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ORIGINAL PAPER

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Mechanisms of benthic algal recovery following spates: comparison of simulated and natural events

Abstract We conducted a manipulative field experiment to examine individual and interactive effects of scour and short-term nutrient enrichment (4 h exposure) on post-spate recovery of benthic algae in a desert stream. We then compared recovery from these simulated-spate conditions to algal recovery patterns following a natural spate that increased water-column nutrient levels for 2 weeks. That event differentially scoured communities on artificial substrata in place for a long-term experiment, significantly reducing biomass in 49-day-old communities but causing no significant reduction of biomass in older, 133-day-old communities. Thus, we were able to examine recovery of scoured and non-scoured benthic algal communities under natural post-spate conditions. Both natural and simulated spates reduced actual and relative abundances of diatoms within communities. In the manipulative experiment, scoured communities accrued biomass more rapidly than those not subjected to scour, but short-term enrichment had no effect. Accrual of diatoms and green algae was stimulated by the scour manipulation, while cyanobacteria maintained equal rates of growth in all treatments. Following the natural spate, diatom and green-algal densities increased in scoured communities, but recovery of algal biomass was slow on both scoured and non-scoured substrata, primarily because cyanobacteria, the dominant algal group on all tiles, did not increase under exposure to highly nitrate-enriched waters. Rates of algal cell accrual were inversely correlated with the amount of algal biomass present at the start of a recovery sequence. Algal immigration rates measured immediately after the natural spate and during an interflood period in the same season did not differ, indicating that the algal drift pool was not augmented by disturbance. Benthic algal recovery following spates is strongly influenced by the degree of scour generated by the event, but recovery patterns are also affected by the length of post-spate enrichment and the taxonomic composition of the affected community.

Introduction

The effects of disturbance on ecosystem structure and function depend on multiple factors which can act independently or interactively. Recovery of disturbed communities is influenced by the severity of direct disturbance effects, such as biomass removal via mortality or export, as well as disturbance-related modification of physical and chemical habitat characteristics. Fires in grasslands, for example, remove biomass from the community, thus increasing light availability to persistent vegetation, but can also alter the pool of inorganic nutrients in the soil through a variety of mechanisms (Ojima et al. 1990). Post-fire recovery of these communities via vegetative reproduction of survivors is stimulated both by release of these individuals from competition and increased availability of resources (Ojima et al. 1990; Svejcar 1990). Similar rapid recovery occurs in benthic algal communities in stream ecosystems following disturbance by spates (Fisher et al. 1982; Power and Stewart 1987; Stevenson 1990). Spates affect primary producers in streams in ways that are analogous to the effects of fire in grasslands. Waters in spate often carry elevated dissolved-nutrient loads (Ortega et al. 1988; McDiffett et al. 1989; Grimm 1992), while the scouring effects of such disturbances can remove a substantial amount of algal biomass from stream substrata (Biggs and Close 1989; Entwistle 1989; Grimm and Fisher 1989). Moreover, detachment of benthic algae by scour elevates concentrations of drifting cells (Hamilton and Duthie 1987; Cazaubon 1988), increasing the pool of potential immigrants available for recolonization. Each of these mecha-

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nisms might be expected to enhance post-spate recovery of benthic algal communities, yet their relative contributions to the recovery process have not been elucidated.

Here, we report results of a manipulative field experiment designed to assess individual and interactive effects of biomass removal by scour and short-term elevation of nutrient concentrations on post-spate recovery of benthic algal communities. We compare results of this simulated spate with algal recovery following a natural spate which resulted in prolonged enrichment of stream surface waters and which differentially scoured attached communities on artificial substrata. Finally, we compare algal colonization rates on clean substrata immediately following the natural spate with those observed during an interflood period in the same season to assess the influence of elevated densities of algal immigrants on recovery.

Materials and methods

Site description and preliminary observations

Our study site was an unshaded, gravel-bed reach located at an elevation of 650 m in Sycamore Creek, a spatially intermittent stream in the Sonoran Desert of central Arizona, United States. At baseflow, surface waters in this system are typically high in dissolved phosphorus [30–70 μg · l^{-1} soluble reactive phosphorus (SRP)] but nitrate-nitrogen (NO_3-N) levels fluctuate considerably and often fall below 10 μg · l^{-1} (Grimm 1992). Enrichment experiments conducted in Sycamore Creek during late spring, summer, and fall have shown that algal growth is stimulated by nitrate enrichment during early stages of succession (Grimm and Fisher 1986), but such stimulatory effects diminish as periphyton biomass increases (Peterson and Grimm 1992). High algal biomass can be maintained during these times by proliferation of cyanobacterial and diatom taxa capable of nitrogen fixation (Peterson and Grimm 1992). The system is subjected to periodic spates during two distinct rainy seasons (late winter/early spring and summer). Spates often mobilize coarse sand and pea gravel, scouring attached algae to varying degrees from gravel, cobble, and boulders. During all seasons, spates in Sycamore Creek elevate NO_3-N concentrations in the water column above baseflow levels of <100 μg · l^{-1} to concentrations that frequently exceed 1000 μg · l^{-1} (Grimm 1992; Grimm and Fisher 1992). Algal colonization of denuded substrata is rapid, often generating a visible film of diatoms within 1–2 days of flood recession (Fisher et al. 1982; Grimm and Fisher 1989; Peterson et al. pers. obs.).

Manipulative experiment

Design, sample collection, and processing

We introduced unglazed ceramic tiles (28 cm^2) into Sycamore Creek on 17 May 1990 and allowed 3 weeks for algal biomass to accrue before subjecting attached communities to experimental manipulation. Tiles were attached with silicon caulk, in groups of six to ten, to the upper surfaces of 21 flat cinder blocks (20–25 cm long, 20 cm wide, 4 cm deep). These blocks were placed on the gravel stream bed with the attached tiles at 5–8 cm depth. Stream discharge decreased from 0.046 to 0.023 m^3 · s^{-1} during the study (17 May–4 July). On 14 June, when manipulations were imposed, discharge was 0.032 m^3 · s^{-1} and current velocity over tiles was 14.0 ($\pm$0.04 SE) cm · s^{-1}. Minimum/maximum water temperature ranged from 16.1/26.7° C on 17 May to 21.7/30.6° C on 4 July. Concentrations of NO_3-N, NH_4-N and SRP varied from 0 to 27 μg · l^{-1}, 17 to 54 μg · l^{-1}, and 18 to 30 μg · l^{-1}, respectively.

