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TEMPORAL SUCCESSION IN A DESERT STREAM ECOSYSTEM FOLLOWING FLASH FLOODING[1]

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Abstract. Recovery of a desert stream after an intense flash flooding event is described as a model of temporal succession in lotic ecosystems. A late summer flood in Sycamore Creek, Arizona, virtually eliminated algae and reduced invertebrate standing crop by 98%. Physical and morphometric conditions typical of the preflood period were restored in 2 d and the biota recovered in 2–3 wk.

Algal communities responded rapidly and achieved a standing crop of nearly 100 g/m² in 2 wk. Community composition was dominated by diatoms early in succession and by filamentous greens and blue-greens later.

Macroinvertebrates also recolonized denuded substrates rapidly, largely by immigration of aerial adults and subsequent oviposition. Growth and development were rapid and several generations of the dominant mayfly and dipteran taxa were completed during the 1st mo of recovery. Invertebrate dry biomass reached 7.3 g/m² in 1 mo.

Gross primary production (P_g) measured as O_2 increased in a similar asymptotic fashion and reached 6.6 $g \cdot m^{-2} \cdot d^{-1}$ in 30 d. P_g exceeded community respiration (R) after day 5 and P_g/R averaged 1.46 for the remainder of the 2-mo sequence. This ecosystem is thus autotrophic and exports organic matter downstream and by drying, laterally. Uptake of nitrate and phosphorus were proportional to net primary production and exhibited a marked downstream decline in concentration during both light and dark periods.

Temporal trajectories of various community and ecosystem attributes are compared with those suggested by Odum (1969) to be diagnostic of successional status. Agreement was poor in attributes which are especially modified in open, frequently disturbed ecosystems such as streams.

Key words: aquatic insects; desert stream; flooding; nutrient dynamics; primary production; stream; succession.

INTRODUCTION

Succession has been a productive, if controversial area of investigation in ecology. Most research contributing to the conceptual base of the field has been done in terrestrial ecosystems, particularly forests, and extrapolation of these ideas to aquatic systems has been difficult and confusing. This is due in part to short life-spans of aquatic organisms relative to disturbance frequency, difficulty in identifying discrete communities in lakes and streams, and the ephemeral nature of spatial relationships in a mobile aqueous medium.

These problems are compounded in running waters where current imposes a spatial vector on temporal change, inexorably transporting the biota and products of biotic activity downstream. Some components move slowly (e.g., benthos, particulate nutrients) and others more rapidly (plankton, dissolved nutrients). Upstream feedback is minimal; thus adjacent organisms or communities may exhibit unequal interaction, depending on their orientation vis à vis direction of flow. Upstream organisms may greatly influence those downstream, but the reciprocal influence is less pronounced or absent.

Because of the overriding influence of current, succession in streams has often been viewed as a longitudinal pattern in space rather than temporal change at a given site. Several workers have described longitudinal changes in stream fauna and flora (Huet 1959, Kuehne 1962, Hynes 1970); however, these attempts yield rather empirical descriptions of zonation that are specific to a given drainage and do not allow generalization. Vannote et al. (1980) have viewed continuous changes in functional attributes of running waters, such as detrital processing and transport.

Temporal succession at a single stream site has been examined after disturbances such as dredging (Hannan and Dorris 1970, Pearson and Jones 1975), drought (Harrison 1966), poisoning (Dimond 1967), and hail (Brock and Brock 1969), and in each case distinctive changes occurred as the stream recovered to near its original state. By far the most frequent agent of stream disturbance is flooding. Recovery following flooding has been described for selected components of streams; the time required varied greatly depending upon stream type, severity of disturbance, and the parameter measured (Hoopes 1974, Bilby 1977, Siegfried and Knight 1977, Bane and Lind 1978), but generally several months to a year or more are required for complete recovery. While recovery or succession is thus easily discernible in streams after floods, its study is confounded by continually flowing water and additional stochastic flooding events which occur dur-

