> Hust.*	<i>A. stewartii</i> Patr.
<i>Diatoma hiemale</i> v. <i>mesodon</i> (Ehr.) Grun.*	<i>Meridion circulare</i> Ag.*	<i>A. subrostrata</i> v. <i>appalachiana</i> Camburn & Lowe
<i>Eunotia curvata</i> (Kütz.) Lagerst.*	<i>Navicula contenta</i> Grun.*	<i>Coconeis placentula</i> Ehr.
<i>Fragilaria vaucheriae</i> (Kütz.) Peters.	<i>Tetracyclus repestris</i> (A. Br.) Grun.*	<i>Cymbella</i> sp.
<i>Frustulia rhomboides</i> v. <i>amphipleuroides</i> Grun.*		<i>Eunotia pectinalis</i> v. <i>minor</i> (Kütz.) Rabh.
<i>Gomphonema gibba</i> J. Wallace		<i>E. sp.</i>
<i>G. parvulum</i> Kütz.		<i>Frustulia rhomboides</i> (Ehr.) de Toni
<i>Navicula mutica</i> v. <i>tropica</i> f. <i>rostrata</i> Krasske*		<i>Gomphonema dichotomum</i> Kütz.
<i>N. radiosa</i> v. <i>tenella</i> (Bréb.) Grun.*		<i>Navicula angusta</i> Grun.
<i>Nitzschia parvula</i> Lewis*		<i>N. cryptocephala</i> Kütz.
<i>Synedra socia</i> Wallace		<i>N. hassiaca</i> Krasske
<i>S. ulna</i> (Nitzsch.) Ehr.		<i>N. minima</i> Grun.
CHLOROPHYTA		<i>N. placenta</i> Ehr.
<i>Spirogyra</i> sp.*		<i>Navicula</i> sp.
<i>Mougeotia</i> sp.*		<i>Neidium</i> sp.
		<i>Nitzschia</i> sp.
		<i>Pinnularia</i> sp.
		<i>Synedra ulna</i> v. <i>ramsei</i> (Herib.) Hust.
		CHLOROPHYTA
		<i>Cosmarium</i> sp.
		<i>Scenedesmus</i> sp.
		<i>Stigeoclonium</i> sp.
		CYANOPHYTA
		<i>Oscillatoria</i> sp.
		<i>Schizothrix calcicola</i> (Ag.) Gom.

* Occurs exclusively in this watershed.

TABLE 3. Biovolume ($10^3 \mu\text{m}^3 \text{mm}^{-2}$) and relative abundance by biovolume (in parentheses) of the 11 most common algal taxa from enrichment experiments.