On 14 June we randomly partitioned cinder blocks into four groups and subjected algal communities within each to one of the following treatments: (1) scoured then soaked for 4 h in nutrient-enriched stream water (S/E); (2) scoured but not enriched (S/NE); (3) not scoured, but soaked for 4 h in enriched water (NS/E); and (4) neither scoured nor enriched (Control). Additional cinder blocks supporting clean ceramic tiles were introduced into the stream to assess the importance of immigration and reproduction of new colonists to recovery.

Scouring was accomplished by inverting cinder blocks and dragging the surfaces of attached tiles over clean, wet aquarium gravel. Each block that supported a community prescribed for enrichment was placed in an aluminum pan containing 4 l of filtered stream water amended with $NaNO_3$ and Na_2HPO_4 to yield 1270 μg · l^{-1} of NO_3-N and 330 μg · l^{-1} of SRP. These values represent average concentrations of these nutrients in Sycamore Creek flood water (N. B. Grimm, unpubl. data). Aluminum pans were placed in the stream during the 4-h enrichment to maintain a water temperature close to that of the ambient stream. Stream-water enrichment following spates in Sycamore Creek can persist for 1 day to several weeks (Grimm unpubl. data). In choosing a 4-h incubation, rather than a more realistic longer period, we weighed the benefits of a realistic exposure length against the substantial costs of artifacts that would be generated by extended retention of treated communities in an environment that differed in temperature, current regime, and colonization pool from the natural stream.

Four replicate tiles were collected from separate blocks within each treatment immediately after manipulation (day 0) and 1, 3, 5, 7, 14, and 21 days thereafter. Upon collection, each tile was partitioned into thirds and algae from each subsection were removed, using a razorblade, toothbrush, and washbottle, into a separate vial for determination of ash-free dry mass (AFDM), chlorophyll a, or algal cell densities and taxonomic composition; these three scrapes were randomly assigned to each variable. AFDM was determined as dry mass (60° C, 48 h) lost upon combustion (550° C, 4 h). Chlorophyll a was measured spectrophotometrically after samples were drawn onto Whatman GF/A filters and pigments extracted in boiling methanol (Tett et al. 1975). Samples used to determine algal cell densities and community composition were preserved, on site, with Lugol's solution (American Public Health Association 1989) and a subsample was later mounted in a syrup medium (Stevenson 1984) for quantitative counts via light microscopy. We randomly chose three out of four replicates from each treatment to estimate densities of live diatoms (intact frustules containing chloroplasts) and non-diatom algae from counts of at least 500 cells at 1000× magnification; at least three 100-μm wide transects of varying lengths were scanned for each count. Only common taxa (chosen via qualitative preliminary scans of samples) were identified to species; sub-dominant and rare taxa were enumerated at the generic or divisional level. Filamentous cyanobacteria were enumerated as 10-μm lengths since trichome crosswalls were not always evident and, thus, cell counts of these taxa would be unreliable.

Triplicate water samples were collected from both the surface stream and enriched stream water and analyzed for SRP (molybdate-blue method, Murphy and Riley 1962), NO_3-N (cadmium-reduction method, Wood et al. 1967), and NH_4-N (phenol-hypochlorite method, Solorzano 1969) content. Duplicate water samples were taken from aluminum pans following the 4-h enrichment to determine the amount of nutrients taken up by algae during the incubation. To quantify nutrient loss attributable to adsorption to the cinder blocks themselves, we leached clean blocks in distilled water in the lab for three weeks (equal to the length of in-stream incubation of blocks supporting tiles), replacing water every 2 days, and sampled nutrients before and after a 4-h incubation in enriched water.

Statistical analyses

Changes in dissolved nutrient concentrations in aluminum pans during 4-h incubations were detected using t-tests. To examine the

relationship between attached algal biomass and NO_3-N removed from solution during enrichment, we estimated the total periphyton biomass on blocks within each pan by multiplying the mean AFDM $\cdot$ cm^{-2} on tiles collected from a given block by the total exposed surface area (top+sides) of that block. We then calculated pan-specific NO_3-N uptake rates and NO_3-N uptake per unit biomass for each block, and tested for differences between treatments using t-tests.

Initial effects of scour/enrichment manipulations of AFDM, chlorophyll a, and taxonomic structure of algal communities (i.e., arcsine-square root transformed relative abundances of individual taxa or algal divisions) were assessed using two-factor analysis of variance (ANOVA).

The relative influences of biomass removal by scour and short-term enrichment on algal community dynamics were assessed using a three-factor [time (0–21 days)×enrichment (0, 1)×scour (0, 1)] ANOVA on AFDM, chlorophyll a concentrations, and algal cell densities (all natural-log transformed to homogenize variances). Cell density data were acquired up to day 14 only. Significances of interaction terms between factors were used to infer differences in accrual rates. All statistical tests were performed using the Statistical Analysis Systems (SAS Institute 1990).

Natural spates

Design, pre-spate conditions, and sampling procedures

Five weeks after completion of the manipulative experiment, in August 1990, Sycamore Creek experienced spates on three consecutive days (13, 14, 15 August). The last and largest of these events differentially affected algal communities attached to two sets of ceramic tiles which had been in the stream since either 4 April (133 days old; April-start) or 27 June (49 days old; June-start), 1990. These tiles were secured in depressions within 70×35×10 cm concrete blocks so that their upper surfaces were flush with the surface of the concrete, thus reducing the chance of displacement during high discharge events. April- and June-start tiles were interspersed among 14 concrete blocks distributed in a 2×7 matrix atop pea-gravel substrata; at baseflow, tile surfaces were submerged at depths of 8.5–15.0 cm. Pre-spate stream discharge was 0.003 $m^3 \cdot s^{-1}$. Current velocity over the sampler array had been declining in the previous weeks and was negligible over most samplers. Minimum/maximum measures of water temperature during this time ranged from 21.1/31.7° C on 8 August to 25.0/32.2° C on 31 August.

Algal communities on April-start tiles exhibited no significant loss of biomass during the 15 August spate (see Results). In contrast, the younger, June-start communities were visibly scoured by this event. Thus, we were able to track recovery of two established algal communities, one affected by scour (June-start; scoured) and one not (April-start; non-scoured), under an enrichment regime and immigration densities typical of a natural spate. Following the 15 August spate, a set of clean ceramic tiles was added to the sampler array to track new post-spate colonization.

We collected four replicate tiles, randomly selected from separate blocks, from each set (April, June, New) at 1, 3, 5, 7, 9, and 16 days following the 15 August spate. This recovery sequence was terminated by another spate on 5 September. As in the manipulative experiment conducted in June, samples were partitioned into three equal subsets and processed, as previously described, for determination of AFDM, chlorophyll a, and algal densities and taxonomic composition. Chlorophyll a samples from these collections fell victim to a spectrophotometer malfunction and could not be analyzed. Taxonomic analyses of these samples were carried out at the species level, allowing us to calculate total algal biovolume and species-specific relative biovolume as well as actual and relative cell densities. Species-specific counts were converted into biovolume by measuring dimensions of 10–25 cells (for common taxa) and using formulae of geometric shape that approximated cell shapes (Kirschtel 1992). Biovolumes of rare taxa were calculated from measurements of one to several individuals.

