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Temporal variation in enrichment effects during periphyton succession in a nitrogen-limited desert stream ecosystem

CHRISTOPHER G. PETERSON[1] AND NANCY B. GRIMM

Department of Zoology, Arizona State University, Tempe, Arizona 85287 USA

Abstract. Periphyton succession was studied over 89 d in longitudinally adjacent reaches (a riffle and run) in Sycamore Creek, a spatially intermittent desert stream. Effects of nitrogen limitation were assessed by comparing algal development on clay saucers containing either nitrate-enriched or unenriched agar. We evaluated effects of grazing on periphyton accrual by amending agar in half the substrata from each enrichment condition with an insecticide (Malathion). Early successional (25-d) communities on unenriched substrata were dominated by *Epithemia sorex*, a diatom capable of N_2 fixation; non-fixing diatoms dominated enriched communities. NO_3-N enrichment increased algal diversity (H') and delayed late-successional dominance by *Calothrix*, a heterocystous cyanobacterium. Replacement of diatoms by cyanobacteria was likely facilitated by autogenic changes in nutrient and light conditions within the periphyton and temporal increases in water temperature.

Three measures of algal biomass exhibited nearly linear increases in all treatments over the 3-mo study. Enrichment enhanced standing crops of chlorophyll *a* and ash-free dry mass (AFDM) in both reaches, an effect most pronounced within the first 3–4 wk. Algal populations unable to fix N_2 were stimulated by enrichment but remained in low abundance on unenriched substrata whereas biovolume of N_2-fixing populations was lower on enriched substrata relative to controls.

Malathion reduced the density of only one common grazer, the moth larva *Petrophila jaliscalis*, which was abundant only in the riffle. Addition of Malathion to enriched substrata in this habitat had no significant effect on net primary productivity or total algal biovolume but resulted in increased chlorophyll *a* and AFDM, suggesting that *Petrophila* did influence algal communities, but by a mechanism that remains unclear.

Spatial heterogeneity of nutrient supply in this system contributes to maintenance of algal diversity; but over long successional seres diversity declines regardless of enrichment owing to autogenic changes that occur during succession. Our results confirm earlier observations that low nitrogen availability limits accrual of algal biomass following spates and constrains algal community structure in Sycamore Creek. However, highly significant early successional differences in algal standing crop and community structure among enrichment treatments were eliminated or much reduced in mid to late stages of succession. We propose that this temporal change in enrichment response was caused by development of a thick periphyton mat that reduced availability of both water-column or substratum-derived nutrients to algae, and increased reliance on internal nutrient recycling.

Key words: periphyton, succession, nitrogen limitation, nitrogen-fixing algae, cyanobacteria, desert stream, grazers, *Petrophila*, long-term enrichment bioassay.

Sources of inorganic nutrients in aquatic systems are spatially and temporally heterogeneous (Pringle 1990). Such patchiness is manifested on microscales, (e.g., nutrient release from retreats of insect larvae [Pringle 1985, Hershey et al. 1988, Power 1991]) and on much broader spatial scales. For example, discrete zones of nutrient efflux from benthic sediment are common in freshwater lakes (Cox 1988), tidal and subtidal marine systems (Höpner and Wonneberger 1985, Pollehne 1986), and streams

(Triska et al. 1989, Coleman and Dahm 1990, Grimm et al. 1991). Nutrient enrichment can significantly alter algal community composition, biomass, and productivity (e.g., Stockner and Shortreed 1978, Grimm and Fisher 1986, Pringle 1990). The rate and pattern of algal succession is also affected by enrichment (Grimm and Fisher 1986, Stevenson et al. 1991), but autogenic changes associated with periphyton development may feed back to influence nutrient availability and mitigate enrichment effects (Bothwell 1989, Pringle 1990, Stevenson et al. 1991). Thus, spatial variation in nutrient supply can generate corresponding heterogeneity in algal community structure and biomass and influence succession (Pringle 1990).

[1] Present address: Natural Science Department, Loyola University–Chicago, 6525 N. Sheridan Road, Chicago, Illinois 60626 USA.

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Benthic-algal abundance, distribution, and community structure can also be modified by invertebrate grazers. Ingestion of cells reduces algal biomass and may alter community structure (Colletti et al. 1987, Steinman et al. 1987, Dudley and D'Antonio 1991). Stimulatory effects generated from excretion of nitrogenous compounds by grazers (Flint and Goldman 1975, Grimm 1988, McCormick and Stevenson 1989), enrichment during gut passage of viable algal cells (Cuker 1983), or release of non-grazed algae from competition (Lamberti et al. 1989, McCormick and Stevenson 1989) have also been suggested. Furthermore, grazing effects often interact with light (Feminella et al. 1989, Winterbourn 1990) or nutrient limitation (Sumner and McIntire 1982, McCormick and Stevenson 1989, Steinman et al. 1991) to yield community dynamics that differ from those caused by variation in any of these controlling factors alone.

Our primary objective was to assess the single and interactive effects of nitrogen limitation and invertebrate grazing on periphyton succession during long interflood periods in Sycamore Creek, a spatially intermittent Sonoran Desert stream in central Arizona. Parent bedrock in the upper portion of Sycamore's 505-km² catchment consists mostly of basaltic lava (Thomsen and Schumann 1968), thus dissolved phosphorus levels in this system are typically high (ca. 30–70 μg/L soluble reactive phosphorus [SRP]; Grimm 1992). At base flow, nitrate-nitrogen in the surface stream often falls below 10 μg/L; enrichment experiments in Sycamore Creek have shown N to limit algal growth at concentrations ≤55 μg/L (Grimm and Fisher 1986). The major influx of inorganic N into the surface stream occurs via intrusion of nitrate-rich water from the hyporheic at discrete areas of upwelling (Grimm et al. 1991, Valett 1991). Nitrate levels decrease downstream from these zones owing to assimilation by benthic autotrophs (Grimm et al. 1981, Grimm 1992). Sycamore Creek experiences seasonal, often intense spates in early spring and late summer separated by extended periods of stable, low discharge during which algal and invertebrate biomass rapidly increases to high levels (Fisher et al. 1982, Grimm and Fisher 1989). Thus, following severe spates, a template characterized by nitrate-replete upwelling zones and nitrate-deficient downstream areas is rapidly established upon which algal succession proceeds from nearly bare, uniform substrata to an often dense mosaic of periphyton.

We simulated conditions of nutrient heterogeneity using clay saucers containing either nitrate-enriched or unenriched agar as substrata for algal community development (cf. Fairchild et al. 1985). To reduce densities of invertebrate grazers, we added an insecticide (Malathion) to half the substrata from each enrichment condition. Using this approach, we hoped to assess individual and interactive effects of nutrients and grazer activity on periphyton succession over a relatively long period (3 mo) without being compromised by site-specific differences between natural upwelling zones and nutrient-poor downstream areas.

