Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream

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Abstract. Resistance, resilience, and patterns of succession were evaluated for periphyton and macroinvertebrates of Sycamore Creek, Arizona, between 1984 and 1987. During this period, 35 flash-flood disturbances occurred, ranging in magnitude (peak discharge) from 0.2 m³/s to 58 m³/s; peak discharge of the largest flash floods exceeded base flow by 3–4 orders of magnitude. Macroinvertebrates and algal assemblages dominated by diatoms were more resistant, i.e., showed less change in response to spates, than macroalgae (filamentous Chlorophyta) and cyanobacterial mats, but resistance of all groups declined with increasing disturbance magnitude. Biota showed little resistance to events large enough to move substrata.

Twenty sequences of postflood succession were analyzed to characterize resilience and patterns of recovery. Resilience was very high compared with other streams and other ecosystems, because of high rates of biotic production in this desert stream. Resilience of periphyton (as indicated by recovery of total chlorophyll *a*) was highest in summer and autumn, while macroinvertebrate resilience (in terms of density or biomass) did not differ among seasons.

In many sequences, recovery curves of macroinvertebrate and algal standing crops were linear or asymptotic; however, macroinvertebrates declined precipitously during later stages of five successional sequences, primarily because of declines in the dominant collector-gatherers. These organisms reproduce continuously and have short life cycles, so declines cannot be explained by synchronous emergence. We propose instead that declines are caused by food quality limitation. Sustained high rates of macroinvertebrate consumption and use of autochthonous detritus are possible only if bacterial conditioning (and immobilization of nitrogen) can increase the N content of this material, which is halved with each gut passage. During many sequences, bacterial conditioning is probably limited by nitrogen, which is known to limit autotrophic processes in this stream. This suggests that productivity at higher trophic levels may be influenced by availability of a limiting nutrient not only to primary producers but to microconsumers.

Key words: desert streams, periphyton, macroinvertebrates, collector-gatherers, disturbance, succession, stability, nitrogen limitation, food quality.

Disturbance has received substantial recent attention by ecologists (Holdgate and Woodman 1978, Sousa 1979, Cairns 1980, Mooney and Godron 1983, Sousa 1984, Pickett and White 1985). Most agree that disturbance may be defined as a discrete event that causes significant mortality and is to some degree unpredictable (e.g., Resh et al. 1988). Disturbance is the context in which ecosystem stability is judged. Resistance (to deflection of state variables across the disturbance) and resilience (rate of recovery after disturbance) are measurable features of stability which have been used to characterize ecosystem or community response (Holling 1973, Orians 1975, Webster et al. 1975, Connell and Sousa 1983). Effects of disturbance on ecosystems typically have been studied by examining responses to single events, yet series of perturbations may have more impact than iso-lated events (e.g., Vogl 1980). Empirical support of this notion is lacking.

Interest in effects of disturbance on stream biota and lotic ecosystem structure and function has surged in the last few years (Ward and Stanford 1983, Webster et al. 1983, Reice 1985, Resh et al. 1988, Fisher 1989). Studies of recovery after spates (e.g., Fisher et al. 1982, Power and Stewart 1987) or colonization of denuded substrata (e.g., Sheldon 1984) are common today but were first suggested much earlier (Shelford and Eddy 1929). Several papers from a recent workshop (e.g., Minshall 1988, Power et al. 1988, Pringle et al. 1988, Resh et al. 1988) urged further studies of disturbance in streams. Minshall (1988) reviewed the fairly extensive literature on experimental studies of disturbance, but pointed out that these studies suffer somewhat in that manipulation is done at inappropriate

scales (see also Fisher 1987). Resh et al. (1988) stated that disturbance is perhaps the dominant organizing factor in streams and outlined design considerations for comparative studies of disturbance. We hope this paper will provide a basis for such comparisons.

Sousa (1984) stressed the importance of characterizing disturbance regime in studies of perturbation effects on communities and pointed out that disturbance has been characterized better in intertidal (e.g., Sousa 1979, McGuinness 1987) than in freshwater ecosystems. A disturbance regime may be described by magnitude, areal extent, frequency, and predictability of disturbances, and such descriptors should be independent of their effects on biota. Desert stream flash floods vary in intensity (a measure of force, e.g., peak discharge), for example, and this may lead to differences in severity (a measure of destruction caused by the event, e.g., % reduction in standing crop). Areal extent of spates may depend on whether rainstorms are localized in upstream or downstream portions of desert catchments and on the capacity of deep channel alluvium to absorb floodwaters between perennial reaches.

The ubiquity of hydrologic extremes as a constraint on stream ecosystems surely argues for study of damage caused by high discharge and subsequent recovery processes exhibited by stream communities. The classic concept of succession has recently merged with stability theory with recognition that succession is a major component of resilience (Pickett et al. 1987, Fisher 1989). Succession occurs in hot desert streams following devastating flash floods (Fisher et al. 1982), but mechanisms of resistance rather than resilience may be more important in streams where spates are more frequent but less severe (e.g., Fisher and Grimm 1988, but see Peckarsky 1986, 1987). While many studies exist of succession after disturbance in a variety of ecosystems, these are often anecdotal and based upon change following single events. Pre-disturbance state may not be adequately described. Studies of succession in ecosystems dominated by long-lived organisms (e.g., forest trees) are further hampered by the necessity of inferring change by comparing sites at different successional stages (Pickett 1988). In streams, on the other hand, organisms are more short-lived. This is particularly true of desert streams, where several successional sequences may occur in a single year.

In this study we describe resistance to 27 and recovery following 20 of 35 spates that occurred in a desert stream over a three-year period. Objectives were to describe disturbance frequency and magnitude, to evaluate resistance of macroinvertebrates and periphyton as a function of disturbance magnitude, to determine whether patterns of successional change are repeatable, and finally, to interpret these patterns in terms of cause and mechanism (sensu Pickett et al. 1987).

Study Site

Streams of Arizona's Sonoran Desert experience spates (flash floods) that are among the most severe in North America (Baker 1977). Because the climate of this hot desert region produces only 15 cm of precipitation annually, most of which falls as rain during the months of January–March and again during the summer "monsoon" of late July–September, modal streamflow is low (0.01–0.05 m^3/s in summer, 0.1–0.5 m^3/s in winter). During a summer flash flood, discharge rises rapidly and flood recession occurs within hours (Fig. 1A). As a result, abiotic conditions and physical structure of the system are quickly restored, and recovery occurs while discharge is relatively stable. In contrast, discharge may remain elevated for some time after winter rains, and stream discharge usually declines exponentially during spring recovery periods (Fig. 1B).