Statistical analyses

Pre- and post-spate values of AFDM, cell densities, and cell biovolume (all ln-transformed), and relative abundances and biovolumes (arcsine-square-root transformed) within each tile set were compared using t-tests. Differences in post-spate accrual rates of AFDM or algal cells between scoured and non-scoured communities were detected using a test for heterogeneity of slopes (Freund et al. 1986).

Comparisons among recovery sequences for both simulated and natural spates

Rates of algal accrual on tiles from all treatments, including clean tiles, from both manipulative and natural experiments, were estimated with the least-squares solution for the rate of change in ln-transformed cell densities during 14 or 16 days of community development. We employed cell densities in this analysis, rather than a mix of density and biovolume, so that criteria with which accrual rates were assessed were comparable between studies. Average accrual rates from each sequence were plotted against mean ln-transformed biomass attached to tiles at the start of that sequence to ascertain whether a relationship existed between initial algal biomass on substrata and cell accrual rates. Pearson correlation coefficients were used to assess the strength of this relationship for all taxa combined, and separately for taxa within each major algal division (diatoms, green algae, cyanobacteria).

We used algal cell accumulation on clean tiles over the first 24 h of incubation as a measure of immigration rate (cf. Stevenson and Peterson 1989) to assess differences in the algal immigration pool between the post-spate period in August and the June interflood period.

Results

Manipulative experiment

Nutrient uptake during enrichment

Nitrate-N concentration was significantly ($P<0.001$) reduced during the 4-h exposure of both scoured and non-scoured algal communities to enriched stream water (Fig. 1a). Incubation of clean blocks had no influence on NO_3-N concentration (Fig. 1a) indicating that the observed decrease in NO_3-N was attributable to biological uptake. Concentration of SRP was significantly reduced in all pans during incubation as well, but also declined significantly ($P<0.001$) in the presence of algae-free cinder blocks, suggesting abiotic adsorption of dissolved phosphorus to a component of the block. Hence, we limit further discussion of nutrient dynamics to nitrate.

The amount of NO_3-N removed from enrichment basins per hour did not differ appreciably ($P=0.084$) between scoured and non-scoured treatments (0.405 ± 0.029 SE and 0.532 ± 0.057 mg NO_3-N $\cdot h^{-1}$, respectively) (Fig. 1b). Because of the large difference ($P<0.001$) in periphyton biomass between treatments, however, the amount of NO_3-N taken up per unit biomass was significantly greater ($P<0.001$) in scoured communities (5.6 ± 0.39 µg NO_3-N $\cdot$ mg^{-1} AFDM) then in non-scoured communities (1.5 ± 0.17 µg NO_3-N $\cdot$ mg^{-1} AFDM) (Fig. 1b).
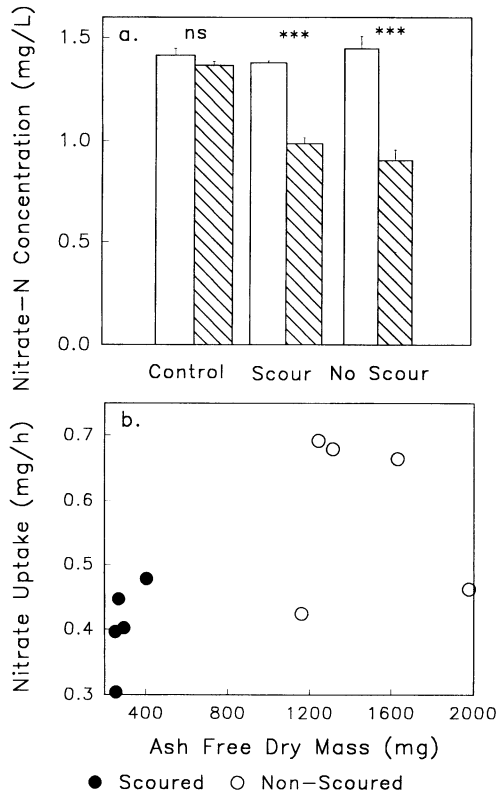
Fig. 1 a Mean NO_3-N (+1 SE) concentration in enriched stream water before (*open bars*) and after (*shaded bars*) a 4-h incubation of algae-free cinder blocks (control) and cinder blocks supporting scoured or non-scoured algal communities. **b** Relationship between NO_3-N uptake rates during 4-h incubations and estimated total algal biomass within each enrichment basin. (*Full circles* scoured, *open circles* non-scoured), *ns*=not significant, ***difference between means significant at $P<0.001$)

Fig. 2 a–c Changes in mean (±1 SE) **a** AFDM **b** algal cell densities and **c** chlorophyll *a* over 21 days for communities subjected to the following treatments: control (*open circles*), non-scour/enriched (*closed circles*), scour/not enriched (*open triangles*), scoured/enriched (*closed triangles*), and new colonization tiles (*open diamonds*)

Algal community response to enrichment and scour

Scour manipulation of attached algae resulted in significant reduction of AFDM, chlorophyll *a*, and algal cell densities (two-factor ANOVA, scour effects: all $P<0.001$), but enrichment had little or no effect (enrichment effects: AFDM $P=0.080$; Chlorophyll *a* $P=0.189$; cells $P=0.868$) (Fig. 2). Algal taxonomic structure (i.e., relative abundances of diatoms, green algae, and cyanobacteria) was also unaltered by 4-h exposure to enriched stream water. On the day of nutrient/scour manipulation, non-scoured communities were numerically dominated by the N_2-fixing diatom *Epithemia sorex* Kütz. [78.3%±3.3 SE (NS/E and control, collectively)] with the cyanobacteria *Anabaena* (5.2%±1.3 SE) and *Calothrix* spp. (2.7%±0.7 SE) as sub-dominants. Scour significantly altered taxonomic structure within the periphyton, principally via reduction in percent contribution of diatoms ($P<0.001$) (*E. sorex* reduced to 43.7%±5.2) and concomitant increase in relative abundance of cyanobacteria ($P=0.018$) (*Calothrix* and *Anabaena* increased to 8.6%±4.8 and 19.5%±5.9, respectively) (Fig. 3).