	Control	Ca	N	P	Ca+P	Ca+N	N+P	Ca+N+P
				BIG HURRICANE BRANCH (clearcut)				
<i>Achnanthes lanceolata</i>	0.4 (6.6%)	0 (0%)	4.9 (5.4%)	1.4 (5.4%)	11.0 (11.9%)	1.2 (1.9%)	24.9 (43.8%)	6.1 (5.5%)
<i>Achnanthes minutissima</i>	0.8 (13.1%)	0 (0%)	10.2 (11.3%)	0.2 (0.8%)	5.0 (5.4%)	13.3 (21.1%)	0.8 (1.4%)	13.0 (11.7%)
<i>Fragilaria vaucheriae</i>	0.9 (14.8%)	7.7 (9.0%)	10.4 (11.6%)	1.7 (6.6%)	3.7 (4.0%)	10.4 (16.6%)	12.8 (22.5%)	4.6 (4.1%)
<i>Gomphonema parvulum</i>	1.0 (16.4%)	2.8 (3.3%)	11.8 (13.1%)	0.2 (0.8%)	3.5 (3.8%)	0.5 (0.8%)	1.3 (2.3%)	4.7 (4.2%)
<i>Navicula mutica</i> v. <i>tropica</i> f. <i>rostrata</i>	0.4 (6.6%)	0 (0%)	8.2 (9.1%)	0.6 (2.3%)	6.3 (6.8%)	9.2 (14.6%)	3.7 (6.5%)	0 (0%)
<i>Synedra socia</i>	0.3 (4.9%)	8.9 (10.4%)	1.1 (1.2%)	1.3 (5.0%)	11.0 (11.9%)	8.9 (14.1%)	2.2 (3.9%)	15.6 (14.1%)
<i>Synedra ulna</i>	0 (0%)	8.5 (10.0%)	0.2 (0.2%)	3.1 (12.0%)	6.0 (6.5%)	1.9 (3.0%)	3.2 (5.6%)	9.6 (8.6%)
<i>Synedra ulna</i> v. <i>ramisei</i>	0 (0%)	0.1 (0.1%)	2.8 (3.1%)	0 (0%)	4.5 (4.9%)	0 (0%)	0 (0%)	2.3 (2.1%)
<i>Spirogyra</i> sp.	1.0 (16.4%)	47.3 (55.5%)	0.5 (0.6%)	11.9 (45.9%)	33.5 (36.3%)	3.8 (6.0%)	0.5 (0.9%)	49.9 (45.0%)
				HUGH WHITE CREEK (reference)				
<i>Achnanthes lanceolata</i>	0 (0%)	0 (0%)	0 (0%)	0.01 (0.8%)	0 (0%)	0 (0%)	0.01 (1.7%)	0 (0%)
<i>Achnanthes minutissima</i>	0.01 (1.6%)	0.05 (5.6%)	0.01 (1.8%)	0 (0%)	0 (0%)	0.03 (2.7%)	0 (0%)	0 (0%)
<i>Eunotia rhomboidea</i>	0.03 (5.0%)	0.12 (13.4%)	0.03 (5.5%)	0.28 (23.1%)	0.09 (19.4%)	0 (0%)	0.03 (5.1%)	0 (0%)
<i>Fragilaria vaucheriae</i>	0 (0%)	0.14 (15.6%)	0.19 (35.5%)	0.21 (17.6%)	0.18 (38.8%)	0.09 (8.2%)	0 (0%)	0.02 (11.0%)
<i>Gomphonema parvulum</i>	0 (0%)	0.20 (22.3%)	0 (0%)	0.26 (21.5%)	0 (0%)	0.20 (18.3%)	0.07 (11.9%)	0.04 (22.1%)
<i>Meridion circulare</i>	0.15 (24.5%)	0.15 (16.8%)	0.22 (41.1%)	0.42 (34.7%)	0.19 (40.9%)	0.19 (17.4%)	0.10 (17%)	0.08 (44.2%)
<i>Synedra socia</i>	0 (0%)	0.06 (6.7%)	0.04 (7.4%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
<i>Synedra ulna</i>	0 (0%)	0.14 (15.6%)	0 (0%)	0.28 (23.1%)	0 (0%)	0.41 (37.4%)	0.14 (23.8%)	0 (0%)

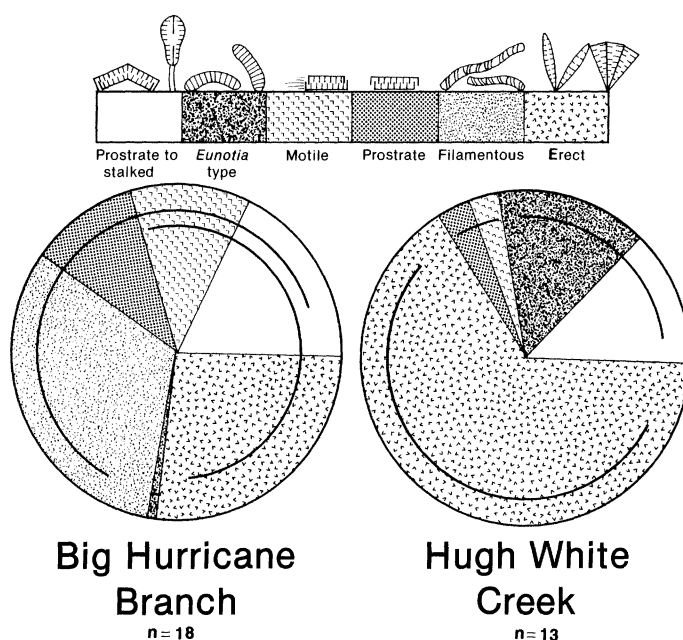


FIG. 2. Relative distribution of algal physiognomies in pooled samples from Big Hurricane Branch (clear-cut) and Hugh White Creek (reference). Lines connecting "pie" sections indicate physiognomies that are not significantly different from each other (t -test, $\alpha=0.05$).

the substrata with all three nutrients added had the least algal biovolume. As with chlorophyll, the clearcut stream supported significantly more biovolume than the reference stream across all nutrient treatments (Fig. 1).