The study was conducted over a 3-yr period (June 1984 to July 1987) in Sycamore Creek, a mid-sized, spatially intermittent stream draining a 505-km² watershed of mountainous terrain with elevations ranging from 425 to >2000 m. Study sites on Sycamore Creek are at 600–700 m in Sonoran desertscrub. The stream in these mid-reaches is composed of six discrete perennial sections, flowing over shallow bedrock overlain by alluvial deposits ranging in size from fine pea-gravel to large (>30 cm diameter) boulders. Approximately 45% of the wetted channel length is cobble-boulder riffle, 45% is runs of fine gravel/coarse sand substrata, and the remaining sections are deep pools on bedrock or sand. Average water temperature is 20–30°C in summer and 10–20°C in winter.

Riparian vegetation consists of large trees such as sycamore (*Platanus wrighti*), cottonwood (*Populus fremontii*), willows (*Salix exigua* and *Salix goodingii*), mesquite (*Prosopis glandulosa*), ash (*Fraxinus pennsylvanica velutina*), and walnut (*Juglans major*). These are restricted to high flood-flow stream margins and provide little shade to the stream; shrubs such as seepwillow (*Baccharis salicifolia*) and burro bush (*Hymenoclea monogyra*) occur along wetted stream margins but because of their height (<2 m) do not shade the stream appreciably. Light levels reaching the stream bottom thus are high and large standing crops of algae (>200 g ash-free dry mass/m^2) can develop when interflood periods are long. Trophic structure of the stream is based upon algae, either through direct consumption (grazing) or more often detritivory on material of autochthonous origin.

Methods

As soon as possible after each spate (2–6 d) and then at 7–10 d post-flood and weekly thereafter we collected samples of macroinvertebrates, algae, and water for determination of macroinvertebrate densities, biomass, and community structure; chlorophyll *a* standing crop and algal community structure; and inorganic nutrients (nitrate- and ammonium-nitrogen and soluble reactive phosphorus). Primary study sites were located at two of the six perennial sections of Sycamore Creek. Several major tributaries enter between these sites; thus, they differ in modal discharge, drainage area, and susceptibility to spates.

We measured stream discharge on each sampling date as the product of cross-sectional area and flow velocity at the upstream ends of the two primary study sites. Peak discharge (Q_{max}), a measure of disturbance magnitude, was estimated for each study site by measuring widths (w) between high-water marks (small debris carried by floods forms a conspicuous line at the flood margins) and depths (z) from the substrate to a tape stretched between the high-water marks on each side of the channel. This method probably underestimates maximum discharge of sediment-scouring spates since sand is redeposited upon recession of flow. Peak discharge was calculated from channel cross sectional area and the Manning equation (Richards

1982), which estimates velocity as a function of slope (9 m/km in Sycamore Creek) and bed roughness (we used a factor of 0.05). For Sycamore Creek, the expression for estimating peak discharge is thus:

$$Q_{max} = 1.9wz^{5/3} \qquad (1)$$

At peak discharge during this study, w ranged from 10 to 30 m and hydraulic radius (z, approximately equal to depth) ranged from 0.25 to 1.0 m. Beginning in 1986, stage height at the upstream study site (Site 1) was monitored continuously with a pressure transducer (Environmental Monitoring Systems), and peak discharge was calculated using equation 1 (where z = mean depth at peak discharge).

Algal percentage cover was mapped at seven fixed transects each in two riffles and one run at Site 1 and in a single run at Site 2. Since transects were fixed, changes in algal distribution could be described for exact locations (±5 cm) on the streambed. In this paper we report only chlorophyll *a* data; changes in algal patch structure during succession will be examined in detail in a later paper (N. B. Grimm and S. G. Fisher, unpublished). Maps of percentage cover for each reach were used to calculate areal coverage of each algal type on each date. Total chlorophyll *a* for each algal type was calculated as areal extent × chlorophyll *a* per m^2 for that algal type; values for all algal types were summed to obtain total chlorophyll *a* for the reach. This patch-weighted sampling scheme permits more accurate assessment of standing crop than would a random sampling method for algae distributed in a highly patchy fashion (Busch 1979). Algae were sampled with five 26-cm^2 cores per algal patch type taken through algal mats to ≈2 cm sediment depth. Each sample was halved in the laboratory. One subsample was filtered, frozen, and then extracted in methanol (Tett et al. 1975) for determination of chlorophyll *a*. Ash-free dry mass (AFDM) was measured as mass loss between dried (60°C, 48 hr) and combusted (550°C, 2 hr) subsamples.

Five random samples for macroinvertebrates were collected along a single run at Site 1 on each sample date. Cores enclosing an 80-cm^2 area were inserted into sandy sediments to a depth of 10 cm, sediments were removed and samples elutriated in the field through a 250-μm-mesh net. Animals were killed in 10% for-

malin and later preserved in 70% ethanol. Samples were sorted and enumerated by taxon (Ephemeroptera and Trichoptera to species and Diptera to family, except *Crypotolabis* sp. (Tipulidae) and *Probezzia* sp. (Ceratopogonidae), which were counted separately). Lengths of major taxa were measured for certain samples and biomass determined from species-specific length-mass regressions of L. J. Gray (Ottawa University, personal communication), P. C. Marsh (Arizona State University, personal communication), and Smock (1980). Wet mass of all animals in other samples was measured after blotting on a preweighted piece of nitex netting. Wet mass of all animals except snails and *Helicopsyche mexicana* (Trichoptera) was converted to dry mass using a dry:wet mass ratio of 0.13, determined independently on samples of similar taxonomic composition ($n = 11$, SE = 0.01). Wet masses of snails and *Helicopsyche* were determined separately and converted to AFDM using AFDM:wet mass ratios of 0.072 and 0.043, respectively ($n = 5, 3$; SE = 0.0074, 0.002). Large, mobile invertebrates (such as late-instar odonates and hemipteran predators) were excluded from dry mass estimates because they are inadequately sampled by coring.

Triplicate water samples were collected in polyethylene bottles at the up- and downstream termini of each of the four algal transect reaches. Analyses for nutrients were completed on filtered (Whatman GF/F glass-fiber filters) samples within 4–24 hr of collection. Nitrate was determined by the cadmium-copper reduction technique (Wood et al. 1967), ammonium by the phenolhypochlorite method (Solorzano 1969), and soluble reactive phosphorus by the molybdate blue method (Murphy and Riley 1962). Flux of inorganic N (grams per day) was calculated as the product of ammonium- + nitrate-N and stream discharge.