Examination of changes in AFDM, chlorophyll *a*, and algal cell numbers over the 21 days following manipula-
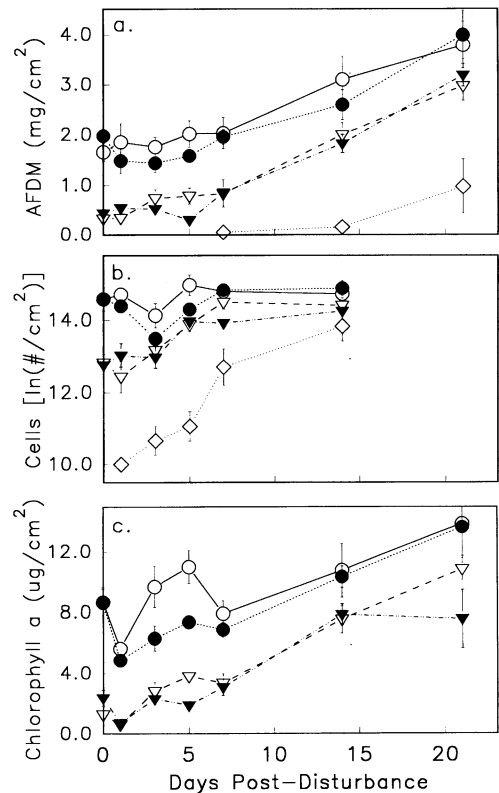
tion with a three-factor (scour×enrichment×time) ANOVA revealed that each of these biomass estimators increased during recovery, that each was significantly affected by scour, and that, while chlorophyll *a* concentrations were lower in enriched communities, enrichment had no significant effect on either AFDM or cell densities (Fig. 2, Table 1). Further, highly-significant scour × time interactive effects indicated more rapid biomass accrual on scoured versus non-scoured substrata for all variables (Table 1).

Comparison of algal accrual rates indicated differences among algal divisions in response to our manipulations (Table 2). Within a given division, highest rates of cell accrual occurred on newly introduced clean tiles, although, for cyanobacteria, accrual on clean tiles was highly variable. Cyanobacteria collectively exhibited significant growth on both scoured and non-scoured tiles, with no apparent effect of either scour or enrichment. In contrast, cell numbers of both diatoms and green algae increased significantly on scoured substrata, but exhibited no net increase in non-scoured communities, regardless of enrichment conditions.
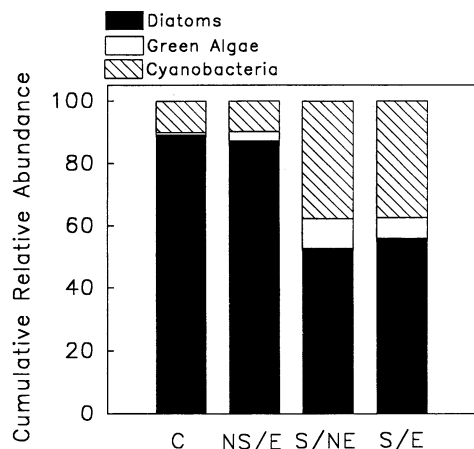
Fig. 3 Relative contribution to total algal densities of the three major algal division to communities exposed to each of four experimental treatments on day 0, immediately following scour and/or nutrient manipulation (*solid* diatoms, *open* green algae, *shaded* cyanobacteria)

Natural spates

Discharge and nutrient characteristics

The three spates that occurred in Sycamore Creek between 13 and 15 August differed in magnitude and in their effect on instream nutrient concentrations (Fig. 4). The first of these events was not of high enough magnitude to mobilize sand and gravel on the stream bed, but greatly increased tubidity in the surface stream and deposited a thin layer of silt over artificial and natural sub-

strata. Stream discharge after this event, on the morning of 14 August, was $0.018 \ \mathrm{m}^3 \cdot \mathrm{s}^{-1}$, up from pre-spate levels of $0.003 \ \mathrm{m}^3 \cdot \mathrm{s}^{-1}$. Nitrate-N concentration jumped from 11 to 284 $\mu g \cdot l^{-1}$ and SRP increased to 67 $\mu g \cdot l^{-1}$ from pre-spate levels of 43 $\mu g \cdot l^{-1}$. The second spate, on 14 August, occurred in two waves, the first which increased discharge to $0.363 \ \mathrm{m}^3 \cdot \mathrm{s}^{-1}$ and elevated NO_3-N and SRP concentrations to 585 and 426 $\mu g \cdot l^{-1}$, respectively. A second distinct front, 40 min after the first, carried NO_3-N loads of 1121 $\mu g \cdot l^{-1}$; discharge of this event peaked at $1.893 \ \mathrm{m}^3 \cdot \mathrm{s}^{-1}$, 1.5 h after the initial wave, and declined to $0.100 \ \mathrm{m}^3 \cdot \mathrm{s}^{-1}$ by the next morning when NO_3-N had dropped to 748 $\mu g \cdot l^{-1}$. At 0730 hours on 15 August, before post-spate samples could be collected, the initial front of a third spate raised stream depth from 8 to 80 cm within 2 min. Discharge and NO_3-N concentrations continued to rise for 1 h when discharge peaked at 61 $\mathrm{m}^3 \cdot \mathrm{s}^{-1}$. Nitrate-nitrogen rose steadily to 2867 $\mu g \cdot l^{-1}$ at 1330 hours, but SRP levels remained relatively stable throughout the event (Fig. 4). Within 24 h, discharge had returned to $0.110 \ \mathrm{m}^3 \cdot \mathrm{s}^{-1}$ and NO_3-N and SRP had declined to 1673 and 164 $\mu g \cdot l^{-1}$, respectively. Nutrient concentrations declined steadily thereafter, but did not reach pre-spate levels for 2 weeks.

Community resistance and recovery

The large, 15 August spate deposited a 2-cm layer of gravel over concrete sampling devices; these blocks were carefully excavated to reveal that each sampler supported a patchwork of scoured and non-scoured tiles. We saw no evidence that attached algal communities were affect-

Table 1 Results of three-factor ANOVAs on ln-transformed values of AFDM, Chlorophyll a, and algal cell densities. Numerator degrees of freedom (df) for F statistic are given; denominator df are as follows: AFDM and chlorophyll a, 84; cell densities, 48. Probabilities (P)<0.05 are in bold. Since no 3-way interaction was significant, these values are not presented

| Source	AFDM			Chlorophyll a			Cell density		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Scour	1	180.9	**<0.001**	1	278.0	**<0.001**	1	131.8	**<0.001**
Enrichment	1	1.2	0.279	1	5.4	**0.023**	1	2.8	0.103
Age	6	46.7	**<0.001**	6	41.2	**<0.001**	5	19.9	**<0.001**
Scour×enrichment	1	0.2	0.686	1	0.2	0.68	1	1.1	0.302
Scour×age	6	4.3	**<0.001**	6	9.0	**<0.001**	5	7.8	**<0.001**
Enrichment×age	6	1.5	0.188	6	2.2	0.054	5	1.0	0.449

