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BENTHIC DIATOM DISTRIBUTION IN A PENNSYLVANIA STREAM: ROLE OF pH AND NUTRIENTS[1]

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ABSTRACT

Buffalo Creek is in a forested watershed in eastern Pennsylvania and is relatively acid in upstream reaches (pH~6), becoming alkaline downstream (pH~8). Temperature, nitrogen (NO_3-N) and phosphorus (O-PO_4) increase significantly downstream whereas N/P declines. Nutrient-diffusing substrata were deployed in triplicate at an upstream and downstream site. Six treatments included two concentrations of nitrate, two concentrations of phosphate, nitrogen + phosphate, and a control. Substrata were collected after 18 days, scraped and analyzed for accrual of chlorophyll a *and algal community structure. Chlorophyll* a *and algal biovolume were greatest downstream across all nutrient treatments. At the community level, accrual appeared to be limited by phosphorus at upstream sites. Downstream accrual also may have been phosphorus-limited, but the results were equivocal. Benthic algae on all treatments at both sites were ~96% diatoms. Minimal overlap in species composition was observed between upstream and downstream sites. Of the 75 species of diatoms encountered in the study, 58 species did not occur at the upstream site and 10 species did not occur at the downstream site. The upstream site was depauperate in species and dominated by* Eunotia exigua *(Bréb. ex Kütz.) Rabh., which showed a positive response to phosphorus and accounted for over 50% of the biomass across treatments. The downstream site showed a four-fold increase in species richness. Communities at this site contained some species that appeared to be phosphorus-limited, e.g.* Melosira varians *Ag., and others that seemed to be nitrogen-limited, e.g.* Diatoma vulgare *Bory and* Navicula seminulum *Grun. We conclude that extreme conditions upstream (low pH, high N/P) result in a species-poor community dominated by acidophilous phosphorus-limited diatoms. Increases in downstream nutrients and pH result in a relatively rich and diverse community.*

Key index words: artificial substrates; diatom distribution; nutrients; stream characterization

The distribution and abundance of stream algal periphyton is influenced by a variety of physical, chemical and biological parameters (Hynes 1970). Physical and chemical parameters that have been demonstrated to influence lotic periphyton quality and quantity include nutrients (Stockner and Shortreed 1978, Crawford 1979, Marcus 1980, Peterson et al. 1983, Pringle and Bowers 1984, Grimm and Fisher 1986, Lowe et al. 1986), light (Busch 1978, Sumner and Fisher 1979, Gregory 1980, Keithan and Lowe 1985, Steinman and McIntire 1986), current speed (McIntire 1966, Stevenson 1983, 1984, Keithan and Lowe 1985, Steinman and McIntire 1986, Lamb and Lowe 1987) and pH (Hancock 1973, Van Dam et al. 1981, Maurice et al. 1987). Concurrent changes in these parameters with stream order as well as changes in stream communities have been observed by many investigators and addressed in the river continuum concept (Vannote et al. 1980). The river continuum concept (Vannote et al. 1980) predicts that in forested watersheds periphyton should reach maximum abundance in areas of the river that are wide enough not to be heavily shaded by riparian vegetation and are shallow enough to allow light penetration to the substratum. These conditions are often characteristic of third-to-sixth-order streams. The continuum concept makes no predictions about qualitative differences in longitudinal distribution of algal periphyton although it is hypothesized that "the biological organization in rivers conforms structurally and functionally to kinetic energy dissipation patterns of the physical system" (Vannote et al. 1980). Given a river continuum with longitudinal differences in physical and chemical parameters (current, light, pH, nutrients) qualitative differences in the distribution of algal populations should be expected. These differences should reflect population level responses to longitudinal shifts in important niche components.

In this study, we examined differences in periphytic algal distributions in a first and fourth-order section of Buffalo Creek, eastern Pennsylvania. Our specific objective was to examine nitrogen and phosphorus availability in Buffalo Creek and to determine the role of these nutrients in structuring communities of attached algae.