We calculated resistance as percent change in state variables between preflood and postflood samples. For statistical analyses, percentages were converted to proportions, made positive by adding 1.0, and subjected to an arcsine square-root transformation. In certain cases when postflood values were higher than preflood values, we set resistance to 1.57, the highest possible transformed value, which corresponds to zero change. Values for resistance therefore range from 0 to 1.57, with the lower number corresponding to lower resistance.

As one measure of resilience, we calculated the slope of the regression of a parameter (e.g., chlorophyll *a*) against days since flood. A minimum of the first three points was used, and additional points were added until the regression was significant ($p < 0.1$). Thus in most cases resilience values correspond to recovery rates for the early stages of the sequence. We used stepwise multiple regression analysis to evaluate effects of a suite of independent variables on invertebrate density. The transformation X = ln(value + 1) was used in this analysis. Time of recovery to pre-disturbance state was used as an alternative measure of resilience.

Results

Disturbance regime

Effects of spates may depend upon both magnitude and frequency of disturbance. Magnitude is probably most directly tied to resistance, while frequency and timing of disturbances dictate time available for recovery and thus exert more influence on resilience. Between June 1984 and July 1987, 35 spates occurred (not all were studied), ranging in magnitude from 0.2 m^3/s to 58.4 m^3/s (Fig. 2A). The 35 spates were treated in our analyses as 49 distinct events because disturbance magnitude differed greatly between sites. In 8 cases, for example, flash floods arising in a tributary catchment affected Site 2 but not Site 1. In 8 cases when spates occurred at both sites Q_{max} at Site 2 exceeded that at Site 1. There were 6 events when Q_{max} at Site 1 > Site 2; we attributed this to absorption of floodwaters by channel alluvium between the sites.

Based upon observations recorded immediately after each event, spates with Q_{max} > 2–3 m^3/s were competent to move coarse sand, resulting in changes in geomorphic structure. Physical effects of very small spates (Q_{max} < 1 m^3/s) were restricted to deposition of silt in backwaters and along stream margins. All spates resulted in discharge increases above base flow of at least one order of magnitude; peak discharges of large flash floods were thousands of times base flow (Fig. 1).

Disturbance frequency may be expressed as number of spates per year; Sycamore Creek averages six spates per year (Fisher and Grimm 1988). Fourteen, 11, and 10 spates occurred in 1984–1985, 1985–1986, and 1986–1987, respec-
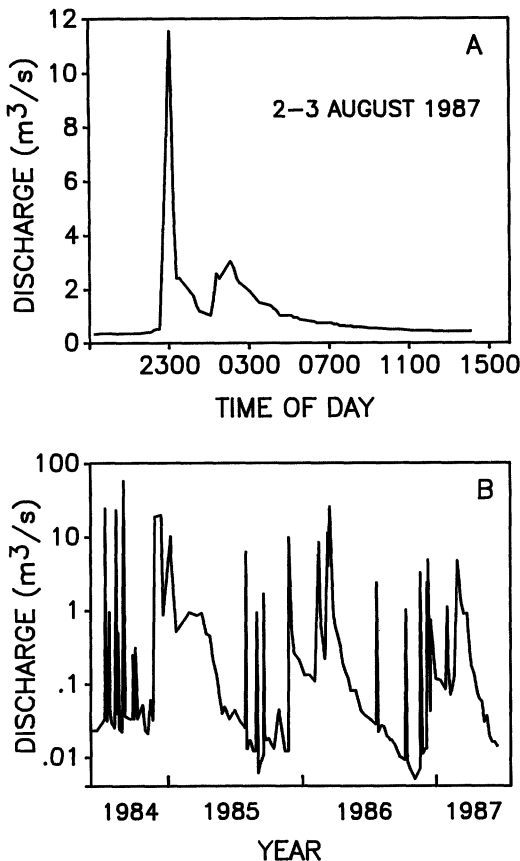
FIG. 1. (A) Summer flash-flood hydrograph for Sycamore Creek, Arizona. Note almost instantaneous rise in discharge to 12 m³/s (over base flow of <0.1 m³/s), rapid recession, and secondary discharge peak. (B) Three-year hydrograph for Sycamore Creek, Arizona, 1984–1987. Note abscissa is log scale.

tively. Spates were clumped in late summer and early spring and were irregularly spaced (Fig. 1B). As a result, interflood successional sequences varied in length from 1 day to 158 days (Fig. 2B).

Resistance

Resistance was measured for 27 spates satisfying the following criteria: a) maximum discharge known; b) preflood data collected ≤7 d before the event if days since flood at time of sample ≤30, or ≤14 d before the event if days since flood at time of sample >30; and c) postflood data collected ≤10 days after the event. Resistance of periphyton standing crop in runs
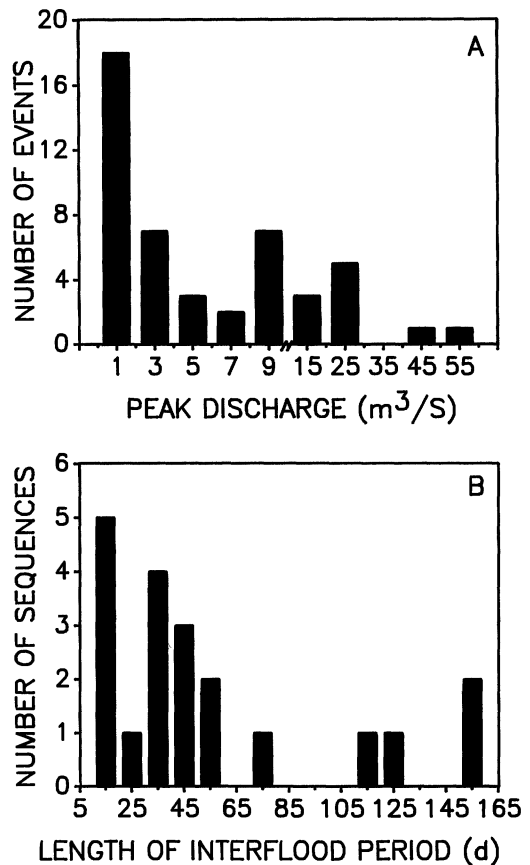
FIG. 2. Frequency histograms of disturbance magnitude (A) and successional sequence length (B) for Sycamore Creek, 1984–1987.

(as total chlorophyll *a*) was negative correlated with Q_{max} ($r = -0.50$, $p = 0.0073$; Table 1); thus larger spates, as expected, cause greater reductions in standing crops. There was no difference in chlorophyll *a* resistance (adjusted for Q_{max}) between cobble riffles and sand-gravel runs (analysis of covariance, $p = 0.6$).