Methods

We monitored algal succession under different nutrient/grazer regimes in two longitudinally adjacent reaches at an elevation of 700 m in Sycamore Creek. The upstream reach was a 50-m run with a homogeneous pea-gravel (diameter = 5–10 mm) substratum, 20–30 cm depth, and current velocity of 5–10 cm/s. The second reach was a riffle, 70 m long, with a mixed substratum of pea gravel, cobbles (ca. 60–200 mm), and boulders (>250 mm). Riffle depth ranged from 5 to 15 cm with variable current of 10–20 cm/s. Vegetation within and directly adjacent to the channel was dominated by seepwillow (*Baccharis salicifolia* (Ruiz & Pavon) Pers.) and aquatic macrophytes (mostly *Rorippa nasturtium-aquaticum* (L.) Schinz & Thell., *Ranunculus* sp., and *Zanichellia palustris* L.).

Nitrate-N content of stream water was 13 μg/L at the beginning of the study, increased to 54 μg/L on day 25, then declined to 20–34 μg/L over the final 6 wks. SRP concentration ranged from 19 to 81 μg/L during the study. Concentrations of these two nutrients did not differ appreciably between study reaches. Water temperature, measured between 0800 and 1000 h, varied from 19 to 22°C.

Inverted clay saucers (upper diameter = 6.4 cm, lower diameter = 9.0 cm, height = 3.2 cm) were filled with 2% agar and amended or not to create four conditions as follows: nitrate added (as 0.05 M NaNO₃) (+N), Malathion (0.4%) (+M), both (+N+M), or neither (Control). Each saucer was attached to an 11 × 11-cm plexiglas plate by a 5.4-cm galvanized steel bolt and

wingnut. Closed-cell foam pads were placed between the saucer's upper interface with a 3.1-cm washer and lower interface with the plexiglas to create a seal when the wingnut was tightened. Each saucer assembly was bolted to one end of an L-shaped aluminum support with the free end embedded in the stream bed to stabilize the saucer.

Substrata were introduced on 13 April 1989, 18 d after a small spate. In the run, saucers were placed in blocks of four (one of each treatment) at 4-m intervals down the reach. Bed morphometry in the riffle was more heterogeneous than in the run, and saucer placement was dictated by location of adequate sites. At 2-wk intervals, agar in all saucers was replaced with a fresh agar cake, appropriately amended, to renew supply of NO_3-N and/or Malathion over this relatively long-term study. Agar in control saucers was similarly replaced. This procedure caused no apparent loss of algal material.

Three replicate saucers from each treatment, selected randomly from each reach, were collected on days 8 (riffle only), 12 (riffle only), 25, 40, 55, 68, and 89 to measure net periphyton productivity (NPP), determine invertebrate densities, and estimate chlorophyll a, ash-free dry mass (AFDM), and algal species composition and abundances. Macroinvertebrates were collected by rinsing the substratum with stream water and removing sedentary organisms (i.e., *Petrophila*, and attached chironomid and caddisfly larvae) from retreats with forceps. These organisms were retained in 250-μm mesh netting and preserved in 70% ethanol for later identification and enumeration. Saucers were then submerged in the stream until metabolism assays were run.

We measured net primary production (NPP) of periphyton on each saucer within closed-bottom, cylindrical plexiglas chambers (volume = 750 mL stream water) fitted with floating lids with motor-driven paddles as described by Grimm and Fisher (1984). Saucers were pre-incubated in the dark to reduce oxygen concentration within chambers; NPP was then measured during a 15–30-min incubation in the light. Water samples were taken at the start and end of the light incubation with a 10-mL syringe through ports in chamber lids and assayed for dissolved oxygen using a modified micro-Winkler technique (Busch and Fisher 1981). NPP measurements were made between 1000 and 1400 h, when light was above saturation (>1000 μmol quanta/m^2/s).

Following NPP measurements, saucers were sealed in plastic bags and transported on ice to the lab; periphyton from the upper 88 cm^2 (entire saucer minus lower rim and upper washer) was removed using a razor blade, toothbrush, and wash bottle. The resulting algal slurry was homogenized with a hand-held electric mixer and brought up to volume, when 25 mL were removed and preserved in Lugol's solution for later algal identification and enumeration. Two additional 50-mL aliquots were filtered through Whatman® GF/A filters. One subsample was frozen, then chlorophyll a was extracted in boiling methanol (Tett et al. 1975). The second was used to determine AFDM as dry mass (60°C, 48 h) lost upon combustion (500°C, 4 h).

Permanent algal slides were prepared by mounting an aliquot of the preserved subsample in syrup (Stevenson 1984a). We estimated densities of live diatoms (intact frustules containing chloroplasts) and nondiatom algae from counts of no fewer than 500, and typically >1000 cells. All counts were made at ×1000 magnification; at least three 500-μm wide transects of varying lengths were scanned on each slide. We enumerated filamentous cyanobacteria as 10-μm lengths since trichome crosswalls were not always evident, and thus counts of individual cells of these taxa would be unreliable. Species- or genus-specific counts were converted to biovolume by measuring the dimensions of 10–25 cells of each taxon and using formulae of geometric shapes that approximated cell shapes (Kirschtel 1992).

Differences among treatments, within each reach type, in community parameters (i.e., chlorophyll a, AFDM, NPP, total algal biovolume, diversity [H', Shannon 1948]), and taxon-specific parameters (i.e., densities of common invertebrate and algal taxa or taxocenes) were assessed using a 3-factor analysis of variance (ANOVA). Class variables used in this ANOVA were community age (typically five levels: 25, 40, 55, 68, and 89 d), Malathion, and enrichment (both two levels—0 or 1). Data were natural-log (ln) transformed prior to analysis to render variances and means independent. Algal taxonomic data on day 68 and chlorophyll a data for day 89 were unavailable. To assess temporal changes in enrichment and grazing effects over successional time, we conducted separate 2-way

ANOVAs (enrichment, Malathion) on riffle data for each date (8, 12, 25, 40, 55, 68, and 89 d). On days 8 and 12, data were collected only from the riffle; we omitted these data from 3-factor ANOVAs to ensure comparability of riffle and run results.

Differences in algal community structure with successional time and among treatments were assessed by examining differences in relative biovolume (arcsine-square-root transformed prior to analysis; Zar 1974) of common taxa on enriched and control substrata using a 1- or 2-factor ANOVA.

Results

Community-level responses to enrichment and Malathion

Twelve invertebrate taxa that colonized clay saucers over our 89-d study were classified as grazers because, as either scrapers or collector/gatherers (sensu Cummins 1973), they likely ingested algae as a major component of their diet (Table 1). Of these, chironomid larvae were numerically most abundant (Fig. 1). Densities of mayfly nymphs and midge larvae decreased significantly during periphyton succession in both reach types (Fig. 1, Table 1). *Fallceon*, the most abundant mayfly, was not encountered on run substrata beyond day 40, but persisted on riffle saucers through 68 d (Fig. 1). *Physella virgata* (Gastropoda:Pulmonata) increased with time on both riffle and run substrata, but occurred in much greater abundance in the riffle (Fig. 1). In addition to *Physella*, six other taxa were most abundant on riffle substrata; no grazers occurred in significantly higher densities in the run than in the riffle (Table 1).