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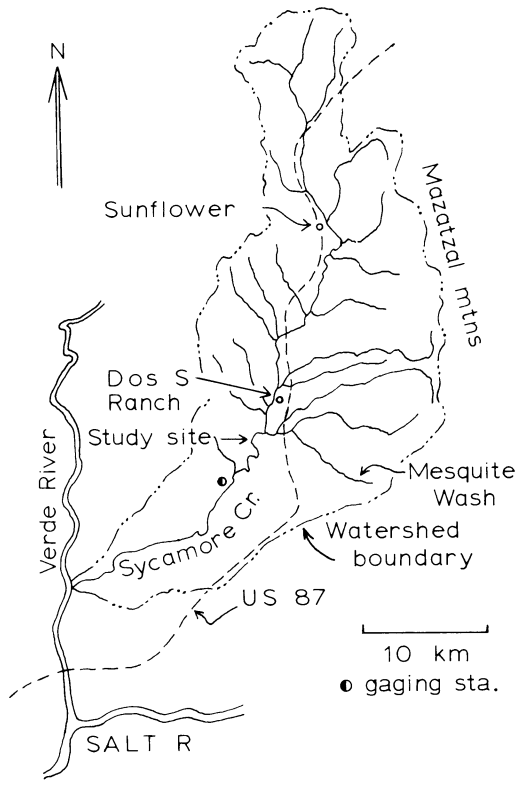

FIG. 1. Sycamore Creek watershed, Maricopa County, Arizona. Study site is 200 m below confluence of Sycamore Creek and Mesquite Wash.

ing the recovery period. Since current is an agent of disturbance via removal of organisms, and floods accentuate this process, stream communities tend to have the characteristics of immature (Margalef 1960, 1968) or pioneer communities (Odum 1969). In rapid streams of mesic areas, and in streams which flood frequently, recovery or succession is truncated, and organisms adapted to high rates of exploitation by current dominate communities. To examine succession in streams properly, a system with infrequent yet catastrophic flooding with relatively stable physical and chemical features during interflood periods is required. Several streams of the desert Southwest (USA) provide this combination of characters and are ideally suited to studies of succession in running waters.

This paper describes changes which occur in a Sonoran desert stream after flash flooding. Emphasis is on temporal change in a single 500-m study reach; however, spatial patterns within this reach are also considered. Strictly speaking, succession is a process of change at the community or lower levels of organization (Drury and Nisbet 1973); however, other workers have described successional change in terms of emergent, or more properly "collective," properties of communities (Margalef 1960, 1968, Odum 1969). The purpose of this paper is to describe simultaneous changes in algal and invertebrate populations and biomass, gross photosynthesis and community respiration, and nutrient dynamics of this stream ecosystem during postflood recovery. Temporal trajectories of these attributes are then compared to generalizations about succession proposed by Odum (1969) and Margalef (1968).

STUDY SITE

Physical organization of Sonoran Desert streams

In the Southwest, lowland streams are permanent only when fed by precipitation inputs occurring at higher elevations of quite large watersheds. Often this precipitation recharges aquifers which drain slowly throughout the year into deep and porous stream channel sediments. Geological faulting in this area of the Basin and Range Province occasionally brings impervious bedrock to or near the surface, and when this occurs in stream channels, water also is forced to the surface. From these "sources" water may flow at the surface for a few metres or for several kilometres before seeping once again into the sand. In some systems, these discrete permanent segments occur one after another in sequence, separated by dry sandy stretches traversed by underflow. The intermittent pattern of surface flow is obliterated during winter and other high-flow periods when the stream occupies its entire channel just as do streams in mesic regions.

Isolated stream segments normally form in summer when evapotranspiration increases and discharge declines. If winter precipitation is high, the stream does not dry back to permanent, isolated segments until late summer. This was the case in 1978–1979, one of the wettest winters of this century in Arizona.

Because the permanent desert stream ecosystem is a small trickle sustained by an enormous watershed, rare isolated cloudburst events in the drainage subject variable portions of the stream to massive destruction. Recession of floods is rapid and the physical structure is restored in hours or (rarely) days, but with a much reduced biota. The reestablishment of the biota is of central interest to this research.

Sycamore Creek

Sycamore Creek (33°45′N, 111°30′W) is a tributary of the Verde River, 32 km northeast of Phoenix, Arizona (Fig. 1). The stream drains a watershed of 505 km² which ranges in elevation from 427 to 2164 m. The drainage is rugged mountainous terrain composed of igneous and metamorphic rocks with shallow overlying soils and unconsolidated alluvial sediments (Thomsen and Schumann 1968). Annual precipitation ranges from 39 cm/yr at 510 m to 51 cm/yr at 1040 m, and peaks bimodally in winter and summer. While winter precipitation is usually gentle and spans one or more days, summer rain occurs as short, localized thunder-

storms. Pan evaporation in the area is 313 cm/yr; thus the stream is frequently intermittent, especially in summer.