Resistances of three algal patch types (diatoms, filamentous green algae, and cyanobacterial mats) were compared with each other (as chlorophyll *a*) and with resistance of invertebrates (density). Algal patch types are assemblages with distinctive growth forms and other gross features which are characterized by different relative abundances of taxa, although all types may have representatives of each major group (Busch 1979). Resistance of all algal types decreased with Q_{max} (Table 1); significant negative correlations were found for the diatom-

TABLE 1. Resistance to spates (as % change across an event) of major periphyton groups and invertebrates in Sycamore Creek, Arizona, 1984–1987. Spates are listed in order of disturbance magnitude (Q_{max} = maximum discharge). For periphyton, resistance reflects change in chlorophyll a of each type, while for invertebrates, resistance reflects change in density.

Q_{max}	Chlorophyll a	Bacillariophyceae	Chlorophyta	Cyanobacteria	Invertebrates
0.2	+7	+63	+82	−100	
0.3	−13	+147	−70	−100	−65
0.3	−42	+[a]	−43	−68	
0.5	+2	+22	−34	−55	
1.0	−73	+	−87	−75	+137
1.1	−42	−31	−77	−100	
1.2	−42	−75	+344	−100	
1.7	−14	+3811	−64	−100	−3
1.9	−86	+1035	−95	−99	
2.1	−93	+146	−100	−100	
2.3	−91	+	−100	−100	
2.4	−36	+388	−73	−94	−64
2.4	−79	−66	NP[b]	−100	−91
3.3	−78	+	−100	−82	+139
3.5	−91	−66	−95	−100	−98
4.9	−58	−80	NP	NP	
6.3	−79	+295	−100	−100	−83
7.2	−78	+431	−94	−100	−99
8.5	−99	−99	−100	NP	−97
9.9	−100	−100	−100	−100	−97
19.0	−95	−27	−100	NP	
19.6	−99	+41	NP	NP	
23.0	−95	−79	−100	−100	
23.4	−96	−91	−100	−100	−21
24.7	−94	−68	−100	−100	
46.9	−97	−95	−100	−100	
58.4	−94	−86	−100	−100	−92

[a] + Denotes post-flood appearance of algal patch which was absent before the flood.
[b] NP = not present before or after flood.

dominated assemblage ($r = -0.53$, $p = 0.004$) and filamentous green algae ($r = -0.45$, $p = 0.026$). The relationship between resistance and disturbance magnitude (Q_{max}) was not linear, however. Above a threshold of $Q_{max} = 1$–2 m^3/s filamentous green algae and cyanobacteria were essentially eliminated. Resistance differed significantly among groups; diatoms were most resistant followed by invertebrates, filamentous green algae, and bluegreen bacteria (a posteriori comparisons of adjusted means, $p < 0.05$).

Resistance of invertebrate density was measured only for runs; however, resistance of each algal assemblage was compared between runs and riffles using a two-factor analysis of covariance, with Q_{max} as the covariate. Again, algal types differed significantly in resistance ($p < 0.001$) and resistance declined with Q_{max} ($p <$

0.001), but there were no significant differences between the two reach types ($p = 0.25$).

Resilience

Our analysis of postflood change was restricted to 21 sequences >10 d in length sampled ≤10 d after a spate and at least twice thereafter. In 1 case we combined 2 sequences separated by a minor flood that had negligible effects on chlorophyll a and invertebrate densities. Invertebrate data were available for 15 of the 21 sequences. Thirty-three percent of the sequences examined were <1 mo in length, whereas 24% exceeded 2 mo.

Periphyton colonization was always rapid (Figs. 3A, 4A), with diatoms, in particular, visually evident within hours of flood recession.
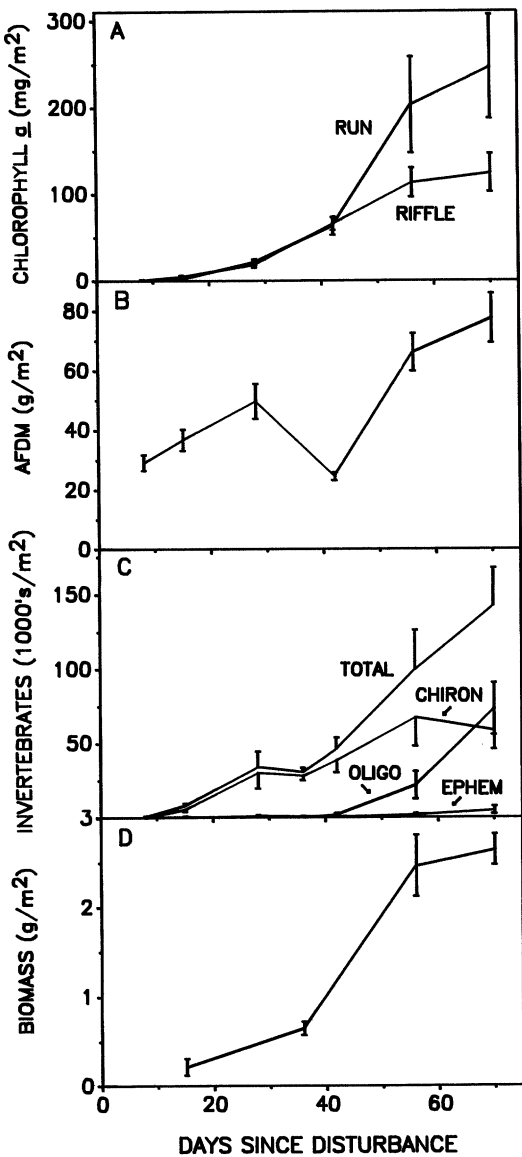
FIG. 3. Successional patterns for a winter successional sequence of chlorophyll *a* (A), total benthic ash-free dry mass (B), macroinvertebrate density (C), and macroinvertebrate biomass (D) following a 9.9 m³/s spate on November 25, 1985 in Sycamore Creek, Arizona. Values shown are means ± standard error, *n* = 5.
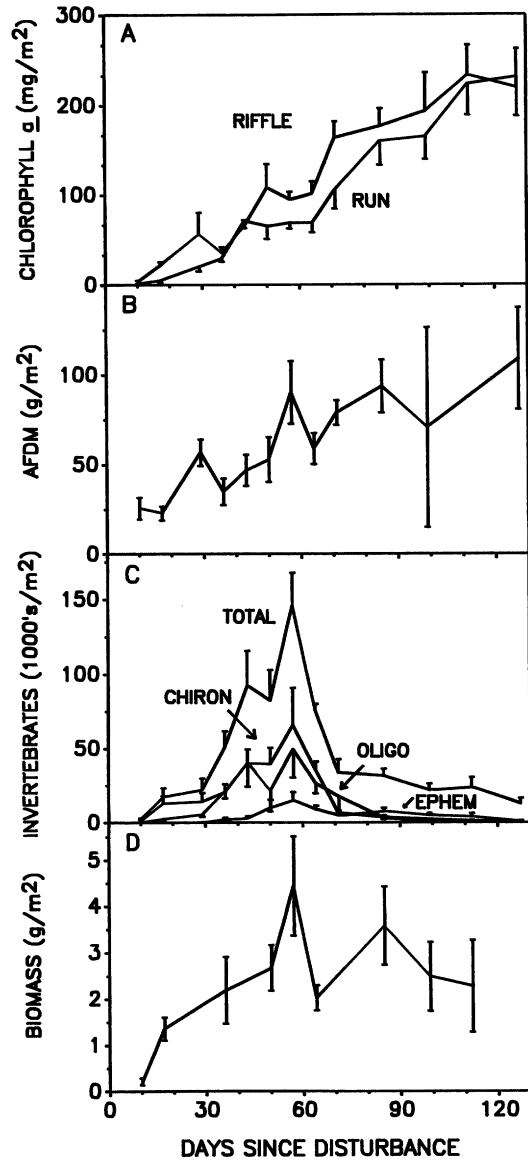
FIG. 4. Successional patterns for a spring–summer successional sequence of chlorophyll *a* (A), ash-free dry mass (B), macroinvertebrate density (C), and macroinvertebrate biomass (D) following a 26 m³/s spate on March 17, 1986 in Sycamore Creek, Arizona. Values shown are means ± standard error, *n* = 5.