Only two grazers were deterred by Malathion. The moth larva *Petrophila jaliscalis* (a common, seasonally abundant grazer in this system [Grimm, unpublished data]) was less abundant on Malathion substrata in both reach types, but occurred in much greater numbers in the riffle (Fig. 1, Table 1), attaining a maximum of 26 individuals on a single unenriched saucer on day 55. *Psephenus murvoshi*, another sedentary insect encountered only on riffle substrata, also was significantly inhibited by Malathion (Table 1) but never occurred in high densities (i.e., never greater than one individual per substratum).

After 12 d of periphyton development we could easily see an enrichment effect; enriched substrata were entirely covered by lush, green periphyton growth, whereas periphyton on unenriched substrata was patchily distributed, more flocculent, and light brown. These visual differences became less pronounced with time; enriched and unenriched communities appeared similar by 89 d.

Two periphyton biomass measures, AFDM and chlorophyll *a*, exhibited similar temporal changes and responded similarly to enrichment and Malathion (Fig. 2, Table 2). Both measures increased steadily throughout succession, showing no reduction in accrual rate in later successional stages, and were significantly enhanced by enrichment in both reach types (Fig. 2, Table 2). The addition of Malathion resulted in higher chlorophyll *a* and AFDM standing crops in the riffle, but had no effect on periphyton biomass in the run. Further, when enriched and unenriched riffle substrata were analyzed separately, only enriched communities showed a significant positive response to the insecticide (AFDM, $p = 0.010$; chlorophyll *a*, $p < 0.001$) (Fig. 2).

Net primary productivity on day 25 and thereafter was unaffected by enrichment (Fig. 2, Table 2). Net productivity of run communities increased with time, but periphyton on riffle substrata showed no consistent temporal change in NPP (Fig. 2, Table 2). Malathion did not affect NPP in either reach type, although when enriched and unenriched communities were analyzed separately, net productivity of unenriched communities was significantly lower on saucers containing Malathion (2-factor ANOVA, $p = 0.039$).

Total algal biovolume increased throughout the study in both reach types, but was unaffected by enrichment or Malathion between 25 and 89 d (Fig. 3, Table 3). When biovolumes of nitrogen-fixing and non-fixing taxa were analyzed separately, however, combined biovolume of the seven N_2-fixers was significantly greater on unenriched than enriched substrata. Collective biovolume of the 123 non-fixing taxa was greater under conditions of NO_3-N enrichment (Fig. 3, Table 3). Biovolume of N_2-fixers increased steadily through succession on both enriched and unenriched substrata in both reach types. In contrast, non-fixer biovolume in the run showed no significant temporal change in
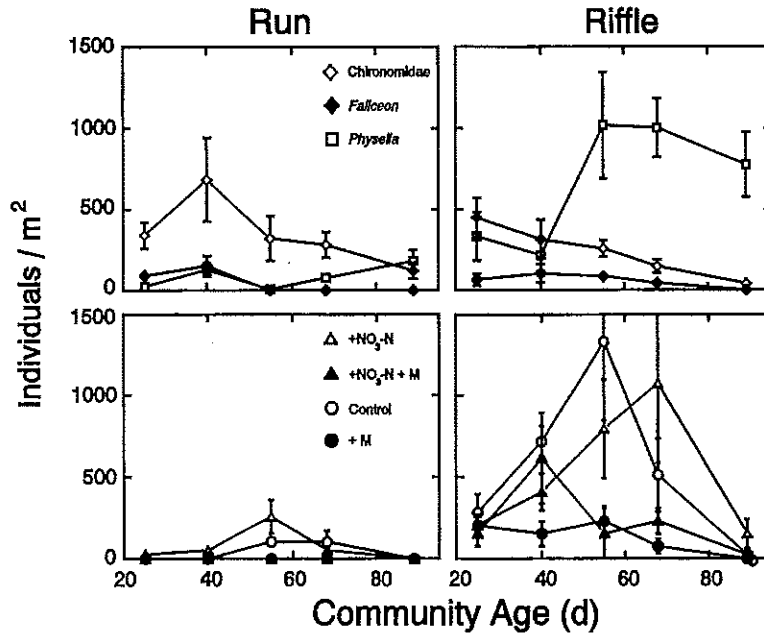
Fig. 1. Mean density (±1 SE) of common grazers in run and riffle habitats. Upper panels—Density of Chironomidae, *Fallceon* spp., and *Physella virgata* averaged over all treatments (n = 12 on first three dates; n = 20 on last two dates). Lower panels—Density of *Petrophila jaliscalis* on unenriched and enriched substrata with and without Malathion (n = 3 on each date).

either enriched or unenriched communities. In the riffle, biovolume of non-fixers increased with age on enriched substrata (2-factor ANOVA; $p = 0.007$), but remained unchanged on unenriched saucers (Fig. 3).

Malathion did not affect collective biovolume of N_2-fixers or non-fixing taxa in either reach (Table 3). Two non-fixing taxa did increase significantly in biovolume in the presence of the insecticide. *Achnanthes minutissima* was more abundant on saucers containing Malathion in both reach types (run: $p = 0.032$, riffle: $p < 0.001$). Basal cells of *Stigeoclonium* also occurred in higher densities in Malathion treatments in the riffle ($p = 0.015$), but not in the run.

Relative effects of NO_3-N enrichment and grazing on periphyton communities changed during succession. On riffle substrata, biomass (AFDM, chlorophyll a, and total algal biovolume) was 3–7× higher in enriched than in unenriched communities on days 8 and 12, but this ratio declined to 1–2 in older communities (days 25–89) (Fig. 4). Enrichment significantly affected AFDM in early successional stages (days 8, 12, and 25; Table 4), but had no effect in later stages, except on day 55. Enriched substrata sup-

ported more chlorophyll a on all dates except days 40 and 68 (Table 4), although these differences were strongly influenced by chlorophyll increases on +N+M substrata (Fig. 2). Total biovolume and NPP were enhanced by NO_3-N enrichment on day 12 only (biovolume: $p = 0.001$, NPP: $p < 0.001$). Although the 3-way ANOVA indicated a significant Malathion effect in the riffle, when each date was analyzed separately the insecticide enhanced biomass only on day 55 (Table 3), the time of maximum *Petrophila* density (Fig. 1).