The primary study site (at 610 m elevation) is a 500-m section of Sycamore Creek. Bedrock is shallow and surface flow occurs during most of the year. While floods may be intense, modal summer discharge is only 0.03 m^3/s. At this time, the stream is shallow (5 cm) and wide (5–6 m) and current velocity averages near 15 cm/s. Stream substrate consists primarily of coarse sand and gravel which is up to 1 m deep. Riparian vegetation in this lower Sonoran Desert scrub life zone consists of cottonwood (*Populus fremontii*), walnut (*Juglans major*), sycamore (*Platanus wrightii*), and ash (*Fraxinus velutina*). Although these trees achieve considerable size, they are sparsely distributed along a stream channel that is >20 m wide. The stream thus receives full sunlight during most of the day.

Sycamore Creek is characterized by moderately hard, calcium and magnesium bicarbonate water with conductance values near 500 μS/cm and total alkalinity near 250 mg/L as $CaCO_3$. Summer pH varies from 7 to 8. Soluble reactive phosphorous is relatively stable at ≈50 μg/L. At the time of this study, nitrate-nitrogen was 50–300 μg/L. Except during floods, the water is clear with little apparent suspended material.

Floods of summer 1979

Despite record precipitation and widespread flooding in Arizona during winters of 1977–1978, 1978–1979, and 1979–1980, no summer floods occurred in the Sycamore Creek drainage during this period until August 1979, when three scouring floods occurred in rapid succession (6, 12, and 16 August). Peak discharge at the study site on these three dates was 7.0, 3.0, and 2.0 m^3/s respectively, and in each case discharge dropped to 0.25 m^3/s within 48 h (Fig. 2). Based upon observations of several floods in the watershed, a discharge of 1.0 m^3/s is sufficient to "reset" the system through scouring, abrasion, and mobilization of bed materials. While winter floods are often characterized by gradually increasing (and decreasing) discharge, summer flash floods are abrupt events characterized by a discrete flood wave. Discharge at a single point can increase instantaneously 100-fold or more, thus apparently precluding behavioral avoidance responses by mobile organisms. A detailed account of a flash flood wave is presented in Fisher and Minckley (1978). After flooding, the system was periodically sampled to document recovery. The sequence was terminated by a 3 m^3/s flood on 29 October, followed by several months of high and fluctuating discharge characteristic of winter.

Methods

In general, data presented here focus on a single postflood recovery sequence at a single site; however,

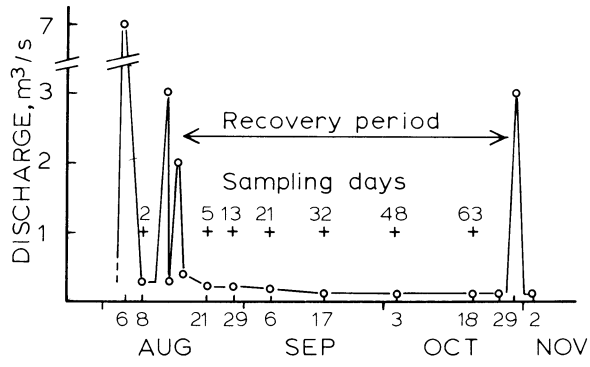

FIG. 2. Stream hydrograph and primary sampling dates, August–November 1979.

this detailed study is part of a more expansive study of flood impact on stream ecosystems and occasionally data are reported from other sites and dates. Samples were taken and measurements made mostly on days 2, 5, 13, 22, 32, 48, and 63 following major flooding. Most data were collected in late morning; however, on 6–7 September (day 22) samples were taken periodically over a 24-h period. Data will be presented as temporal trajectories of various community and ecosystem attributes after flooding.

Physical-chemical properties

Stream morphometry was determined by measuring width and depth at 15 transects in the reach. Discharge was estimated by stream cross-sectional area and velocity near the reach midpoint. Photosynthetically active radiation (PAR) was measured with a Lambda Instruments quantum probe or estimated from curves developed with this instrument. Water samples for chemical analysis were taken in polyethylene bottles at 0, 175- , 325- , and 500-m points in the reach. Samples were transported on ice and filtered immediately upon return to the laboratory (<2 h) (Whatman® GF/F glass fiber filters, pore size 0.7 μm). Analyses were performed on refrigerated samples within 2 d.