Maximum chlorophyll *a* reached in any single sequence varied from 75 to 404 mg/m², with lower maxima generally associated with short sequences (Table 2). Average maximum chlorophyll *a* values were remarkably similar among seasons (Table 2). Increases in chlorophyll *a*

standing crop were either linear (11 sequences) or asymptotic (9 sequences); in the latter cases stable standing crops were reached within 12–100 d. In one sequence, there was no change in chlorophyll *a*. Times required for preflood standing crops to be reached varied from 9 to

TABLE 2. Comparison of resilience and maximum standing stocks of periphyton (chlorophyll *a*), benthic organic matter (AFDM), and macroinvertebrates (density and biomass) of successional sequences in Sycamore Creek as a function of season. Resilience measures are slope of increase after spates and time to reach preflood levels (chlorophyll *a*) or 40,000 individuals/m^2 (macroinvertebrate density). Parenthetical values are standard errors and number of values. All comparisons were by analysis of variance; means with the same superscripts do not differ significantly (Newman-Keuls test, $p < 0.05$).

Parameter	Season	Slope[a]	Time (d)	Maximum	
Chlorophyll *a* (mg/m^2)	Winter–Spring	1.66 (0.65, 5)^z	78 (9.2, 4)^z	208	(27.1, 6)^z
	Summer	5.62 (1.03, 5)^y	21 (6.1, 3)^y	188	(41.8, 7)^z
	Autumn	4.03 (0.75, 6)^y	20 (3.2, 6)^y	188	(33.9, 8)^z
AFDM (g/m^2)	Winter–Spring	0.41 (1.33, 4)^z		221	(54.3, 6)^z
	Summer	6.72 (1.26, 3)^y		258	(51.0, 7)^z
	Autumn	1.47 (0.88, 3)^z		202	(12.0, 8)^z
Invertebrate Density (1000's/m^2)	Winter–Spring	1.33 (0.56, 5)^z	40 (4.2, 5)^z	92	(22.4, 5)^z
	Summer	1.37 (0.98, 4)^z	20 (4.1, 5)^y	30	(9.2, 5)^y
	Autumn	2.45 (1.04, 4)^z		68	(21.7, 5)^{zy}
Invertebrate Biomass (g/m^2)	Winter–Spring	0.057 (0.003, 4)^z		4.24 (0.55, 5)^z	
	Summer	0.069 (0.030, 4)^z		1.65 (0.49, 5)^y	
	Autumn			1.71 (0.38, 5)^y	

[a] Analysis of variance performed on natural log-transformed data; means given are back-transformed.

97 d. Although this measure of resilience is dependent on flood history because preflood standing crops also vary with time since flood, longer recovery times were required in winter–spring than in summer and autumn (Table 2). Seasonal differences were significant ($p < 0.0001$). In addition, slopes of chlorophyll *a* recovery were significantly higher in summer and autumn than in winter–spring (ANOVA on natural log-transformed slopes, $p = 0.024$).

Macroinvertebrates colonized rapidly after flooding. Densities reached 20,000 individuals/m^2 in 8–36 d and 40,000 individuals/m^2 in 13–52 d (Table 2). Time to 40,000 individuals/m^2 was significantly shorter ($p < 0.01$), in warm, low-flow seasons (summer and autumn, e.g., Fig. 4C) than in winter and spring sequences (e.g., Fig. 3C). Slopes of macroinvertebrate recovery did not differ among seasons, however ($p = 0.26$). Maximum densities were 15,000–146,000 individuals/m^2 and were lowest in summer (Table 2). Maximum macroinvertebrate biomass varied from 0.50 to 5.43 g/m^2 among the 15 sequences; maximum biomass was highest in winter sequences (Table 2). Increases in biomass after spates paralleled those in density (Figs. 3, 4).

In most sequences, the macroinvertebrate fauna was dominated by Oligochaeta and Chironomidae (Figs. 3, 4). Ephemeroptera (*Fallceon*

(*Baetis*) *quilleri* and *Tricorythodes dimorphus*), the tipulid *Cryptolabis* sp., Trichoptera (*Cheumatopsyche arizonensis* and *Helicopsyche mexicana*), and the snail *Physa virgata* were occasionally abundant.

We used multiple regression analysis to identify variables that best explained variation in macroinvertebrate density over the 3-yr period of the study. Independent variables included in the analysis were days since disturbance, discharge at the time of sampling, discharge of the last spate, water temperature, day length, dissolved inorganic nitrogen (DIN) concentration, and chlorophyll *a*. Whereas the first six of these variables explained ≈70% of variance in chlorophyll *a* (Fisher and Grimm 1988), only 40% of variance in invertebrate density was explained by four of the variables: days since disturbance (partial correlation $r = 0.27$); DIN flux ($r = 0.50$); chlorophyll *a* ($r = 0.41$); and day length ($r = 0.28$). Furthermore, while the disturbance-related variables days since disturbance, discharge, and discharge of the last spate accounted for most of the chlorophyll *a* variance (Fisher and Grimm 1988), these variables were only weakly correlated with macroinvertebrate density. Other, unmeasured factors must explain postflood variation in invertebrate standing crop.