Successional patterns in algal species composition

Under ambient NO_3-N concentrations (i.e., on control substrata), benthic algal communities in both riffle and run were overwhelmingly dominated by N_2-fixing taxa (Fig. 5). Seven of 130 algal taxa encountered in 95 samples were presumed able to fix atmospheric nitrogen: three heterocystous cyanobacteria (*Anabaena* sp., *Calothrix* spp., *Nostoc* sp.) and four diatom species within the family Epithemiaceae, all containing cyanobacterial endosymbionts (*Epithemia sorex*

TABLE 1. Effects of enrichment, Malathion, and community age on abundances of invertebrate grazers (3-factor ANOVA on ln-transformed densities), and preferences for riffle or run habitats (generated from reach-type × enrichment × age ANOVA on ln-transformed densities from control and NO_3-N-enriched substrata). Degrees of freedom for F-statistic = 1,44. A significant positive (+) or negative (−) response is denoted as +++ or −−− ($p < 0.01$), ++ or −− ($0.05 > p > 0.01$), + or − ($0.10 > p > 0.05$). Age effects are denoted as "E", "M", or "L" for taxa that reached maximum density in early, middle, or late succession, respectively. "•" = < 5 individuals were encountered on all substrata; ns = not significant; NP = not present. RF = most abundant on riffle substrata; none = no habitat preference.

	Enrichment		Malathion		Age		Habitat	
Taxon	Run	Riffle	Run	Riffle	Run	Riffle	Preference	p
Ephemeroptera								
Fallceon spp.	ns	ns	ns	−	E	E	RF	0.052
Tricorythodes dimorphus Allen	ns	ns	ns	ns	E	E	none	0.443
Other Ephemeroptera	•	•	•	•	•	•	•	•
Trichoptera								
Helicopysche mexicana Banks	−	+	ns	−	E	ns	none	0.722
Ochrotrichia sp.	•	•	•	•	•	•	•	•
Diptera								
Chironomidae	ns	ns	ns	ns	E	E	none	0.824
Stratiomyidae	NP	ns	NP	ns	NP	ns	RF	0.005
Cryptolabis sp.	•	•	•	•	•	•	•	•
Coleoptera								
Psephenus murvoshi Brown	NP	ns	NP	−−	NP	ns	RF	0.002
Lepidoptera								
Petrophila jaliscalis Schaus	ns	ns	−−−	−−−	M	M	RF	0.001
Gastropoda								
Physella virgata Gould	ns	ns	ns	ns	L	L	RF	0.001
Gyraulus sp.	ns	ns	ns	−	ns	ns	RF	0.001

Kütz., *E. turgida* (Ehr.) Kütz, *Rhopalodia gibba* (Ehr.) O. Müll., *R. gibba* var. *ventricosa* (Kütz.) H. & M. Perag.). *Epithemia sorex* was dominant on unenriched substrata by day 25 in both reaches and remained so in the riffle through day 55. This species was replaced within 89 d in both run and riffle by *Calothrix*, a filamentous cyanobacterium which made up 94.8% (SE = 0.8%) of total algal biovolume in the run and 78.5% (SE = 5.9%) in the riffle (Fig. 5).

In contrast to unenriched communities, early successional (25-d) communities on enriched substrata contained relatively few *E. sorex* and were dominated by the stalked diatom *Cymbella affinis* Kütz. (relative biovolume: run = 53.9% [SE = 4.7], riffle = 39.7% [SE = 7.0]). The monoraphid diatoms *Achnanthes lanceolata* (Bréb.) Grun. and *A. minutissima* Kütz. and the filamentous chlorophyte *Stigeoclonium* also contributed sig-

nificantly to algal biomass under enriched conditions (Fig. 5); the last two taxa sustained their relative abundance throughout the 89-d sequence. As with unenriched communities, 89-d enriched communities were dominated by *Calothrix*, but to a lesser degree than controls; *Calothrix* contributed only 56.0% (SE = 10.76) and 53.6% (SE = 6.5) to algal biovolume in the run and riffle, respectively. Under enriched conditions *Oscillatoria*, a non-heterocystous cyanobacterium, accounted for 11.7% (SE = 5.0) of algal biovolume in run communities and 18.2% (SE = 6.6) in the riffle on day 89.

Relative biovolume of *Synedra ulna* (Nitz.) Ehr. was not affected by enrichment, but this alga was conspicuous in its obligatory early successional status. This pattern was most evident in the riffle where *S. ulna* attained maximum relative biovolume of 22.9% (SE = 3.4) in 12-d
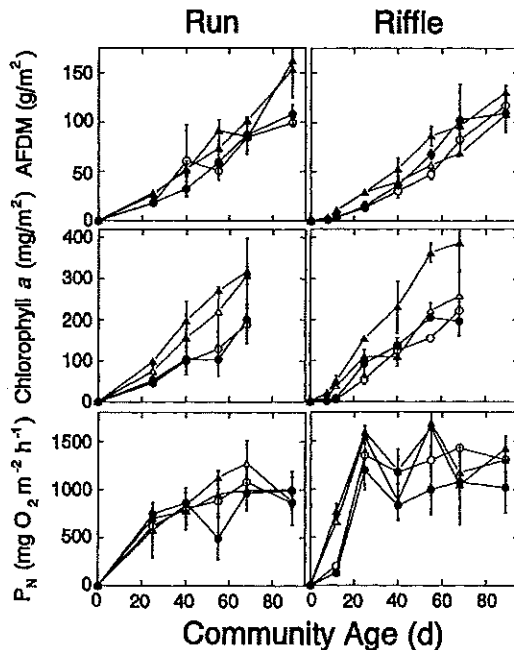
Run   Riffle

FIG. 2. Mean (±1 SE) ash-free dry mass (AFDM), chlorophyll a, and net primary productivity (P_N) of periphyton communities in run and riffle habitats. Symbols and number of replicates as shown in Figure 1 (lower panels).

control communities, formed 8.0% (SE = 3.5) of control communities and 6.3% (SE = 2.3) of enriched communities on day 25, but was not encountered after day 40 (Fig. 5).

Algal diversity (H') on day 25 did not differ with NO_3-N enrichment (Fig. 6). Over the entire sequence, however, diversity was greater in enriched communities relative to controls (p < 0.001), was similar between reach types, and declined throughout succession (p < 0.001) (Fig. 6). Although diversity of riffle and run communities did not differ significantly, a significant reach-type × age interaction (p = 0.004) reflected the fact that $Calothrix$ established dominance more rapidly on run substrata than in the riffle (Fig. 5).