Nitrate was determined after reduction to nitrite in cadmium-copper columns (Wood et al. 1967). Nitrite was then measured by a diazotization technique (Strickland and Parsons 1972). This method measures nitrate + nitrite. Ammonium was determined using the phenolhypochlorite method of Solorzano (1969). Soluble reactive phosphorus was measured colorimetrically (after Murphy and Riley 1962) and total dissolved phosphorus was determined as soluble reactive phosphorus after persulfate digestion. Conductivity was measured with a Markson® model 10 conductivity meter (Markson Science Inc., Del Mar, California, USA), pH by electrode, and alkalinity by titration with H_2SO_4. Chloride was measured titrimetrically with $Hg(NO_3)_2$, and sulfate turbidimetrically with $BaCl_2$. The ammonium-molybdate method of Golterman

(1969) was used for colorimetric determination of silica as reactive silicate.

Primary producers

Algae in Sycamore Creek are distributed in several distinct patch types, easily recognized by eye and possessing significantly different microscopic and compositional properties (e.g., species composition, density, chlorophyll content) (Busch 1979). Areal coverage of these patches was determined on sampling dates by a line intercept method (Lewis and Taylor 1967) applied at 15 permanent transect sites in the study reach. Resolution of the transects was 10 cm. On each date three to six samples of each patch type were taken to assay biomass, chlorophyll *a*, and algal community structure for these algal assemblages. Samples consisted of 51.3 cm^2 sediment cores taken to a depth of 0.5 cm.

In the laboratory, each sample was suspended in distilled water, subsampled, and counted in a Palmer cell. Filamentous algae were enumerated with Olson's (1950) grid method. Community structure was based on algal volumes, determined geometrically for each taxon. Remaining suspended algae were drawn upon a glass fiber filter (Whatman® GF/A) which was then divided in half. One half was combined with half of the sediments remaining, dried at 90°C, and combusted at 500° to determine ash-free dry mass, hereafter referred to as "biomass" but including detrital material as well. The remaining half filter and sediment were extracted in methanol followed by spectrophotometric determination of algal pigments (Tett et al. 1977). Estimates of biomass, chlorophyll *a*, and community structure for the stream ecosystem were then computed by weighting patch data by areal coverage of each patch type.

Estimates of gross primary production (P_g) and respiration (R) in terms of milligrams of O_2 per square metre per hour are based on measures of temperature (T, °C), light intensity (L, in Einsteins per square metre), biomass (B, ash-free dry mass in grams per square metre), chlorophyll *a* concentration (C, in milligrams per square metre), and equations for predicting rates of these processes:

$$R = 5.74\, B^{0.26}\, (1.10^T)$$

$$P_g = 6.41\, C^{0.61}\, (1.04^T) L^{0.31}$$

This simple model was developed for Sycamore Creek algal assemblages in summer 1978 for a range of light (0.1–7.6 $E \cdot m^{-2} \cdot h^{-1}$), temperature (19–30°), nitrate (NO_3-N = 0.03–0.16 mg/L), and phosphorus (SRP = 0.05–0.10 mg/L) which encompass those extant during this recovery sequence. The model was parameterized with empircal measures of dissolved oxygen change in light and dark plexiglas chambers incubated in situ for 0.5 to 1.0 h (Busch and Fisher 1981).

Chlorophyll and biomass values during this recovery sequence did not reach the range over which the model was developed until 5 and 10 d after flooding, respectively. Estimates for those early days are extrapolations beyond model conditions and should be viewed with caution.

Confidence limits (95%) of the model vary with state variables but over the range of conditions applied are ±10–20%. It should be emphasized, however, that P_g and R values reported in this paper are estimates, not empirical measurements. P_n is taken as the difference between P_g and R over a 24-h period.

Macroinvertebrates

Invertebrates were taken with core samplers on eight dates following flooding. A minimum of 12 cores (to 10-cm depth) was taken in a stratified random sampling regime on each date. Samples were elutriated, retained on a 270-μm mesh screen, preserved in Kahle's fluid and sorted under a dissecting microscope. Larger, more mobile aquatic insects (e.g., some beetles, hemipterans) were counted in 1-m^2 quadrats and sampled with a dip net.