MATERIALS AND METHODS

This investigation was conducted in the Buffalo Creek Drainage in east-central Pennsylvania during July and August, 1985. Buffalo Creek originates from tributaries in a mountainous forested watershed (76°52′–77°15′ long., 40°52′–41°05′ lat.), passes through a largely agricultural valley, and joins the Susquehanna River as a fourth-order stream (Fig. 1). Two sites were selected for periphyton investigation: Hartleton, the upstream site, is a first-order section, and Cowan, the downstream site, is a fourth-order

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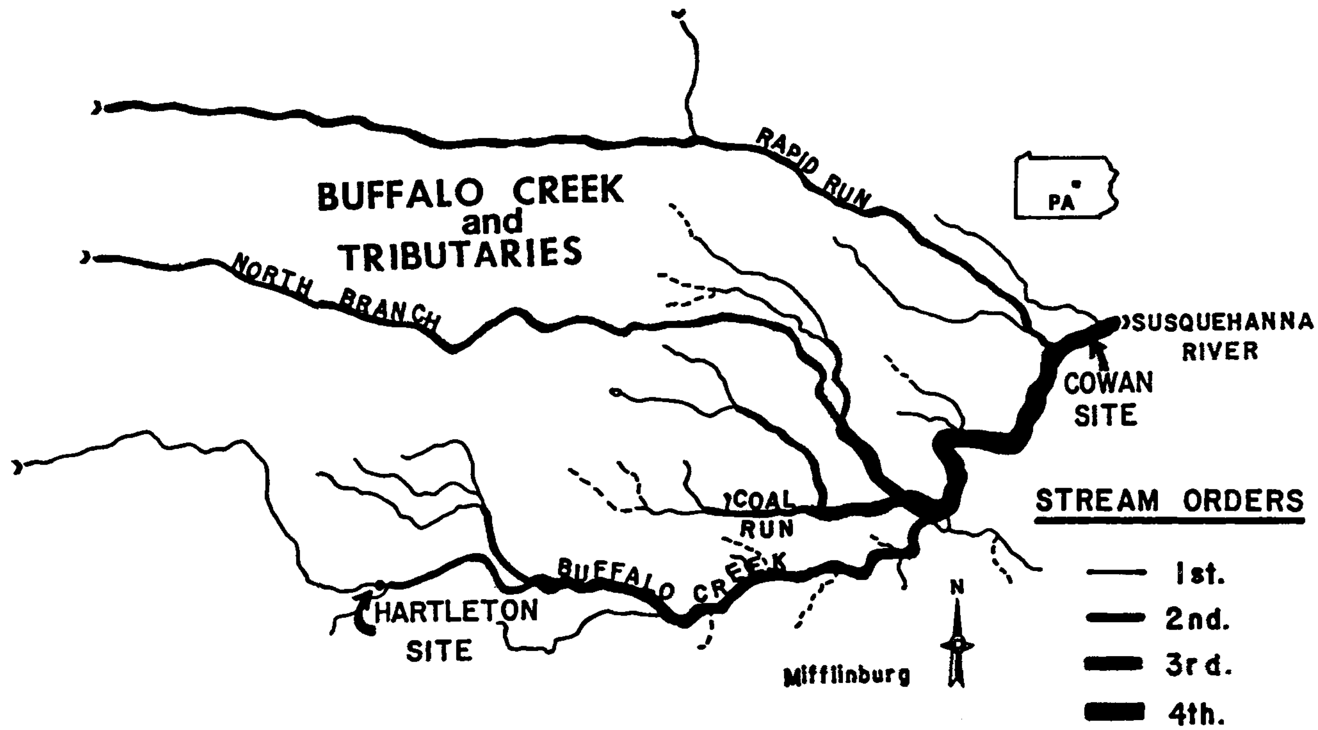

FIG. 1. Location of Hartleton and Cowan sampling sites on Buffalo Creek.

section of Buffalo Creek. Initial investigation suggested that the two sites were similar in flow rate [Mean ($\bar{X}$) = 22.8 cm], depth ($\bar{X}$ = 28 $cm \cdot s^{-1}$) light (study range of 110–2000 $\mu E \cdot m^{-2} \cdot 5^{-1}$) availability, and substrate composition, but differed in pH, nutrient chemistry, and periphytic flora.