A total of 47 algal taxa, all but seven of which were diatoms, were observed in community analyses of the two streams. The t -tests performed on log-transformed biovolume data using nutrient treatments as replicates revealed several taxa whose distributions varied significantly with respect to watershed (Table 2). Sixteen algal taxa were significantly more abundant in the clearcut stream. Ten of these taxa were collected exclusively from this watershed including *Spirogyra* sp. which was the most abundant alga in the clearcut stream and accounted for more than 40% of the total biovolume in several samples. *Spirogyra* responded most positively to calcium and phosphorus, either alone or in combination (Table 3).

Two species of *Achnanthes*, *A. lanceolata* and *A. minutissima* were significantly more abundant in the clearcut stream and contributed a substantial portion to the biovolume of several of the nutrient treatments. The greatest occurrence of *A. lanceolata* was in the N+P treatment

where the biovolume averaged $24.9 \times 10^3 \mu\text{m}^3/\text{mm}^2$ and represented 44% of the community biovolume. *Fragilaria vaucheriae*, *Gomphonema parvulum*, *Synedra ulna*, and *S. socia* were also abundant in the clearcut stream (exceeding $9 \times 10^3 \mu\text{m}^3/\text{mm}^2$ in at least one treatment).

Six diatom taxa occurred exclusively in the reference stream in spite of the overwhelming preponderance of total algal biomass in the clearcut stream. These taxa were *Achnanthes detha*, *Eunotia exigua*, *E. rhomboidea*, *Meridion circulare*, *Navicula contenta* and *Tetracyclus rupestris* (Table 2). Only *M. circulare* and *E. rhomboidea* contributed a significant portion of the biovolume in this watershed.

The distribution of algal biovolume based on physiognomic form was analyzed, assigning each algal taxon to a group based on how it is associated with the substratum. Designated physiognomic groups were erect, filamentous, prostrate, prostrate to stalked, motile, and *Eunotia* type (attaching by 1 or both ends). The two watersheds displayed relatively large differences with respect to which form was most prevalent (Fig. 2). In the reference stream most algal biovolume was in the form of erect cells with *Meridion circulare*, *Fragilaria vaucheriae*, and

Synedra ulna forming the bulk of this group. The next most abundant forms were *Eunotia* type and prostrate to stalked. The former form included all species of *Eunotia* and the latter those taxa that may be either prostrate or form a stalk (*Achnanthes minutissima* and *Gomphonema parvulum*). The least abundant forms were prostrate and motile. Prostrate forms include all species of non-stalk-forming monoraphid diatoms and motile forms include all species of non-stalk-forming biraphid diatoms. The filamentous physiognomic form was absent from the reference stream.

In Big Hurricane Branch filamentous forms were most abundant (Fig. 2); however, the data set is highly skewed with a large biovolume of filamentous forms in some samples and none in others. Once the data were log transformed to reduce skewing, the most important forms in the clearcut stream were erect, prostrate to stalked, and motile. The *Eunotia* type form was almost absent from this watershed.

Discussion

Benthic algal accumulation did not respond significantly to nutrient addition in either stream, although a trend toward increased algal biomass with nutrient addition in the clearcut stream suggested that light may not be limiting in this stream. Both independent measures of algal accumulation, chlorophyll and biovolume, were significantly lower in the reference stream than in the clearcut stream across all nutrient treatments. We interpret this as strong evidence that light is limiting to algal accumulation in the forested watershed. Furthermore, trends in total biovolumes with nutrient addition were not apparent in the reference stream. In fact, little difference was seen between the control and the seven nutrient treatments (Fig. 1). Lack of response to nutrient addition again suggests that algal accumulation is controlled by some other factor in this stream. We feel that light is that factor although unmeasured covariates cannot be ruled out. Light limitation of photoautotrophs in forested second-order streams is a widely accepted phenomenon. A similar increase in periphyton biomass following logging was reported by Lyford and Gregory (1975) and Murphy and Hall (1981) in Oregon who attributed periphyton increase to increased light availability. Experi-

ments in Carnation Creek on Vancouver Island (Shortreed and Stockner 1983, Stockner and Shortreed 1978) showed that phosphorus was limiting to periphyton accumulation when light availability was above a threshold level of 50–60 g-cal cm⁻² day⁻¹. These stream experiments provided convincing evidence for limitation by either light or phosphorus depending on stream site and climate-controlled solar radiation. Phosphorus limitation has also been reported for a tundra stream (Peterson et al. 1983) and a forested stream in northern Michigan (Pringle and Bowers 1984).