Food habits of individual taxa were determined by methods of Gray and Ward (1979). Each determination used 5–10 individual guts (foreguts and midguts) from the same species. Gut contents were filtered onto Millipore® HA filters. After clearing the filter, percentage composition of food material was assessed from areal measurements using a Whipple grid. Food habits of nine taxa comprising 85% of total numbers and biomass present were determined in this manner. Trophic classification of remaining taxa was based on our field and laboratory observations and on Merritt and Cummins (1978).

Results and Discussion

Physical-chemical properties

While the flash floods which reset the system and initiated the recovery sequence ranged from 2 to 7 m^3/s, flood wave recession was rapid and relatively stable conditions characterized the 63-d recovery period. In flood the channel was bank-full, nearly 15 m wide, 0.5 m deep, with current velocity near 1.0 m/s. Within 2 d (8 August), width was halved, depth reduced to 6.3 cm, and velocity to 0.62 m/s. Depending upon supply and size of sediments, the stream bed remains mobile at this site until velocity drops to ≈0.5 m/s. On average this occurred by day 5, although mid-channel regions continued to transport bed materials for ≈10 d. While it is reasonable to consider recession of the flood wave as the beginning of recovery for the system as a whole, substrate stability is requisite to colonization by algae and many invertebrates. As a result, recovery of biota progressed from stream periphery to center.

From days 2 to 63 stream width decreased by 28%, depth by 22%, and mean velocity by 34% (Table 1). The 500-m study section thus experienced recession

TABLE 1. Morphometric, physical, and chemical features of Sycamore Creek during postflood recovery. Concentrations in milligrams per litre unless otherwise noted. All data are means for the study section except nitrogen and phosphorus which are for the upstream site only (0 m). Dots denote no data.

Date	8 Aug	21 Aug	29 Aug	6 Sep	17 Sep	3 Oct	18 Oct
Days after flood	2	5	13	21	32	48	63
Width (m)	7.2	6.6	6.3	6.0	5.7	5.4	5.2
Depth (cm)	6.3	7.2	6.4	6.4	5.7	4.4	4.9
Surface area (m^2)	3600	3300	3120	3000	2850	2680	2600
Discharge (m^3/s)	0.28	0.22	0.2	0.18	0.1	0.1	0.11
Mean velocity (m/s)	0.62	0.46	0.5	0.47	0.31	0.42	0.41
Temperature (°C)	29.6	26.3	27.3	30.2	28.5	24.4	22.4
Conductance (μS/cm)	610	630	560	540	530	570	560
pH	7.7	8.6	8.0	7.9	8.0	7.9	8.0
Alkalinity (meq/L)	3.8	4.2	4.1	4.1	...	3.6	4.0
Cl^-	24	23	24	24	23	23	23
SO_4-S	32	29	30	32	28	30	33
Si	7.1	7.8	6.8	7.0	7.0	7.3	7.2
NH_3-N	0.017	0.005	...	...	0.014	...	...
NO_3-N	0.44	0.140	0.120	0.075	0.070	0.100	0.087
Soluble reactive *P*	0.094	0.065	0.070	0.062	0.056	0.054	0.056

of both areal and volumetric boundaries. From day 5 to 63, 700 m^2 of stream channel (19%) was left dry (exposed). This phenomenon potentially affects communities by concentrating mobile organisms and removing (by stranding) nonmotile ones.

During the diel run on 6–7 September 1979, stream temperature ranged over 7°–8° C (23.0°–30.8°). Midday stream temperature ranged from 22.4° to 30.2° during the 2-mo study period. Water is cooled below air temperature by high rates of evaporative cooling which occur at relative humidities near 15% at this time of year (Naiman et al. 1973). Air temperature typically varies from 18° to 43° on a daily basis, a 25° range; thus thermal conditions in this desert stream are moderate and remained so during the course of this study.

Most chemical characteristics, such as conductivity, sulfate, chloride, alkalinity, and silica remained remarkably constant through the study period (Table 1). In addition, these constituents showed no significant fluctuation on a diel basis nor did they vary spatially in the 500-m study section. Nitrogen and phosphorus, on the other hand, varied considerably. The predominant form of nitrogen present was nitrate, which declined from 436 μg/L to 70 μg/L over the 2-mo period (station 1). Ammonia-N was not measured at all sites and times; however, on six dates only 4.4% of inorganic nitrogen was present as NH_3-N (n = 24, SE = 1.4). Soluble reactive phosphorus (SRP) at station 1 declined sharply between days 2 and 5, then varied little from day 5 through 63. Both nitrate and SRP declined in concentration as water flowed through the 500-m study reach. Temporal and spatial dynamics of N and P will be discussed later.