Table 2 Cell accrual rates ($b\pm SE$) of taxa within three algal divisions on substrata from four experimental treatments and new-colonization tiles over the 14 days following field manipulations. Probabilities (P) <0.05 are in bold, indicating which rates are significantly different from zero; n=18 for all estimates. Within a given algal division, accural rates bearing the same superscript do not differ significantly (P>0.05, t-test). (S scour, E enrichment, NS no scour, NE no enrichment)

Treatment	Diatoms			Cyanobacteria			Green algae		
	b	SE	*P*	b	SE	*P*	b	SE	*P*
S/E	0.063[a]	(0.020)	**0.005**	0.148[a]	(0.029)	**<0.001**	0.286[ac]	(0.135)	**0.050**
S/NE	0.084[ac]	(0.033)	**0.024**	0.195[a]	(0.036)	**<0.001**	0.183[a]	(0.055)	**0.004**
NS/E	−0.015[b]	(0.024)	0.544	0.152[a]	(0.032)	**<0.001**	−0.162[b]	(0.148)	0.290
Control	−0.048[b]	(0.025)	0.072	0.138[a]	(0.029)	**<0.001**	0.250[abc]	(0.196)	0.221
New colonization	0.173[c]	(0.043)	**0.001**	0.347[a]	(0.173)	0.067	0.402[c]	(0.093)	**<0.001**

Fig. 4 Changes in Sycamore Creek discharge (*D, solid line*) and ambient water-column NO₃-N (*open circles, dashed line*) and PO₄-P (*solid circles, short dashes*) concentration during and after three consecutive spates (indicated by *arrows*) in August 1990
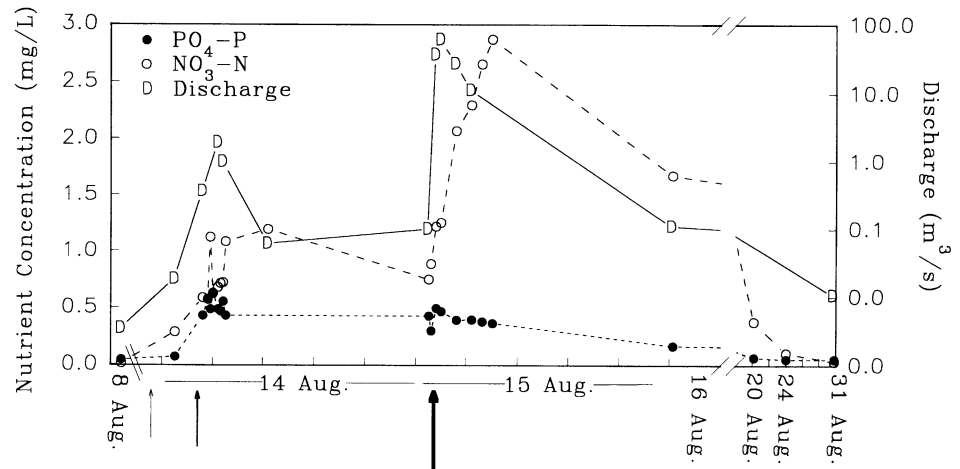
ed by excavation. June-start communities were heavily scoured by the spate, with each tile displaying a mosaic of attached material and exposed tile surface. In contrast, older (April-start) communities appeared unaffected, supporting the same thick, cohesive mats that were present prior to the spates. We assume that attached algae were subjected to spate-induced scour for at least 1 h, during the period of increasing discharge, and that sampling devices were buried as mobilized gravel was redeposited on the declining limb of the hydrograph. The effect of the 24-h burial itself on community structure and function could not be assessed because of the lack of an adequate control.

Community-related differences in disturbance effects were evident from examination of both AFDM and algal biovolume (Fig. 5). The 61-m³ · s⁻¹ spate had no significant effect on AFDM in April-start communities, whereas June-start tiles, which supported ca. half the pre-spate biomass as older communities, lost >80% of their biomass (P=0.003) (Fig. 5a, b). High variability in algal biovolume among replicates precluded detection of a significant reduction in total biovolume in either April- or June-start communities. When partitioned by algal division, however, significant disturbance effects were detected (Fig. 5c, d). Cyanobacteria (primarily *Calothrix* and *Schizothrix* spp.) were common in both communities prior to the 15 August spate, contributing 62.9% (±13.1 SE) to algal biovolume in April-start communities and 46.2% (±11.5) to those established in June; collective cyanobacterial biovolume was unaffected by the disturbance. In contrast, diatoms, which comprised 31.5% (±13.2 SE) and 50.4% (±12.3 SE) of total algal biovolume in April- and June-start communities, respectively prior to the spates, were significantly reduced on all tiles (April-start, P=0.090; June-start, P=0.020) (Fig. 5c, d). *Fragilaria pinnata* Ehr. was the dominant diatom in pre-spate communities, contributing 9.0% (±4.2 SE) to algal biovolume of older communities and 15.8% (±7.2 SE) to June-start communities. This differential susceptibility among algal divisions caused a reduction in the relative contribution of diatoms to total algal biovolume following disturbance from 31.5% to 8.6% (± 3.7 SE) in April-
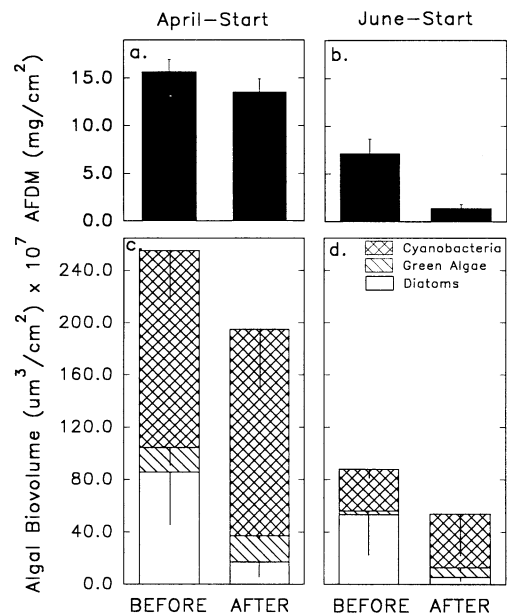

Fig. 5a, b Mean AFDM (+1 SE) and **c, d** division-specific algal biovolume (−1 SE) before and after the 15 August spate for algal communities established in April and June. (*Hatched* cyanobacteria, *shaded* green algae, *open* diatoms)

start communities and from 50.4% to 12.8% (±4.4 SE) on June-start tiles.