Nutrient-diffusing artificial substrata were constructed from clay flower pots filled with agar-nutrient combination using the method described by Fairchild and Lowe (1984). The following nutrient treatments were prepared and deployed in triplicate at each site: control pots containing only 2% agar, low nitrate pots containing 0.05 M $NaNO_3$, low phosphate pots containing 0.05 M KH_2PO_4, high phosphate pots containing 0.5 M KH_2PO_4, and pots containing both nitrate and phosphate in concentrations of 0.05 M $NaNO_3$ and 0.05 M KH_2PO_4. Nutrient levels were chosen on the basis of methods used by Fairchild and Lowe (1984). During the 18-day exposure period, the following physical and chemical factors were periodically measured: water temperature, depth, flow rate, pH, alkalinity, NO_3-N, and O-PO_4. Investigators have found that attached algal communities associated with artificial substrata achieve a maximum "stable standing crop" after a 2-3 week period with a minimal net gain or loss in cell density of standing crop with time (Weber and Raschke 1970, Tuchman and Blinn 1979).

Following the incubation period the pots were retrieved and returned to the lab, and the periphyton was removed. The total volume of periphyton suspension from each pot was recorded. Subsamples of the suspension from each pot were filtered onto Whatman GF/C glass fiber filters (0.45 μm) and ground in 90% acetone (saturated with $MgCO_3$) for chlorophyll extraction. A Turner Model III fluorometer was used to determine chlorophyll *a* concentrations. Subsamples of the homogenate were also filtered onto 0.45 μm Millipore filters, dried, and cleared with clove oil to examine and quantify the algal community. Diatoms were identified to species, and determinations of relative abundance, diversity and evenness were made. At least 500 frustules were counted in each sample. Mean cell volumes of each taxon were estimated by measuring cell dimensions of 10 randomly chosen cells. Densities of each taxon were obtained by multiplying mean cell volume by cell densities. In statistical analyses, biovolumes were used rather than cell numbers since biovolumes are a more direct measure of biomass.

Results were analyzed at both community and population levels. Comparisons of treatment effects on biovolumes of particular taxa and the community as a whole were performed using one-way Analysis of Variance (ANOVA). Duncan's Multiple Range Test was used to order differences in population responses to nutrient treatment (Sokal and Rohlf 1969).

RESULTS

There were no significant differences (*t*-test, $P <$ 0.05) in physical characteristics at the two study sites (Table 1). Depth and flow rate were also similar at both sites with a slight increase in water temperature at the downstream site. Chemical data indicate that pH alkalinity were significantly lower at the upstream site with at least a ten-fold increase in NO_3-N and a fifteen to thirty-fold increase in O-PO_4 at the downstream site. Therefore, the major differences measured between the sites were pH, NO_3-N, and O-PO_4. The N:P ratios also differed (N/P = 11 at Cowan, N/P = 25 at Hartleton).

Chlorophyll *a* concentrations among nutrient treatments at either site were not significantly different (Fig. 2); however, the downstream site had significantly higher chlorophyll *a* values (*t*-test, $P <$ 0.05) when all replicates were pooled. Diatom biovolume versus treatment at Hartleton was not significantly different; however, phosphate treatments resulted in the greatest increase in biovolume (Fig.