Autotrophs

During this study, algae were the only significant autotrophs present at the study site. At other sites and times aquatic vascular plants may be locally abundant in Sycamore Creek, but during the 2-mo study period, no significant vascular plant populations developed.

Seven algal patch types were macroscopically identifiable during the recovery period. These were coalesced to five types for analysis. Patch type 1 was bare sand without visible algae. Biomass measured as ash-free dry mass was low (≈50 g/m^2) as was chlorophyll *a* (≈3 mg/m^2), and the low chlorophyll : biomass ratio (0.08) as well as the rarity of living cells in microscopic examination indicate that this patch consists largely of detritus. Patch type 2, with intermediate biomass and chlorophyll densities, was dominated by diatoms (77% of total algal volume), particularly *Achnanthes exigua, Gomphonema parvulum,* and *Navicula pupula. Cladophora glomerata* and its epiphytes characterized patch type 3. Both biomass (≈240 g/m^2) and chlorophyll *a* (143 mg/m^2) densities were considered high. Blue-green algae such as *Schizothrix calcicola* and *Anabaena variabilis* characterized patch 4. Biomass and chlorophyll were of intermediate density (≈170 g/m^2 and ≈140 mg/m^2, respectively). Finally, patch 5 was dominated by *C. glomerata,* its diatom epiphytes, and various blue-greens. Patch 5 exhibited the highest biomass (≈310 g/m^2) and chlorophyll *a* (≈190 mg/m^2) values amongst the patches. Species diversity (H') based upon biomass for all algae and for the diatom component alone were similar among patches.

Spatial distribution of algal patch types depended upon current. Patch 1 was most prevalent in mid-channel rapid water, and patch 3 was most abundant in quieter, peripheral sites where the dominant *Cladophora* filaments were less subject to removal by scouring. Other distributional factors are undoubtedly operative, but their identification is beyond the scope of this study. Spatial distribution of patches can be

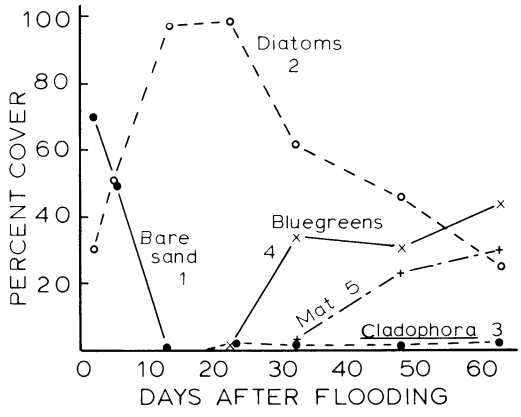

FIG. 3. Percent cover of algal patch types following flooding.

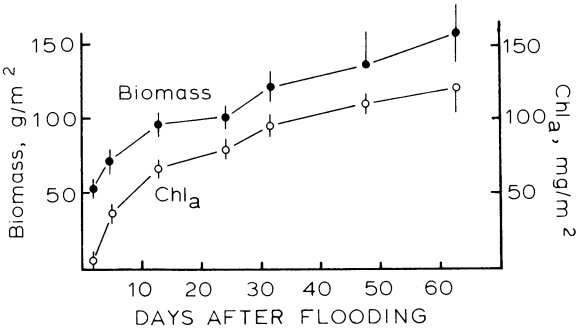

FIG. 4. Recovery of mean biomass and chlorophyll *a* after flooding. "Biomass" is determined as ash-free dry mass and thus includes living and nonliving organic matter. (± 1 SE).

described, however. On a percent coverage basis, the stream ecosystem was rapidly colonized by diatoms (patch 2) which dominated the system during the 1st mo following flooding (Fig. 3). Blue-greens (patch 4) and the *Cladophora*-blue-green mat (patch 5) began to establish late in the sequence, and by the end of the study, dominance was nearly equally shared by patches 2, 4, and 5. Patch 3 (*Cladophora* + epiphytes) was restricted to the channel periphery and was never abundant.

Patch-specific collective properties (such as biomass and chlorophyll) and patch areal coverage data can be combined to describe temporal changes in these properties for the ecosystem as a whole. Biomass and chlorophyll accrued rapidly after flooding and attained nearly 50% of their ultimate levels within 10 d, and >75% within a month (Fig. 4). Species diversity of all algae and of diatoms separately reached levels within 5 d which did not change significantly for 2 mo (Table 2). Likewise, pigment diversity ($O.D._{480}/O.D._{666}$), was stable from day 2 to 63 (Table 2).