Algal biomass, measured as either AFDM or cell densities, did not change in either April- or June-start communities in the 16 days following the spate (Fig. 6). Tests for heterogeneity of slopes showed the two communities did not differ in rates of post-spate cell accumulation, and differed only slightly (P=0.079) in rate of AFDM accrual. As with resistance parameters, patterns of recovery differed among treatments based on differences in responses of among algal divisions (Table 3). On April-start tiles, none of the three algal divisions increased significantly in cell numbers over the 16-day post-spate recovery. In June-start communities, however, both diatom and green-algal cells increased significantly, while cyanobacterial densities remained unchanged. All

Table 3 Growth rates ($b\pm$SE) of all algal taxa combined (total) and taxa within each of three algal divisions on April-start, June-start, and new-colonization tiles over 16 days following the 15 August spate. Probabilities (P)>0.05 are in **bold**, indicating which rates are significantly different from zero; n=24 for all estimates. Within a given algal division, accural rates bearing the same superscript do not differ significantly (P>0.05, t-test)
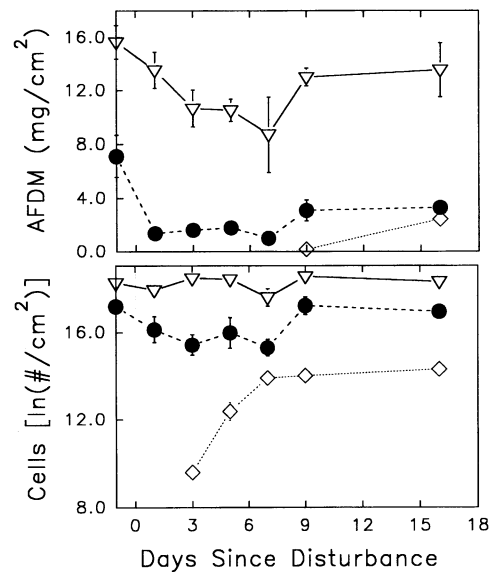
Community type	All taxa			Diatoms			Cyanobacteria			Green algae		
	b	SE	P	b	SE	P	b	SE	P	b	SE	P
April-start	0.009[a]	(0.022)	0.700	0.064[a]	(0.048)	0.195	0.007[a]	(0.023)	0.745	0.040[a]	(0.028)	0.165
June-start	0.080[a]	(0.048)	0.079	0.143[ab]	(0.046)	**0.006**	0.078[a]	(0.048)	0.115	0.097[a]	(0.039)	**0.021**
New colonization	0.289[b]	(0.064)	**<0.001**	0.307[b]	(0.083)	**0.002**	0.298[b]	(0.049)	**<0.001**	0.338[b]	(0.112)	**0.007**

Fig. 6 Mean ($\pm$1 SE) AFDM and cell densities in April-start communities (*open triangles*), June-start communities (*closed circles*), and newly introduced clean ceramic tiles (*open diamonds*) before and for 16 days after the 15 August spate (day 0)

Fig. 7 Relationship between net algal growth rates ($\pm$1 SE) and the amount of biomass ($\pm$1 SE) attached to tiles at the start of each recovery sequence for all algal taxa combined, and for each of the three major algal divisions (*closed symbol* enriched conditions, *open symbols* unenriched, *circles* non-scoured communities, *triangles* scoured communities, *diamonds* new colonization tiles, *closed symbols* that identify growth rates associated with the 15 August spate are surrounded by a *dotted circle*)

three groups exhibited highest post-spate cell accrual rates on clean, newly-introduced tiles (Table 3).

Comparisons of immigration rates and algal cell accrual among recovery sequences

Algal immigration rate (measured as 1 d accumulation on clean tiles) immediately after the August spate (1.79×10^4 cells $\cdot$ cm^{-2} $\cdot$ day^{-1}, SE=0.37×10^4) did not significantly differ (P>0.10) from that measured during the June interflood period (2.26×10^4 cells $\cdot$ cm^{-2} $\cdot$ day^{-1}, SE= 0.44×10^4). Taxonomic composition of these two immigration assemblages differed considerably, however, with diatoms comprising 68.5% ($\pm$ 5.2) of 1-day colonists in mid June but only 15.0% ($\pm$7.1) of August immigration assemblages (P<0.01). Cyanobacteria contributed 30.2% ($\pm$5.1) and 81.3% ($\pm$6.4) to June and August immigration assemblages, respectively. Despite these taxonomic differences, and the large disparity in water-column nutrient

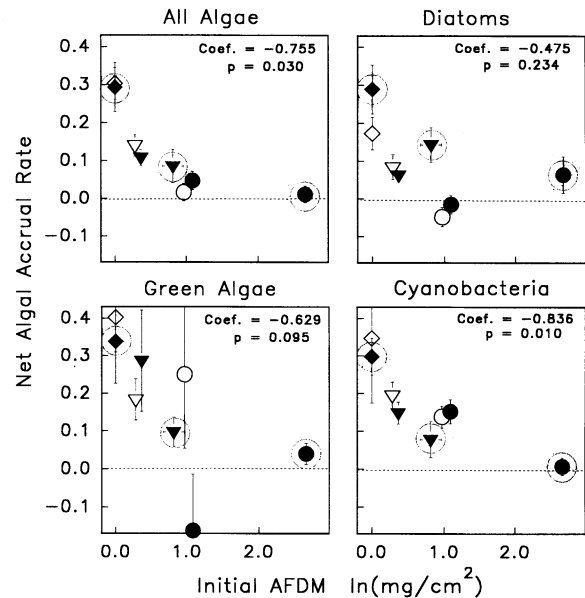concentrations, algal accrual rates on clean tiles did not differ between the June and August colonization periods (Fig. 7).

Rates of cell accrual following natural and simulated spates were inversely correlated with the amount of biomass attached to tiles at the start of a recovery sequence (Fig. 7). When analyzed separately, each of the three algal divisions exhibited different relationships between accrual rate and initial biomass; cyanobacteria emerged as the principal contributor to the observed inverse correlation. Detection of a significant relationship between diatom accrual and initial biomass appeared to be compromised by a propensity in this group for higher rates of accumulation following the August flood relative to those noted during our manipulative experiment in June. Accrual rates of green algae were highly variable and displayed no strong, consistent pattern.

Discussion

Results of this study enabled us to assess the relative importance of three specific factors in driving post-spate recovery of benthic algae in stream ecosystems: (1) stimulation of algal reproduction by nutrient-rich flood waters; (2) stimulation of algal reproduction by scour-induced removal of algal biomass and subsequent release of persistent cells from autogenic constraints; and (3) increased algal immigration rates, as cells suspended into the water column by scour recolonize denuded substrata.