TABLE 1. *Ambient physical–chemical data obtained during nutrient pot incubation period at Hartleton and Cowan sites.*

		Physical-chemical characteristics						
Date 1985	Site	Temp. °C	Depth cm.	Flow $cm \cdot s^{-1}$	pH	Alkalinity mg $CaCO_3 \cdot L^{-1}$	NO_3–N $mg \cdot L^{-1}$	O–PO_4 $mg \cdot L^{-1}$
7/18	Hartleton	17	22.8	20	6.4	0	0.10	0.01
7/22		19.5	22.8	20	6.2	0	0.14	0.01
7/25		19.5	22.8	20	6.2	0.5	0.12	0.01
7/29		19	22.8	25	6.5	1	0.08	0.01
8/2		16	30.5	49	6.0	0	0.10	0.01
8/5		16	22.8	31	6.0	0	0.09	0.01
Mean		17.8	24.1	27.5	6.2	0.25	0.11	0.01
Molarity (μM)							7.5	0.3
Mean N/P = 25								
7/18	Cowan	22	22.8	20	8.6	53	1.8	0.30
7/22		23	22.8	20	8.3	183	1.4	0.35
7/25		23	22.8	20	8.3	66	1.2	0.2
7/29		24	22.8	25	9.1	58	0.9	0.30
8/2		18.5	24.1	54	7.6	47	1.0	0.15
8/5		19.5	22.8	34	7.9	51	1.1	0.18
Mean		18.0	23.0	28.8	8.3	76.3	1.2	0.25
Molarity (μM)							89	8.1
Mean N/P = 11								

3). At the Cowan site, the control was significantly lower ($P < 0.05$) than all of the nutrient treatments.

An initial inspection of periphyton collected from Buffalo Creek revealed that over 90% of the epilithic communities were composed of diatoms. We limited our population level analysis to this algal group. A total of 75 diatom taxa were observed in this experiment. Hartleton yielded 65 taxa, 58 of which were unique to that site.

Three taxa, representing 79% fo the biovolume at Hartleton, showed a significant ($P < 0.05$) response to nutrient treatment (Table 2). In all cases, phosphorus enrichment resulted in the densest growth. *Eunotia exigua* was the most abundant diatom at this site (76% of the control biovolume). Other taxa responding positiviely to phosphorus enrichment at this site included *Navicula radiosa* var. *parva* and *Eunotia praerupta.*

At the Cowan site, eight taxa, representing 39% of the biovolume responded significantly ($P < 0.05$) to nutrient manipulation (Table 3). However, at this site nutrient responses were more varied than at the upstream site. For example, *Melosira varians,* which composed 17% of the community, responded most positively to the high phosphorus treatment, although all treatments yielded significantly ($P < 0.05$) more biovolume than the control. *Diatoma vulgare* responded positively (*t*-test, $P < 0.05$) to nitrogen enrichment whereas *Navicula rhynchocephala* was stimulated significantly ($P < 0.05$) by all nutrient additions. Several other taxa responding significantly ($P < 0.05$) to nutrient enrichment at Cowan displayed a variety of responses, although in most instances the control treatment yielded the lowest biovolume.

DISCUSSION

Interpreting periphyton response to nutrient limitation based on community measurements, such as chlorphyll *a* and biovolume, is often misleading. Our chlorophyll *a* data indicate that the periphyton is not nutrient-limited at either site. Total diatom biovolume suggests that the Hartleton diatom community is not nutrient-limited, but at Cowan it is, although the specific nutrient limitation is not identified. At Cowan, any nutrient addition resulted in significantly more diatom biovolume than the control treatment. It is important to recognize that resource limitation occurs at the population level. Analyzing differences in whole community chlorophyll *a* or biovolume is often uninformative and may lead to erroneous conclusions.

The Hartleton site supported a species-poor community. Reasons for the depauperate flora may in-

TABLE 2. *Analysis of variance for taxa vs. treatments for taxa responding significantly to treatments at Hartleton, upstream site, N:P = 25.*

Taxon	Relative abundance in control by biovolume (%)	Significance level *P* value	Duncan's Mult. Range					
Eunotia exigua (Bréb. *ex* Kütz.) Rabh.	76.4	0.0026	0.5P	0.05P	0.5N	NP	0.05N	C
E. praerupta Ehr.	0.4	0.022	0.5P	0.05P	0.5N	0.05N	NP	C
Navicula radiosa var. *parva* Wallace	2.2	0.0001	0.05P	0.5P	0.5N	NP	C	0.05N
Total	79.0							