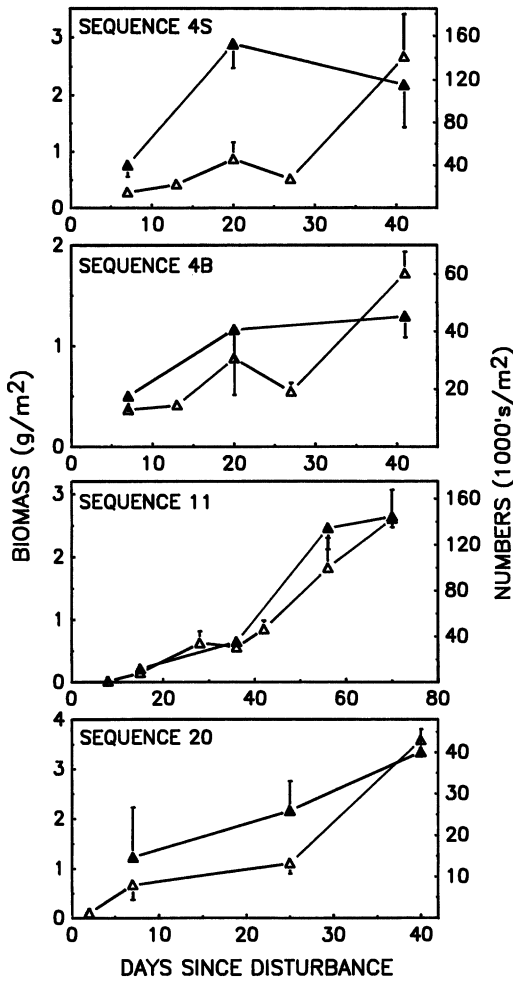We examined each of the 15 sequences for

FIG. 5. Successional patterns of macroinvertebrate density (open triangles) and biomass (closed triangles) in four of the eight sequences showing continual or asymptotic increases in macroinvertebrate density. Values shown are means ± standard error, $n = 5$.
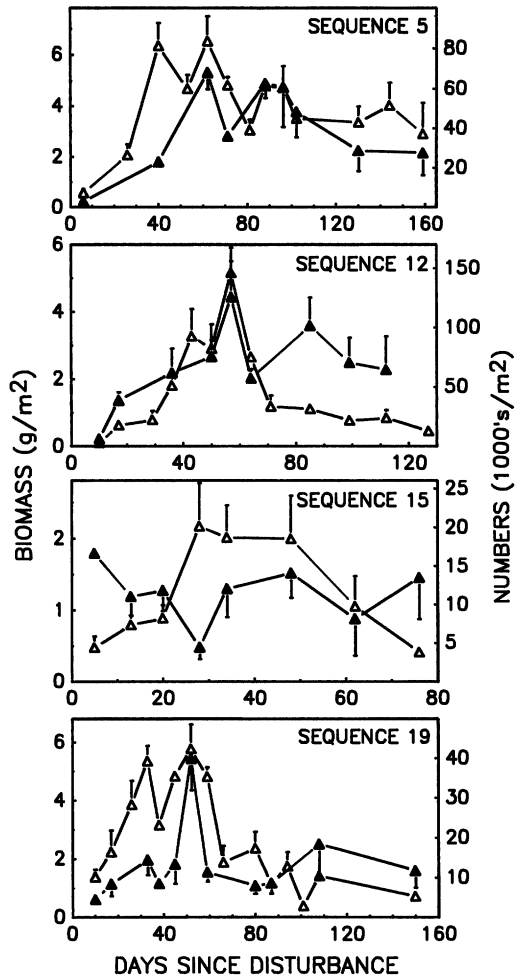
FIG. 6. Successional patterns of macroinvertebrate density (open triangles) and biomass (closed triangles) in four of the five sequences showing late-stage declines in macroinvertebrate density. Values shown are means ± standard error, $n = 5$.

which invertebrate data were available to determine whether distinctive patterns could be identified. Two sequences showed no pattern in macroinvertebrate density: sequence 8 because it was very short (18 d) and sequence 9 because of high variation among samples. Eight sequences showed increases in density that were either linear (e.g., Figs. 3C, 5) or asymptotic. In five sequences, however, macroinvertebrate densities declined dramatically after initial rapid increases (e.g., Fig. 4C). These precipitous declines, or "crashes", in macroinvertebrate density were also seen in biomass in most se-

quences (Figs. 4D, 6) and were attributed to declines in the dominant taxa of the sequence.

Three features characterized the five sequences with crashes: 1) four of the five were the longest sequences (>2 months), 2) in each case DIN flux was either low throughout the sequence or at the end of the sequence, and 3) cyanobacteria appeared in abundance during these sequences only after macroinvertebrates declined. Because many cyanobacteria can fix nitrogen and may increase in abundance when N becomes limiting, the apparent relationship between macroinvertebrate crashes and cyano-

FIG. 7. Macroinvertebrate density in mid–late stages of successional sequences (>1 month after flood) plotted against nitrogen flux (dissolved inorganic nitrogen concentration × discharge), a measure of nitrogen availability ($r = 0.74$, $p < 0.001$).
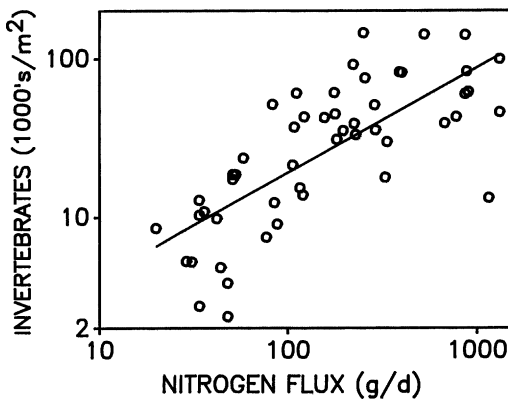
bacterial abundance may be explained by correlation of both groups with a common variable. Natural log-transformed macroinvertebrate densities for samples collected >1 month after disturbance (to eliminate colonization effects) were plotted against natural log of DIN flux (Fig. 7). During late stages of succession macroinvertebrate density was significantly correlated with N availability ($r = 0.74$, $p < 0.0001$).