Algae possess a number of physiological adaptations that allow them to exploit transient increases in dissolved nutrients. Many taxa, for example, "luxury consume" excess supplies of dissolved phosphate (Stevenson and Stoermer 1982; Cembella et al. 1985) and, to a much lesser extent, nitrate (Elfrifi and Turpin 1985) which can then be used for later growth. In addition, benthic algae can greatly increase their rate of nitrate uptake during short-term exposure to nutrient-rich water (Triska et al. 1983; Grimm 1992). Tracer experiments have shown that high stream nutrient concentrations can be reduced significantly by short-term biotic uptake, whether nutrients were augmented via direct injection (Sebetich et al. 1984) or through storm-induced enrichment (Triska et al. 1990).

Given the existence of such adaptations, it follows that short-term exposure to enriched flood waters should stimulate algal growth and accelerate recovery. Growth of algal communities we examined, however, showed little response to either short-term (4 h) or prolonged (2 week) exposure to elevated nutrient concentrations. During short-term enrichment, we noted a significant reduction in nutrient levels within enrichment basins, indicating that biotic uptake of dissolved nutrients did occur. Humphrey and Stevenson (1992) obtained similar results; their 12-h enrichment of artificial stream channels during simulation of a sub-scouring spate failed to stimulate accrual of algal biomass, despite measured increases in the nutrient content of periphyton mats.

There are at least two reasons why short-term enrichment was ineffectual. First, because of constraints to diffusion imposed by the periphyton mat, access to enriched stream water should be limited, primarily, to cells in upper strata of the community (Riber and Wetzel 1987; Horner et al. 1990). Our nutrient-uptake data lend support to this contention. Based on a nitrogen content for microalgae of 3–11% by weight (Ahlgren et al. 1992), the 1.5–5.6 µg N · mg^{-1} AFDM (a 0.15–0.56% increase) for non-scoured and scoured communities, respectively, is minimal. It is doubtful, however, that all attached algae on tiles and blocks had access to enriched water. The fact that equal amounts of NO_3-N were removed from all enrichment basins, regardless of scour treatment (see Fig. 1a), strongly suggests that only cells at the surface of these mats were actively taking up nutrients, with greater uptake per unit biomass by the lower-density, scoured communities as a result. Secondly, excess nutrient stores, sequestered within cells residing at mat surfaces during short-term enrichment, were likely exhausted within one or two cell divisions, and thus would be insufficient to fuel the sustained reproduction needed to generate an appreciable increase in community biomass in the long term. Short-term enrichment may be more important in systems that are strongly limited by phosphorus. Unlike nitrate, the primary limiting nutrient in Sycamore Creek, excess phosphorus can be accumulated and stored as polyphosphate by most algal taxa in quantities sufficient to sustain extended growth during P-limited conditions (Cembella et al. 1985).

Results from our manipulative experiment, and those from other investigations, indicate that the high dissolved nutrient loads carried by flood waters are not essential to induce the initial pulse of benthic algal growth often observed following scour disturbance. Scour manipulations often increase reproduction and/or metabolic activity within algal/bacterial biofilms, even when nutrient concentrations in overlying stream water are low (e.g. Horner et al. 1990; Blenkinsopp and Lock 1992; Peterson and Stevenson 1992). This stimulus is likely driven by re-exposure of persistent cells to light, which attenuates rapidly to limiting levels as algal mats thicken (Jørgensen et al. 1983; Kühl and Jørgensen 1992; Dodds 1992), and to water-column nutrients. Bothwell (1989) demonstrated that, in thin periphyton mats, algal growth is saturated at very low nutrient levels and responds rapidly to minute increases in dissolved nutrients. Thus, following a severe spate, cells within a thin persistent biofilm would be bathed in water carrying nutrient loads far in excess of those needed to saturate growth requirements.

The degree to which accessibility of light and dissolved nutrients to attached algal cells is increased by scour disturbance is dictated, primarily, by the amount of biomass retained on substrata through a scour event. A number of investigators have found the rate of post-spate biomass accumulation in lotic periphyton to be strongly and inversely correlated to the amount of biomass that persists through the disturbance (Stevenson 1990; Uehlinger 1991; Humphrey and Stevenson 1992; this study). Thus, the extent of biomass removal via scour is probably more important than external nutrient regime in regulating algal accrual early in recovery.

While the impact of short-term enrichment on benthic algal recovery appears to be minor, algal standing crops in lotic systems can be greatly influenced by prolonged enrichment (Peterson et al. 1985; Biggs and Close 1989; Lohman et al. 1992; Welch et al. 1992). Previous experiments in Sycamore Creek have shown that NO_3-N additions lasting 7–35 days significantly increase accrual of algal biomass relative to unenriched controls (Grimm and Fisher 1986). The differential effects of the 15 August spate gave us an opportunity to monitor post-spate recovery in scoured (June-start) and non-scoured (April-start) algal communities under prolonged enrichment associated with a natural spate.

Contrary to expectations, algal recovery following this spate was extremely slow, even in June-start communities which had lost >80% of their biomass. We believe both taxonomic and physiognomic factors contributed to

the slow recoveries observed. In both April- and June-start communities, diatom densities were significantly reduced by the spate. April-start communities were dominated by *Calothrix*, a mucilaginous, N_2-fixing blue-green alga whose trichomes intertwined to form a thick, cohesive, extremely resistant mat; diatoms lost in the spate were likely removed from the surface of this mat, while persistent diatom cells were embedded within. Surfaces of cohesive periphyton mats, in addition to imparting high resistance to physical disturbance (Neumann et al. 1970; Peterson et al. 1990; Applegate and Bryers 1991), greatly impede penetration of light (Jørgensen and Des Marais 1988; Ploug et al. 1993) and dissolved materials (Applegate and Bryers 1991). Thus, the lack of post-spate cell accrual in April-start communities likely stemmed from inavailability of allogenic resources to all but those cells at the uppermost surface of these thick algal mats.

Pre-spate characteristics of June-start communities differed from the older, April-start communities in ways that influenced their disturbance response. These communities supported ca. 50% less biomass, contained a large diatom component, and were less structurally cohesive (and, thus, more susceptible to disruption by scour) than those established in April. As in the older communities, diatom biomass on June-start tiles was significantly reduced by the spate leaving a community dominated by cyanobacteria. Densities of both diatoms and green algae increased significantly on June-start tiles after the spate, but community biomass exhibited no significant change because cell densities within the dominant blue-green algal component of the community remained unchanged.