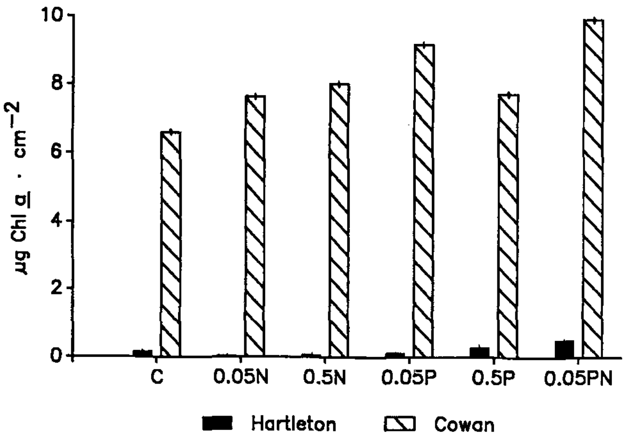

FIG. 2. Nutrient treatment response versus chlorophyll *a* concentration per cm^2 on substrata at Hartleton and Cowan sites.

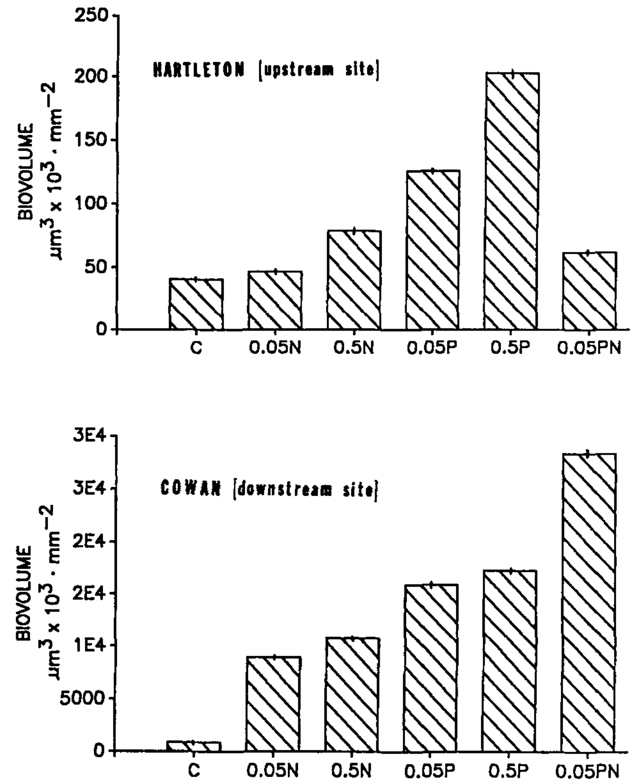

FIG. 3. Community response to nutrient treatments in terms of total biovolume at Hartleton and Cowan sites.

clude the lack of diverse sources of upstream colonizers, a phenomenon common to first-order streams (Vannote et al. 1980). However, Rushforth et al. (1986) found headwater streams in the blast zone at Mt. St. Helens containing as many as 63 diatom species only four months after the eruption of this volcano. A more likely reason for reduced species numbers at Hartleton is the relatively acidic stream conditions in combination with a relatively high N:P ratio. Acid stream conditions often lead to a reduced diatom flora (Descy 1979, Van Dam et al. 1981, Maurice et al. 1987). *Eunotia exigua,* which composed 75% of the diatom biovolume at Hartleton, is one of the most acid-tolerant diatoms known (Hancock 1973, Lowe 1974), and it was the only diatom to survive in moorland pools that were reduced to a pH range of 3.7–4.6 (Van Dam et al. 1981). The N:P ratio of 25 at this site may have also played a role in reducing species diversity, as the community was dominated (89% relative biovolume) by a small population of phosphorus-limited acid tolerant taxa.