Discussion

Stability of the stream ecosystem

Periphyton and macroinvertebrate resistance to spates in Sycamore Creek was generally low, although resistance by periphyton varied according to type. Relatively small flash floods (1–2 m³/s, ≈100× summer base flow) virtually eliminated the more susceptible chlorophytes and cyanobacteria, but larger spates ($Q_{max} > 8$ m³/s, ≈1000× summer base flow) were required to reduce the more resistant diatoms and macroinvertebrate density by >90% (Table 1). Resistance of diatoms and filamentous green algae was inversely correlated with disturbance magnitude, but above a threshold disturbance magnitude, essentially all algae were eliminated. Such a threshold disturbance intensity, above which biota are not resistant, probably exists for most types of disturbance. Threshold magnitude will vary depending on features of the ecosystem (e.g., substratum mobility [Gurtz and

Wallace 1984]) and the biota (e.g., attachment strength). Others have found resistance to disturbance to depend on several factors, including disturbance magnitude (Sousa 1980); certain aspects of predisturbance history, e.g., stability or harshness of habitat (Zaret 1982, Gurtz and Wallace 1984, Peterson 1987) or successional age of the assemblage (Sousa 1980); and growth form, life history characteristics, and life stage of the biota (e.g., Hoopes 1974, Woodley et al. 1981, Power and Stewart 1987).

We reasoned that runs should be less resistant than cobble-boulder riffles because of greater substratum stability of the latter, but this expectation was not borne out by a comparison of chlorophyll a reductions in runs vs. riffles. Since the destructive force of spates is enhanced by scouring action of transported sediment, algae in riffles are subject to scour by sediment transported from adjacent runs, and this scouring may have precluded survival on immobile substrata. Power and Stewart (1987) also were unable to demonstrate a relationship between substratum stability and algal persistence before and after a large spate in an Oklahoma stream.

Difference in resistance among algal assemblages corresponded to differences in growth form and mode of attachment. Cyanobacteria (Anabaena variabilis, Oscillatoria spp.), the least resistant algal type, occur as loosely attached mats along stream margins and are easily transported as water rises. Some filamentous green algae (predominantly Cladophora glomerata) are attached but grow to long, floating filaments within weeks. Variation among spates in resistance of green algae (Table 1) may be due in part to life stage at the time of the disturbance (Power and Stewart 1987). Short, tightly attached young "turfs" may be less easily dislodged than older, senescent filaments or mats. Power and Stewart (1987) tested resistance of two green algal species to simulated scour by turning rocks in a cement mixer and found Rhizoclonium to be more resistant than the unattached Spirogyra. Zygnematalean species (e.g., Spirogyra spp., Zygnema sp., and Mougeotia sp.) are occasionally abundant in Sycamore Creek; differences such as those identified by Power and Stewart (1987) within the broad grouping of Chlorophyta may also account for differences in resistance to the spectrum of spates we studied.

Apparent immediate increases after spates in standing crops of the assemblage dominated by Bacillariophyceae (Table 1) are attributable to high resilience of this assemblage, rather than to high resistance. The assemblage consists primarily of diatoms (especially *Nitzschia fonticola*, *Achnanthes lanceolata*, *Gomphonema tenellum*, *Melosira varians*, and *Navicula radians tenella* [Busch 1979]), with species of *Calothrix*, *Amphithrix*, and *Anabaena* often abundant. Diatom colonization is sometimes visually obvious within hours of flood recession and often we did not sample for several days after the event. In addition, this assemblage may make up a very small percentage of preflood periphyton standing crops but >90% of postflood cover. Even if chlorophyll *a* per unit area is low after spates, total chlorophyll *a* of the diatom-dominated assemblage may be higher than preflood values because of areal increases.

While resistance of algae and macroinvertebrates was low, resilience was very high. Rapid recoveries of standing crops in Sycamore Creek have been noted previously and attributed to warm temperatures, stable low discharge, high light, and consequent high rates of primary and secondary production (e.g., Fisher et al. 1982, Grimm 1987). Times required for biotic recovery in other stream ecosystems after a variety of disturbances vary depending on the severity of the disturbance and the life history features of the organisms involved. For example, benthic nitrifying bacteria recovered completely from flood losses within 10–12 d (Cooper 1983), whereas algae in an Oklahoma stream attained preflood standing crops in 3 wk (Power and Stewart 1987). After the devastation of the Mt. St. Helens volcanic eruption, microorganisms became established in aquatic habitats within several weeks, but algae required a few months (Ward et al. 1983). A year after the eruption, stream algae at several sites were limited to pioneer diatoms (Rushforth et al. 1986). Recovery times of aquatic insect larvae are generally in the order of months (Hoopes 1974, Siegfried and Knight 1977) to a year (Molles 1985), although many insects in Sycamore Creek have very short life cycles and recover within weeks (Table 2; Fisher et al. 1982). Such rapid development times and continuous reproduction may in fact be an adaptation to the regime of severe, infrequent disturbance by flash flooding (Gray 1981).

Patterns of recovery

Although a successional perspective may not be as appropriate to studies of all streams as it is to Sycamore Creek, some authors have proposed that flood history is an important variable in most unregulated streams (Tett et al. 1978, Fisher et al. 1982, Fisher 1983). Chlorophyll *a* standing crop in Sycamore Creek is predictable from days since disturbance, magnitude of the last spate, and discharge (a seasonally varying, but also disturbance-related factor [Fisher and Grimm 1988]). Temperature, day length, and nitrate-N concentration explain just 2–3% of the remaining explainable variation in this parameter. Flood-related variables are important predictors of chlorophyll *a* in New Zealand streams as well (Biggs 1988), and Tett at al. (1978) suggested that length of flood-free periods was the most important factor controlling algal biomass in a Virginia river. In the present study, biotic standing crops were significantly correlated with days since disturbance, at least in early stages, for 17 of 21 (81%) sequences examined for chlorophyll *a* and 13 of 15 (87%) sequences examined for macroinvertebrates. In other streams, however, flood disturbance may have little explanatory power. In Fort River, Massachusetts, light was the single independent variable which explained chlorophyll *a* variation, albeit poorly, over a similar time frame (Fisher and Grimm 1988), and invertebrate density appeared unrelated to flood disturbance in a Pennsylvania stream (D. Arnold, Pennsylvania State University, personal communication).