Discussion

Our results suggest that heterogeneity in nitrogen supply in Sycamore Creek, generated from spatially discrete upwelling zones of nitrate-rich hyporheic water (Grimm et al. 1991, Valett 1991), can cause temporal and spatial variation in periphyton structure and function. Periphyton communities on unenriched substrata differed greatly in species composition

TABLE 2. Results of 3-factor ANOVAs on ln-transformed values of periphyton community variables. Numerator degrees of freedom (df) for F statistic are given; denominator df are as follows: AFDM = 40 (both reach types), Chlorophyll a = 32 (both reach types), Net Productivity = 36 (run), 37 (riffle). Probabilities (p) < 0.05 are bold-faced. Since no 3-way interaction was significant, these values are not presented.

| Variable	Source	Run			Riffle		
		df	F	p	df	F	p
AFDM	Nutrients	1	13.20	**<0.001**	1	11.17	**0.002**
	Malathion	1	0.03	0.865	1	6.16	**0.017**
	Age	4	40.68	**<0.001**	4	67.21	**<0.001**
	Nutr × Mal	1	0.08	0.775	1	0.49	0.490
	Nutr × Age	4	0.36	0.835	4	3.53	**0.015**
	Mal × Age	4	0.38	0.823	4	0.68	0.613
Chlorophyll a	Nutrients	1	26.85	**<0.001**	1	18.21	**<0.001**
	Malathion	1	0.59	0.449	1	10.01	**0.003**
	Age	3	21.00	**<0.001**	3	21.62	**<0.001**
	Nutr × Mal	1	0.68	0.417	1	3.01	0.093
	Nutr × Age	3	0.40	0.757	3	1.31	0.290
	Mal × Age	3	0.15	0.930	3	0.36	0.782
Net productivity	Nutrients	1	1.06	0.310	1	1.31	0.260
	Malathion	1	1.18	0.284	1	3.25	0.080
	Age	4	2.98	**0.032**	4	2.39	0.068
	Nutr × Mal	1	0.05	0.816	1	3.09	0.087
	Nutr × Age	4	0.85	0.505	4	0.19	0.940
	Mal × Age	4	0.22	0.925	4	1.32	0.282
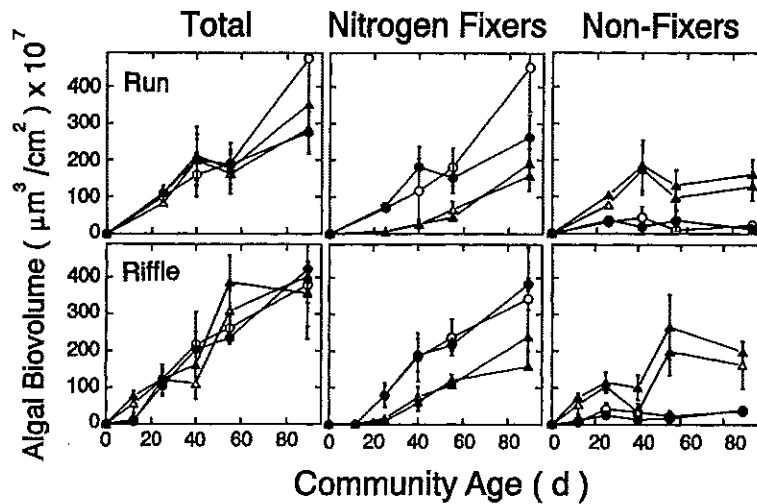
FIG. 3.   Mean (±1 SE) total algal biovolume and biovolume of nitrogen-fixing taxa and non-fixing taxa in run and riffle habitats. $n = 3$ for all means except day-40 control for which $n = 2$. Symbols as in Figure 1 (lower panels).

from those developed on substrata that released NO_3-N. Moreover, enrichment altered successional dynamics by increasing algal diversity and delaying late-successional dominance by cyanobacteria. Community biomass was enhanced by enrichment, but this enhancement became less pronounced as succession proceeded. Thus, the importance of nitrogen enrichment to biomass accrual in this ecosystem decreased with successional time.

TABLE 3.   Results of 3-factor ANOVAs on ln-transformed values of algal biovolume. Numerator degrees of freedom (df) for F statistic are given; denominator df are as follows: run = 31, riffle = 32. Probabilities (p) < 0.05 are bold-faced. Since no 3-way interaction was significant, these values are not presented.

| Variable	Source	Run			Riffle		
		df	F	p	df	F	p
Total biovolume	Nutrients	1	0.23	0.634	1	0.01	0.909
	Malathion	1	0.11	0.740	1	0.46	0.503
	Age	3	12.84	<0.001	3	14.90	<0.001
	Nutr × Mal	1	0.56	0.459	1	0.26	0.616
	Nutr × Age	3	0.08	0.969	3	1.48	0.238
	Mal × Age	3	0.27	0.843	3	0.20	0.895
N_2-fixer biovolume	Nutrients	1	66.21	<0.001	1	39.55	<0.001
	Malathion	1	0.08	0.782	1	0.22	0.646
	Age	3	30.04	<0.001	3	35.69	<0.001
	Nutr × Mal	1	0.00	0.947	1	0.97	0.333
	Nutr × Age	3	4.76	0.008	3	3.00	0.045
	Mal × Age	3	0.78	0.512	3	0.17	0.917
Non-fixer biovolume	Nutrients	1	80.81	<0.001	1	74.67	<0.001
	Malathion	1	0.21	0.649	1	0.68	0.415
	Age	3	1.37	0.270	4	5.38	0.004
	Nutr × Mal	1	0.28	0.602	1	3.21	0.083
	Nutr × Age	3	1.75	0.176	4	2.77	0.058
	Mal × Age	3	0.87	0.634	4	0.38	0.766
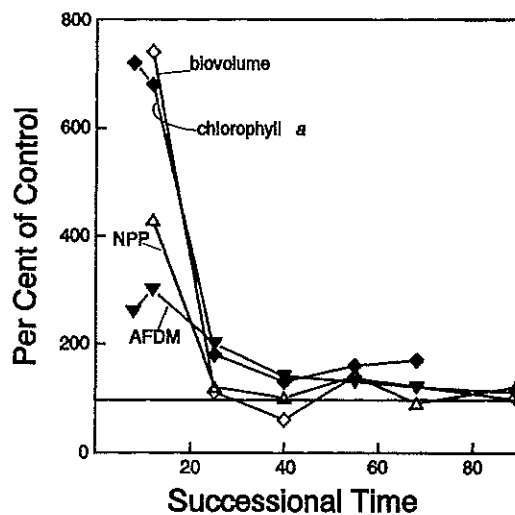
FIG. 4. Biomass (AFDM, chlorophyll a, and algal biovolume) and production of enriched periphyton communities as a percentage of unenriched (control) community biomass ($n = 6$) over 89 d of succession.

Algal succession under enriched and unenriched conditions

Diatoms dominated early successional communities, but the composition of this assem-

blage differed between enriched and unenriched substrata. On unenriched substrata, early successional communities were dominated by *Epithemia sorex*, a diatom containing cyanobacterial endosymbionts that presumably enable this alga to fix atmospheric nitrogen. Cyanobacterial inclusions occur in all three genera within the Epithemiaceae (Geitler 1977) and, in at least one species (*Rhopalodia gibba*), N_2 fixation has been documented (Floener and Bothe 1980). Epithemiacean diatoms often dominate periphyton communities in environments where NO_3-N concentrations are low (Fairchild and Lowe 1984, Bahls and Weber 1988, Mulholland et al. 1991).