At least two factors may be potentially responsible for the nearly four-fold increase in species richness at the Cowan site. First, Cowan is at a fourth-order site on Buffalo Creek. Thus, dozens of first-order streams, potentially diverse in water chemistry and diatom flora, may contribute colonists to the Cowan site through drift. However, Cushing and Rushforth (1984) found no significant difference in diatom diversity among first to seventh-order sites on the Middle Fork of the Salmon River Drainage. No strong chemical clines were found (or recorded) in the Salmon River survey; thus, a more likely cause of increased diatom diversity at Cowan is probably attributable to water chemistry, including the more circumneutral pH, the increased concentration of both NO_3-N and $O\text{-}PO_4$, and the reduced N:P ratio.

At Cowan, a smaller portion of the diatom com-

TABLE 3. *Analysis of variance of taxa vs. treatments for taxa responding significantly to treatments at Cowan, downstream site, N:P = 11.*

Taxon	Relative abundance in control by biovolume (%)	Significance level *P* value	Duncan's Mult. Range					
A. minutissima Kütz.	0.05	0.0129	0.5N	0.05P	NP	0.5P	0.05N	C
Cymbella minuta Hilse *ex* Rabh.	0.84	0.0081	0.5P	0.5N	0.05P	0.05N	NP	C
Diatoma vulgare Bory	0.51	0.0037	0.05N	0.5N	NP	0.05P	0.5P	C
Gyrosigma obtusatum (Sulliv. & Wormley) Boyer	0.57	0.0194	0.5P	0.05N	NP	0.05P	C	0.5N
Melosira varians Ag.	17.1	0.0001	0.5P	0.05P	0.5N	NP	0.05N	C
Navicula cryptocephala Kütz.	6.8	0.0005	0.05N	0.5N	0.05P	C	0.5P	NP
N. rhynchocephala Kütz.	12.9	0.0001	NP	0.05P	0.5P	0.5N	0.05N	C
N. seminulum Grun.	0	0.003	0.5N	0.5P	NP	0.05P	C	0.05N
Total	38.8							

munity responded significantly to nutrient manipulation (eight species composing 39% of the biovolume). In addition, responses were more diverse than at the Hartleton site. At Cowan, some species were phosphorus-limited, some were nitrogen-limited, and some appeared to be co-limited by N and P. The majority of the community at Cowan displayed no response to N and P manipulation. These populations may be regulated by other factors such as light, space, or predation. These data suggest that at the Cowan site, there is a diversification and a potential narrowing of diatom niches. It is likely that autogenic factors such as resource competition for nutrients, space or light, or predation play a more important role at this site. At Hartleton, allogenic factors (reduced pH, sparse nutrients) appear to be more important in structuring the community.

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PHYCOLOGICAL SOCIETY OF AMERICA
ANNOUNCEMENT OF THE GERALD W. PRESCOTT AWARD FOR 1989

The Phycological Society of America will accept nominations for an award to be presented at the Annual Meeting of the Society in Toronto, Ontario, in August 1989. The Award will recognize the author(s) of a scholarly work devoted to phycology in the form of a book or monograph published in English. Edited volumes, individual book chapters, typical journal articles and the like will not be considered. Publications must have *copyright dates of 1987 or 1988.* Authors need not be members of the Phycological Society of America to have their publications nominated for the Award. The value of the Award for 1989 is expected to be $500.

Nominations may be made by any member or non-member of the Phycological Society of America by submitting a brief letter stating the strong points of the scholarly work and a copy of the book or monograph to be considered. It is acceptable and in fact strongly encouraged that authors nominate their own publications. Separate publications by the same author(s) may be nominated. Nominations for the 1989 Award should be sent to the Chairman of the Gerald W. Prescott Award Committee, Dr. J. Robert Waaland, Department of Botany, KB-15, University of Washington, Seattle, Washington 98195, U.S.A., and to be considered must be postmarked not later than April 1, 1989. For further information write the Chair or phone him at (206) 543-7098.