Although macroinvertebrate density is correlated with time since disturbance in Sycamore Creek, disturbance-related variables are poor predictors of density when all data, including late stages of sequences, are analyzed using multiple regression analysis. We suggest several possible reasons for this. First, all appropriate independent variables may not have been included in the analysis. Chlorophyll *a* and benthic AFDM both were used as potential indicators of food availability; however, the dominant macroinvertebrates are collectors of fine alga-derived detritus and do not directly consume algae. These measures may therefore be poorly correlated with true food availability. Second, we did not investigate biotic interactions that might have affected densities during late stages of successional sequences. The im-

portance of biotic interactions is thought to in-
crease during periods of flow stability (e.g.,
Hemphill and Cooper 1983, Power et al. 1985).
Finally, examination of individual patterns of
recovery reveals that the shapes of recovery
curves are in some cases complex (Fig. 6), and
may not fit the assumed linear model of the
multiple regression analysis.

Many sequences showed a strong relation-
ship of density and days since disturbance dur-
ing the initial recolonization period, but in five
sequences, early increases were followed by
marked declines, or crashes (e.g., Figs. 4C, 6).
These crashes appear to be correlated with re-
duced availability of dissolved nitrogen (Fig.
7). We are not suggesting that macroinverte-
brates use nitrogen directly and are therefore
strictly resource limited; rather, we propose a
mechanism explaining the relationship be-
tween macroinvertebrate density and nitrogen
flux and the pronounced population declines
during late stages of long successional se-
quences.

Macroinvertebrates in Sycamore Creek have
high rates of secondary production (Fisher and
Gray 1983, Jackson and Fisher 1986) but very
low assimilation efficiencies ($\approx 10\%$; Fisher and
Gray 1983). Consequently, ingestion rates are
high, amounting to 4 times macroinvertebrate
biomass or approximately one third of total or-
ganic matter in the stream *each day*. Further,
organic matter ingestion exceeds gross primary
production by as much as 400%, but most (90%)
is egested; macroinvertebrates therefore can and
must reingest feces (Fisher and Gray 1983). Only
50% of nitrogen ingested is egested (Grimm
1988); thus, feces are much poorer in quality (N
content or C:N ratio) than food. If feces released
into the environment are colonized by bacteria,
quality may be improved by conditioning, much
as leaves are conditioned by fungal and bacte-
rial colonization in forest streams. Increases in
N content of feces (or decreases in C:N) during
conditioning would require microbial immo-
bilization of N from the medium. If nitrogen
supply rate is limiting, however, N content of
feces will not increase during incubation in the
stream, and as the material is continually re-
ingested, its quality will decline. In this way,
nitrogen limitation may have a direct effect on
macroinvertebrate populations, causing them
to crash when N availability is insufficient to
maintain food quality of particulate materials.

We propose this food quality hypothesis as a

mechanistic explanation for observed declines
in macroinvertebrate density and biomass dur-
ing late stages of long successional sequences.
Food quality changes may be caused not by N
limitation of detrital conditioning but by other
changes in the detrital pool, such as an increase
in the proportion of detritus derived from cy-
anobacteria. We suggest, however, that because
increases in cyanobacterial abundance always
occurred after peaks in macroinvertebrate den-
sity, structural shifts in the algal community to
cyanobacteria could not have caused hypothe-
sized changes in food quality. Of course, we
have not presented data unequivocally linking
N availability to food quality nor food quality
to density, but we present this hypothesis as
the most plausible explanation of observed pat-
terns. The hypothesis could be tested with at
least two predictions: 1) C:N and bacterial col-
onization of benthic detritus will increase with
time following disturbance, and 2) if the system
is enriched with N, then no crash in macroin-
vertebrate density or biomass will occur.

Alternative hypotheses to explain late-stage
crashes in long successional sequences are: 1)
macroinvertebrates are limited by food quan-
tity; 2) crashes are caused by increased preda-
tion; or 3) crashes correspond to a synchronous
emergence of one or a few taxa. The last alter-
native may be addressed with data from our
study and Gray's (1981). Arguments against it
are that biomass curves are similar to density
curves and that taxa exhibiting declines have
continuous reproduction and asynchronous life
histories. The food quantity explanation is un-
likely since ash-free dry mass, a measure of ben-
thic organic matter standing crop, continues to
increase as macroinvertebrate densities crash
(Table 2, Fig. 4). Finally, although increased
predation may account for declines, we were
unable to detect any consistent successional pat-
terns in interstitial predators (primarily larval
Coleoptera, small odonates, and the ceratopo-
gonid, *Probezzia* sp.). Predatory adult beetles,
hemipterans, and large odonates are not ade-
quately sampled by coring methods, so patterns
of change in their abundances are unknown.

Despite our inability to reject the predation
hypothesis, the food quality hypothesis re-
mains the most plausible explanation for late-
stage crashes of macroinvertebrate density. Ni-
trogen limitation in this ecosystem thus may
affect not only primary producers and poten-
tially the grazing food chain through limitation

of primary production (Grimm and Fisher 1986), but also detritivorous consumers through limitation of bacterial conditioning of particulate organic matter. Evidence for similar influence of nutrient availability on higher trophic levels has been obtained from a long term fertilization study of a tundra river (B. J. Peterson, Woods Hole Marine Biological Laboratory, personal communication). Phosphorus fertilization has resulted not only in increased chlorophyll *a* standing crops and primary production (Peterson et al. 1985) but also increased heterotrophic microbial activity (Hullar and Vestal 1988, Peterson et al. 1985), insect growth and abundance (Hershey et al. 1988), and fish growth (L. Deegan, Woods Hole Marine Biological Laboratory, personal communication).

In conclusion, we have convincing evidence that in desert stream ecosystems over the long term (>annual periods) disturbance is indeed a dominant organizing factor. Disturbance by spates has a profound influence on total algal standing crop, macroinvertebrate density, and presumably primary and secondary production. Spates are extremely destructive events, and biota of desert streams show little resistance to spates large enough to alter physical structure or move substrata (>2–3 m³/s peak discharge). Seasonal variation in factors such as light, temperature, or nutrients appears to be less important than disturbance in determining biotic standing crops on longer temporal scales (e.g., Fisher and Grimm 1988, this study), but between spates these variables may strongly influence biota. Rates of recovery (via succession) are usually high, for example, but exhibit some seasonal variation (Table 2). Patterns of succession in macroinvertebrate density are complex. In some sequences, macroinvertebrate populations decline dramatically following an initial rapid colonization period. We suggest that this decline is due to a parallel decline in food quality, brought about by continued reingestion of particulate materials and by nitrogen limitation of microbial conditioning of those materials. This suggests a strong control of productivity at higher trophic levels by element limitation.

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Nancy B. Grimm; Stuart G. Fisher

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