Enrichment delayed dominance of N_2 fixers; early successional communities on NO_3-N enriched substrata supported high proportions of non-fixing taxa. Sites of hyporheic upwelling in the stream channel may similarly enrich periphyton and thus maintain diverse assemblages of non-fixers within N-poor stream reaches dominated by N_2-fixing taxa. In a disturbance-prone system like Sycamore Creek, such sites may supply colonists to newly scoured substrata following spates. Alternatively, viable populations of non-fixing taxa may persist at the base of thick epilithic periphyton mats, then

TABLE 4. Results of 2-factor ANOVAs on ln-transformed values of community variables on each sampling day in the riffle. Degrees of freedom for F statistic are 1,8 in all cases. Probabilities (p) <0.05 are bold-faced. Two-way interactions were never significant and are not presented. A dash signifies that data were not available.

| Variable	Source		Community age (d)						
			8	12	25	40	55	68	89
AFDM	Nutrients	F	23.71	22.02	13.08	3.22	5.77	0.09	0.11
		p	**<0.001**	**<0.001**	**0.007**	0.111	**0.043**	0.776	0.752
	Malathion	F	0.15	0.64	0.04	1.76	18.33	0.83	0.38
		p	0.704	0.807	0.840	0.221	**0.003**	0.389	0.566
Chlorophyll a	Nutrients	F	23.06	76.48	5.89	0.55	53.62	5.14	—
		p	**<0.001**	**<0.001**	**0.042**	0.479	**<0.001**	0.053	
	Malathion	F	0.44	0.33	1.44	3.62	38.62	0.64	—
		p	0.527	0.585	0.265	0.094	**<0.001**	0.449	
Net primary productivity	Nutrients	F	—	59.76	2.48	0.01	3.83	0.44	1.41
		p		**<0.001**	0.154	0.928	0.086	0.528	0.269
	Malathion	F	—	0.61	0.04	0.03	0.77	1.08	0.46
		p		0.457	0.857	0.876	0.406	0.328	0.516
Total biovolume	Nutrients	F	—	23.92	0.29	1.83	3.54	—	0.02
		p		**0.001**	0.607	0.213	0.097		0.906
	Malathion	F	—	2.22	0.04	0.46	0.18	—	0.23
		p		0.175	0.853	0.518	0.680		0.642
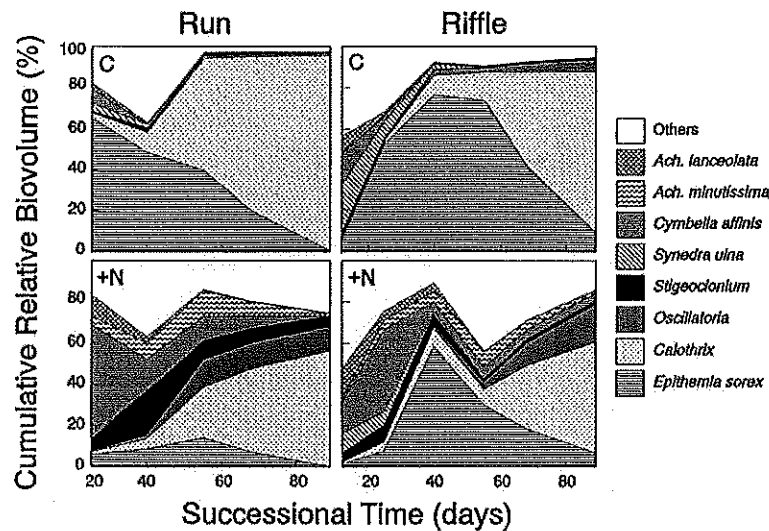
FIG. 5. Changes through successional time in relative biovolume of common taxa on control (C) and enriched (+N) substrata (both without Malathion) in run and riffle habitats. *Epithemia sorex* and *Calothrix* are capable of N₂-fixation.

rapidly proliferate when biomass is reduced by scour during spates. Studies in other systems have identified diatom taxa that dominate early successional communities by virtue of rapid immigration (Stevenson 1984b, McCormick and Stevenson 1991), rapid growth following immigration (Peterson and Stevenson 1989, Peterson et al. 1990), or persistence through scour events and subsequent reproduction (Peterson and Stevenson 1990). These mechanisms need not only apply to large-scale disturbance; similar successional patterns may occur on smaller
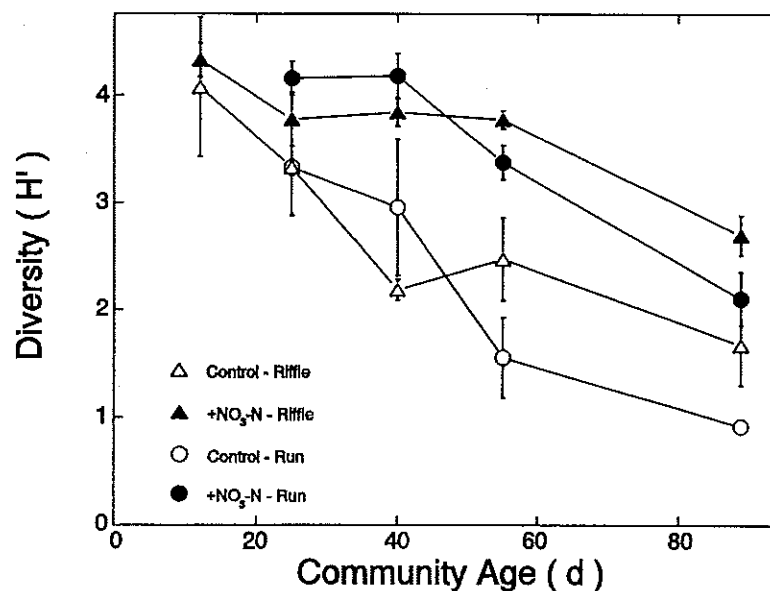

FIG. 6. Mean (±1 SE) algal diversity on control and enriched substrata (both without Malathion) in run and riffle habitats.

scales after localized sloughing of benthic algal mats or detachment of benthic algae by activity of fish or terrestrial vertebrates.

Despite early differences in species composition between enriched and unenriched communities, diatom dominance eventually ($\geq$55 d) shifted under all conditions to dominance by the heterocystous cyanobacterium *Calothrix*. Such shifts commonly occur during benthic algal succession in Sycamore Creek during long inter-spate periods (Fisher et al. 1982, Grimm and Fisher 1989, Fisher and Grimm 1991). Nitrogen supply in this stream declines following spates as flow recedes and inorganic N is used by actively growing benthic algae, favoring nitrogen fixers over non-fixers. Interspecific differences in N_2-fixing abilities among N_2-fixing taxa may influence these successional shifts in community structure. Epithemiacean diatoms fix N_2 less efficiently than heterocystous cyanobacteria (Floener and Bothe 1980) and thus should be out-competed by the latter during long successional seres.