Our results suggest that species composition can be a strong determinant of both community resistance and recovery. In algal communities dominated by diatoms (Peterson et al. 1990) or filamentous green algae (Power and Stewart 1987; Peterson and Stevenson 1992), resistance to disturbance can lessen as communities age, presumably as cells at the base of thick, late-successional mats senescence and dettach. In contrast, communities dominated by mucilage-producing, filamentous cyanobacteria appear less prone to display such patterns of senescence. Many filamentous blue-green algae can fix N_2, photosynthesize under hypoxic conditions (Lee 1980), and shift to heterotrophic growth in the dark (Bastia et al. 1993) – these physiological adaptations would prevent senescence under resource-depleted conditions at the base of thickening benthic algal mats. These adaptations, coupled with development of an interwoven, cohesive physiognomy may confer increased resistance with age to algal communities dominated by filamentous cyanobacteria.

While conferring higher resistance, the fact that post-spate assemblages were dominated by cyanobacteria, rather than diatoms or green algae, likely accounted for the failure of algal biomass to recover rapidly from the August spates. Several lines of evidence suggest that blue-green algae should be poor competitors in the nitrate-rich conditions that characterize the post-spate environment in Sycamore Creek. In the June manipulative

experiment, when NO_3-N levels were low, N_2-fixing cyanobacteria increased in numbers, regardless of treatment or community biomass; populations of diatoms and green algae, in contrast, apparently required access to light and dissolved nutrients via scour to maintain growth. A previous experiment in Sycamore Creek showed that N_2-fixing taxa (primarily *Calothrix*) grew more rapidly, reached greater biomass, and attained a higher degree of dominance on unenriched substrata than on substrata that leached nitrate during an 89-day successional sere (Peterson and Grimm 1992). Reuter and Axler (1992) reported that cyanobacteria-dominated assemblages in Lake Tahoe possessed very low affinities for NO_3-N compared to diatoms, thus should be poor competitors in high-nitrate environments. Laboratory culture experiments on phytoplankton assemblages reveal that, at temperatures similar to those in our study ($24°$ C), complete cyanobacterial dominance shifts to complete diatom dominance as N: P supply ratios increase toward high relative N availability (Tilman et al. 1986).

The immigration rates of 1.8–2.2×10^4 cells $\cdot$ cm$^{-2} \cdot$ day^{-1} measured during this study exceed those reported from other systems [Brettum 1974 (max.=c. 6200 cells $\cdot$ cm$^{-2} \cdot$ day^{-1}); Müller-Haeckel and Håkansson 1978 (max.=c. 10000 cells $\cdot$ cm$^{-2} \cdot$ day^{-1}); Stevenson and Peterson 1989 (max.=c. 2500 cells $\cdot$ cm$^{-2} \cdot$ d^{-1})]. No difference was detected, however, between immigration rates immediately following the August flood and those measured during mid-June, arguing against the kind of spate-induced augmentation of the drift pool noted by Hamilton and Duthie (1987). Algal drift data from two 36-h diel drift/colonization studies conducted in Sycamore Creek (Peterson, unpubl. data), one from 28–29 June 1990 and a second from 20–21 August, indicates that 3 days after the August spate, average algal drift densities were more than twice as high (1572 cells $\cdot$ ml^{-1}), with a much greater diatom component(56%) than during the interflood period in late June (669 cells $\cdot$ ml^{-1} – 10.5% diatoms). This implies that, following the August spate, rapid proliferation and subsequent emigration of diatoms from newly colonized gravel substrata augmented the immigration pool, possibly accounting for enhanced diatom accrual rates following this event. Large post-spate standing crops of persistent algae on both April- and June-start tiles, however, precluded immigration even at these high rates, from significantly contributing to post-spate recovery (cf. Stevenson 1986).

In most stream systems, benthic algal recovery from scouring spates likely initiates from multiple starting points, ranging from substrata that have been denuded of algal biomass to surfaces that vary in the amount and taxonomic content of persistent algae. The scale at which this mosaic is evident depends, at least partially, on the predominant substratum type in a given system. For example, spatial variation in scour effects should be readily apparent in systems where sand and gravel are scarce and large cobbles, boulders, and/or exposed bedrock are common; such substrata contain refugia from scour for attached algae (Dudley and D'Antonio 1991; Peterson

pers. obs.). In such systems, a spate may generate, over a relatively small area of stream bed, an array of algal patches, each differing in the rate and pattern of post-spate recovery. In contrast, spates large enough to mobilize the coarse gravel that predominates in Sycamore Creek denude a large percentage of the stream bed of macroscopic algal growth (Fisher and Grimm 1988; Grimm and Fisher 1989). Larger substrata in such systems do retain pockets of persistent algae through spates (Uehlinger 1991; Peterson pers. obs.; this study), but these patches are often scarce enough to preclude detection by coarse-scale sampling protocols or are not sampled because they occur on substrata that represent only a small percentage of the benthic habitat. Such pockets of persistent algae may serve as sources of propagules of late-successional algal taxa (cf. Uehlinger 1991), represent "hot spots" of both aerobic and anaerobic metabolic activity (Stock and Ward 1991), or, in Sycamore Creek, may house N_2 fixers and thus affect supplies of this important limiting nutrient in this system.

Diatoms typically dominate initial post-spate assemblages in Sycamore Creek by virtue of their rapid recolonization of the large expanses of denuded gravel (Grimm and Fisher 1989), a response more likely driven by the high efficiency with which spates remove algae from substrata rather than the elevated nutrient content of flood waters. There are two likely reasons for this. First, clean gravel substrata should facilitate more rapid new colonization of diatoms than surfaces supporting persistent algal residues. In slow currents, like those present in this study, some diatoms reproduce more rapidly on clean surfaces than on those supporting algal or bacterial biomass (Peterson and Stevenson 1989; cf. Steinman and Parker 1990) – in faster currents, such biofilms can facilitate algal immigration by counteracting the negative influence of current shear (Stevenson 1983; Peterson and Stevenson 1989). Second, as discussed previously, high nutrient concentrations are not necessary to stimulate growth during early stages of algal succession when cell densities are low (Bothwell 1989), thus rapid colonization of clean substrata would be expected regardless of enrichment status. Prolonged enrichment, however, should facilitate persistence of diatoms in the system and delay the shift in dominance to filamentous cyanobacteria that is commonly observed in mid- to late stages of post-spate succession (Fisher et al. 1982; Peterson and Grimm 1992).

Our results demonstrate that patterns of benthic algal recovery following spates are strongly affected by the degree of scour generated by the event. Recovery is also affected by the taxonomic composition of the community, and this apparently dictates the relative influence of post-spate enrichment. We have yet to determine what length, and at what level, spate-induced enrichment will generate significant long-term effects, but it is likely that such criteria will vary greatly as a function of biotic parameters such as algal community age, taxonomic composition and physiognomy, physiological health, biomass, and grazing pressure. These considerations point to the tight coupling of abiotic factors and biotic processes, and

emphasize the need for an intimate understanding of these interactions if we hope to predict the influences of disturbance on the dynamics of natural communities.

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