It has been the custom in aquatic biology to try to elucidate the factors that limit the productivity of entire communities such as the phytoplankton, or in this case, the periphyton. Such an approach is often misleading unless it is coupled with a close scrutiny of population level responses within the community. The benthic algal communities in this study, for example, included up to 47 taxa from three different algal divisions. One should expect a differential response among species to sets of environmental parameters and not a uniform response of the community to the addition of a single limiting resource. In the clearcut stream it is probable that increased light availability and perhaps other covariates had a significant positive effect on 16 algal taxa, nine of which were observed exclusively from this stream. Filamentous green algae, particularly *Spirogyra*, were the predominant algae in the clearcut stream. The response of green filamentous species of the Zygnemataceae to clearcutting has been reported previously (Hansmann and Phinney 1973, Shortreed and Stockner 1983). The requirement of higher light levels for *Spirogyra* and *Mougeotia* may in part be due to their lack of pigment diversity relative to the diatoms which are much richer in carotenoid pigments (Jorgenson 1977, Round 1965). The preponderance of green filaments in the clearcut stream, however, might belie their significance to energy flow in the aquatic food web. Patrick (1977) has shown diatoms to be a preferred food item of invertebrates in mixed algal communities, thus turnover rates of the Zygnemataceae might be much lower than those of diatoms. The 14 diatom taxa that occurred exclusively or significantly in the clearcut stream are more typical of midwestern rivers and streams than mountain streams (Lowe 1974,

Patrick and Reimer 1966, 1975). Hansmann and Phinney (1973) reported a negative response of *A. lanceolata* to clearcutting, however, it is difficult to compare our data with theirs as they reported relative abundance based on cell numbers. Unlike the two *Achnanthes* species, *Fragilaria vaucheria*, *Gomphonema parvulum*, and *Synedra ulna* were important components of the reference stream but maintained significantly higher standing crops in the clearcut stream. Although these taxa are common components of densely shaded streams they are apparently light limited and respond positively to canopy removal.

Six diatom species were found exclusively in the reference stream. All of these taxa appear to be either shade adapted or intolerant of increased light levels. *Meridion circulare*, for example, maintains large populations only in cool streams (Besch et al. 1972, Patrick 1971, Wuthrich 1975). It is interesting to note that this diatom grows abundantly in full sunlight in an Ohio stream but only at temperatures of from 7 to 10°C (Krejci and Lowe, in press). Little is known of the physiological ecology of the other five diatom taxa except that they are encountered primarily in lower order undisturbed forested streams of the Appalachian Mountains (Camburn et al. 1978, Kocielek 1982, Lowe and Kocielek 1984). Controlled experiments are required to determine whether their absence in the clearcut stream was due to increased light or some other factor.

The analysis of algal communities based on physiognomic form revealed some significant differences between the streams. In the reference stream most of the algal biovolume was in the erect form, attached at one end. This may be adaptive in poorly lighted habitats. An erect pennate diatom has a minimum of its cell associated with the substratum while most of the cell length could receive light from almost any angle. The next most abundant form, *Eunotia* type, was established for algae with the ability to attach at one or both ends. The preponderance here of this physiognomy is probably a reflection of *E. rhomboidea* dominance more than an adaptive morphology. Being prostrate in a poorly lighted habitat is probably a poor strategy. Both motile and nonmotile prostrate diatoms may have advantages in avoiding the shear stress in high gradient streams but the trade-off of poorer light conditions may limit this

physiognomy in the reference stream. One might expect that filamentous forms would be relatively efficient at gathering light since they can project from the substratum. Lack of filamentous algae in the reference stream may be a function of light limitation (Hansmann and Phinney 1973, Shortreed and Stockner 1983).

In the clearcut stream there is ample light to support green filaments and the filamentous physiognomy appears to be well adapted. The only form poorly represented in this system is the *Eunotia* type which is significantly less abundant than all others. Physiognomies are more evenly distributed in the clearcut stream than in the reference stream. Reduced and perhaps limiting light availability appears to reduce the physiognomic options of members of an attached algal community and only with ample light can structural complexity develop.

Acknowledgements

This research was supported by NSF grant DEB 8012093 for Long Term Ecological Research at Coweeta Hydrologic Laboratory and was conducted while the senior author was on sabbatical leave at Virginia Polytechnic Institute and State University. We thank M. E. Krejci and H. J. Carrick for technical assistance.

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Received: 29 April 1986

Accepted: 30 September 1986