Seasonal changes in temperature may also have contributed to algal species replacement. Temperature minima and maxima in Sycamore Creek varied from April (14°, 24°C) to July (19°, 32°C) of the year following this study (Peterson, unpublished data). Competitive abilities of algae are temperature dependent; diatoms often dominate phytoplankton communities at low temperatures whereas cyanobacteria are more prevalent at high temperatures (Tilman et al. 1986). Similar temperature-dependent variation in taxonomic structure has also been noted in benthic algae (Duncan and Blinn 1989, Snoeijs and Prentice 1989). *Oscillatoria*, a cyanobacterium that does not typically fix N_2 (but see Paerl and Bebout 1988), increased in abundance along with *Calothrix* during late succession, suggesting that the dominance shift from *E. sorex* to *Calothrix* may have been partially temperature-induced.

The ultimate success of cyanobacteria on N-enriched substrata is less easily explained. Higher water temperatures late in the sequence may have accounted for increasing abundance of some species, but temperature could not have been the sole factor controlling successional change, since enrichment maintained a diverse algal assemblage well into late succession. Taxa that could not fix N_2 were clearly poor competitors in dense, mid- to late-successional com-

munities even when supplied with N, as evident from the lack of significant increase in collective non-fixer density between 25 and 89 d on run substrata (Fig. 5).

We suggest that autogenic changes in microenvironmental conditions within the mat contributed to ultimate cyanobacterial dominance in enriched communities. As mats thicken with development, light penetration decreases (Jørgensen and Des Marias 1988), nutrient diffusion is reduced from both water column (Sand-Jensen 1983, Riber and Wetzel 1987) and the interstitial environment (Katznelson 1989), thus increasing the importance of nutrient recycling (particularly of phosphorus) in the periphyton (Mulholland et al. 1991). In addition, microenvironments within the mat can become hypoxic (Carlton and Wetzel 1987). Diffusion of NO_3-N from clay substrata was probably inhibited by heavy periphyton growth in mid to late succession, generating conditions of low nitrogen availability within mats on both enriched and unenriched substrata. Such conditions should promote dominance by cyanobacteria, many of which fix N_2 and can photosynthesize under hypoxic conditions (Lee 1980).

Although run and riffle communities followed similar successional paths, relative-biovolume plots showed that succession toward cyanobacterial dominance was more rapid on run substrata than in the riffle. Greater turbulence and faster currents associated with riffle habitats may increase influx of water-column nutrients into developing algal mats by strengthening the nutrient-concentration gradient between the water column and mat surface, thus lowering the intensity of competition for nutrients within these communities. This mechanism should be particularly important in nutrient-poor systems (Horner et al. 1990), like Sycamore Creek, and in early stages of succession when community biomass is relatively low (Bothwell 1989). In the slower, less-turbulent run habitats, availability of water-column nutrients to benthic algae should be lower, and competition more intense, because of a thicker diffusive boundary layer at the mat–water interface. Further, algae at the surface of riffle communities would display greater current-induced movement than those in more placid run habitats, allowing greater light penetration (Meulemans 1987) into the periphyton mat. Thus, competition for nutrients, and perhaps

light, likely influenced succession more strongly in run than in riffle communities (cf. Peterson and Stevenson 1990), yielding higher rates of species replacement in the run. The slower rates of succession we observed in enriched communities relative to controls in the run support this contention, at least with respect to nutrients. Grazer densities on substrata were generally greater in the riffle than in the run; these differences may have also affected algal succession. However, given the apparent unpalatability of filamentous cyanobacteria to some benthic invertebrates (Hart 1985), higher grazing pressure in the riffle should have accelerated, not slowed, replacement of diatoms by *Calothrix*.

Enrichment effects on community biomass and production

Nitrate enrichment enhanced accumulation of benthic organic matter and chlorophyll *a*, but had no long-term effect on total algal biovolume. In nutrient-limited systems, recycling efficiency of the limiting nutrient within periphyton communities should be high (Paul and Duthie 1989), and may be sufficient to maintain high steady-state biomass (DeAngelis et al. 1990, Mulholland et al. 1991). In our study, N_2-fixing taxa were able to proliferate and maintain high biomass despite low ambient NO_3-N concentrations, a pattern similar to that observed by Mulholland et al. (1991). In systems where two or more nutrients are in short supply, compensatory mechanisms (such as N_2 fixation) may not operate and unenriched and enriched habitats may support substantially different algal standing crops (cf. Stevenson et al. 1991).

Under some conditions we observed significant increases in AFDM and chlorophyll *a* without concomitant increases in algal biovolume. High bacterial standing crops on enriched substrata likely accounted for the disparate enrichment effects observed for AFDM and algal biovolume. Differences between algal biovolume and chlorophyll *a* standing crop may reflect differences in chlorophyll content of algal cells under the two enrichment conditions. Under nitrogen-limited conditions the amount of chlorophyll per cell decreases (Darley 1982). Furthermore, Paul and Duthie (1989) demonstrated that algal cells in lower strata of thick benthic mats had a lower light compensation point than upper-story cells, suggesting photoadaptation to low light. Shade-adapted cells can contain 2–10× more chlorophyll *a* than cells in high-light environments (Darley 1982) even under conditions of nutrient deficiency (Rosen and Lowe 1984). Thus, algal response to a combination of high NO_3-N concentrations and low light availability within high-biomass enriched communities could account for elevated chlorophyll content without a corresponding increase in algal biovolume. Alternatively, these patterns could have reflected interspecific variation in chlorophyll content among dominant taxa within each enrichment condition. If both bacterial standing crops and chlorophyll *a* density increased in response to nitrogen enrichment as we suggest, then the respiratory demand of the elevated bacterial populations could potentially counteract the product of increased photosynthesis. Such counteractive effects might explain why net primary productivity was unaffected by enrichment despite increases in AFDM and chlorophyll.

These data show that gross-scale measures of community biomass like chlorophyll *a* and AFDM, while appropriate for describing whole-system biomass, may be misleading when used alone (see Stevenson and Lowe 1986) at the scale examined in this experiment. In our study, similar amounts of chlorophyll *a* were carried in "packages" (i.e., species) that differed both functionally (N_2-fixation) and structurally (diatoms vs. filamentous cyanobacteria). Chlorophyll data alone would have provided us with little insight into periphyton community dynamics.

Effects of grazers and Malathion on algal communities

Although Malathion appeared ineffective against all invertebrates except *Petrophila* and *Psephenus*, which are sedentary (or nearly so) and would thus be more chronically exposed to the pesticide, its presence significantly enhanced AFDM and chlorophyll *a* standing crops on riffle substrata. Our data suggest that these grazers influenced periphyton communities, but perhaps by a mechanism other than selective grazing. *Petrophila jaliscalis* constructs silken retreats that are themselves colonized by periphyton, but which may inhibit establishment of

relatively chlorophyll-rich *Stigeoclonium* basal cells and other adnate taxa.

In the presence of Malathion, increases of *Achnanthes minutissima* and *Stigeoclonium*, taxa known to resist grazing by means of small size and tight adhesion (*Achnanthes*—Colletti et al. 1987, Peterson 1987; *Stigeoclonium*—Steinman et al. 1987, Steinman 1991), were unexpected. Malathion is an organophosphate (0,0-dimethyl dithiophosphate of diethyl mercaptosuccinate); phosphate release during degradation of this pesticide may have stimulated growth of *A. minutissima* and basal cells of *Stigeoclonium* at the base of thick periphyton mats. Although phosphorus is plentiful in Sycamore Creek surface waters (Grimm and Fisher 1986, Grimm 1992), concentrations within algal mats may be reduced to limiting levels. Thus, elevated chlorophyll *a* on +N+M substrata may reflect release of these two small taxa (thus no biovolume response) from secondary limitation by phosphorus, a response magnified by increased chlorophyll production associated with shade-adaptation and increased nitrogen availability in this environment (cf. Darley 1982). This interpretation is supported by the fact that positive Malathion responses were manifested only under N enrichment.

Factors controlling organic matter accumulation during succession

Based on studies of organic matter accrual under enriched and unenriched conditions over 3- to 5-wk experiments, Grimm and Fisher (1986) predicted that nutrient-limited periphyton might grow more slowly, but eventually attain the same maximum biomass as nutrient-replete communities. This model assumed that maximum biomass is set by other factors, such as export or grazing rate. Our experiment, conducted over a 3-mo period, enabled us to evaluate these predictions.

Although we found enrichment effects to be most pronounced in early succession (≤25 d in the riffle) and biomass of enriched and unenriched communities did converge, we cannot attribute this temporal variation to attainment of maximum biomass. All measures of periphyton biomass exhibited linear rather than asymptotic increase. Instead, we suggest that temporal decreases in the extent to which

enrichment enhanced biomass accrual were caused by changing conditions within the thickening periphyton mat. These autogenic changes may have led to increased reliance on internal recycling and nitrogen fixation relative to nutrient supply from external sources (cf. Mulholland et al. 1991).

Trophic controls on algal standing crops also likely change during succession. Macroinvertebrates typically colonize and grow more slowly than most algae, and population increases following spates may lag behind increases in algal biomass. Such a lag was evident for *Petrophila*, which reached maximum density in the riffle after 55 d of succession. Grazing effects on chlorophyll *a* and AFDM (difference between riffle substrata with and without Malathion) were significant only on that date. Our manipulation significantly affected only a single abundant invertebrate species, but this insect appeared to greatly influence periphyton standing crop (although the mechanism for this response is uncertain). These results, and those of others (e.g., DeNicola et al. 1990, Dudley and D'Antonio 1991), illustrate that grazer identity and the timing of grazing activity relative to algal successional state can influence algal succession in lotic systems.

Our results demonstrate that the effects of enrichment on algal succession can vary substantially in time and that, under some circumstances, short-term enrichment bioassays may provide only a limited picture of the complex interactions between algal community development and resource supply. In the riffle, AFDM response to enrichment during the first month of our experiment indicated strong nitrogen limitation; this effect was much reduced during the final 2 mo, as biomass accumulation limited algal access to external nutrient supplies. Enrichment enhanced total biovolume on only a single date (day 12), but not thereafter. Although effects on chlorophyll *a* were significant on several dates, they may have been caused by differences in community structure or higher cellular chlorophyll *a* content of heavily shaded basal cells under enriched conditions. Nutrient limitation, like many constraints in lotic ecosystems, should be expected to vary temporally. Results of algal enrichment bioassays may vary with season, successional state (i.e., time since last disturbance), magnitude of last disturbance,

life history characteristics of the major players in a given stream ecosystem, or some interaction among these factors.

Concluding remarks

Pringle (1985, 1990) contends that spatial and temporal heterogeneity of nutrient supply provides a mechanism by which benthic algal diversity is maintained in nutrient-poor systems. Our data support this contention but suggest that, in systems with high productive capacities and long periods between disturbances, an initially heterogeneous array of nutrient sources may become more homogeneous through time owing to autogenic factors associated with algal succession. As periphyton biomass increases through succession, the mat surface represents a continually shrinking percentage of community biomass. With time, allogenic nutrient sources should yield to autogenic nutrient recycling as the primary supplier of nutrients to benthic algae, and large initial differences between biomass of enriched and unenriched communities should diminish. The importance of internal controls in regulating benthic algal standing crops has been suggested by others (e.g., Lock et al. 1984, DeAngelis et al. 1990, Mulholland et al. 1991, Stevenson et al. 1991). The potential for autogenic mechanisms to exceed allogenic mechanisms in relative importance as regulators of algal community dynamics should vary among systems depending on such factors as disturbance frequency, nutrient regime, and the abundance and activity of grazers. In systems, like Sycamore Creek, in which high algal standing crops are maintained over long periods, results of short-term bioassay experiments may be misleading and relatively long-term enrichments may be needed to obtain a complete picture of the dynamic role of nutrients in algal succession.

The role of herbivores in controlling biomass accrual during succession is incompletely understood. Significant grazer effects in our experiment were noted only after sufficient time had elapsed for invertebrate colonization and growth, and only under N enrichment. Conversely, the algal community may influence grazer abundance and distribution. Studies in other stream systems indicate many aquatic invertebrates preferentially graze on certain algal taxa (Hart 1985, Becker 1990) and may track changes in algal biomass (Kohler 1985, Richard and Minshall 1988). Given such selectivity, site-specific differences in algal community structure and biomass related to areas of nutrient efflux would affect spatial distribution of invertebrates and perhaps allow certain populations to persist in the system as a whole.

In this context of temporal and spatial change in successional control, the importance of disturbance timing may be paramount in dictating community composition, maintaining spatial heterogeneity and, by inference, controlling trophic structure in an ecosystem. If interspate periods are long (i.e., disturbance frequency is low), the importance of spatial heterogeneity in nutrient sources with respect to algal biomass may decrease with time. In many systems, waters in spate carry high nutrient loads (e.g., McDiffett et al. 1989, Tate 1990, Grimm 1992) and associated scour can substantially reduce benthic algal biomass. Both of these factors should return algal communities to a state where allogenic controls dominate. In Sycamore Creek, this may shift dominance from cyanobacteria to diatoms, a change that may greatly influence structural and functional properties of the periphyton.

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