The rapid recovery and stable nature of collective properties such as these (and metabolic parameters to be discussed later) belie the rapid, continuous changes in community composition which are simultaneously occurring. Thus, in effect, ecosystem-level collective properties are achieved and persist over a wide range of taxic and physical community structures.

To this point, algal community structure has been presented holistically, i.e., for the entire ecosystem, as the sum of patch-specific structures (Fig. 3). This is analogous to describing forest succession as change in total percent species composition without regard to tree-by-tree replacement processes (e.g., Horn 1975). Our data permit resolution of algal community change at the level of the patch as suggested by Williams et al. (1969) for forests. That is, by examining intact structure of permanent transects through time we can describe the succession of patches at any point on a transect over the 63-d study period.

The method used to construct a transition matrix for Sycamore Creek algae follows Horn (1975). Six patch types were used in this analysis: uncolonized sediments, the four algal assemblages, and algae stranded on dry stream banks due to ecosystem shrinkage accompanying drying (patch 6). Ten-centimetre increments on each of the 15 permanent transects were observed to note transitions among patch types between sampling dates. A transition matrix was then generated for each transect for each pair of sequential observations. These matrices were standardized to a weekly resolution and averaged to yield one transition matrix for the entire recovery period (Table 3, Fig. 5).

The likelihood of a given area of stream remaining the same from one week to the next is indicated by values on the matrix diagonal. These probabilities range from 0.25 for patch 1 (uncolonized sediments) to 1.0 for patch 6 (dry stream bank). Sediment without algae was rapidly colonized, while areas exposed as water receded were removed from the stream and thus

TABLE 2. Selected collective properties of algal communities following flooding.

	Days after flooding						
	2	5	13	22	32	48	63
Diatom *H'*	1.74	2.25	2.31	2.38	2.38	2.26	2.13
Algal *H'*	2.22	2.65	2.71	2.73	2.77	2.73	2.54
$O.D._{480}/O.D._{666}$	1.81	1.86	1.96	1.88	1.93	1.91	1.99
Chlorophyll *a*/biomass (mg/g)	.21	.52	.80	.79	.79	.73	.73

TABLE 3. Patch-specific transition matrix for algal assemblages in Sycamore Creek. Transition probabilities are for 1 wk. See text for description of patches 1–6.

Patch type state 1	Patch type, state 2					
	1	2	3	4	5	6
1	0.25	0.74	0.01	0	0	0.01
2	0	0.58	0.02	0.27	0.03	0.10
3	0	0.17	0.33	0.04	0.04	0.42
4	0	0.22	0.03	0.33	0.35	0.07
5	0	0.08	0.05	0.08	0.71	0.08
6	0	0	0	0	0	1.0

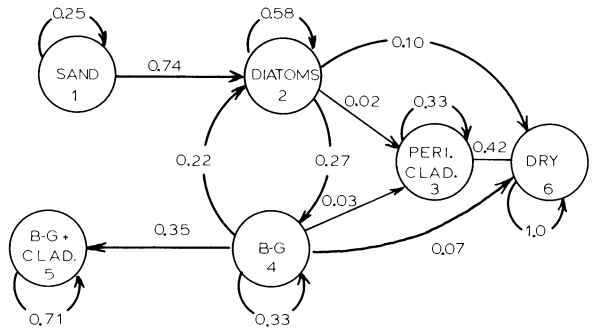

FIG. 5. Transition probabilities between algal patch types. Arrows and associated numbers indicate the probability that the given transition will occur within 1 wk. CLAD = *Cladophora*; BG = blue-green algae; Peri = periphyton.

experienced no change to other patch types. The other patch types ranked in order of their persistence were 5, 2, 4, and 3.

The off-diagonal values in the transition matrix indicate probabilities of change in state in a week's time. For example, the most likely transition from bare sediment was to diatom-dominated assemblages. In general, most probable transitions resulted in an increase in biomass and chlorophyll *a*. An exception was the most probable transition from *Cladophora*-epiphyte assemblages (3) to the stranded state (6). These assemblages tended to be located at the periphery of the

TABLE 4. Numbers and biomass of most abundant invertebrate taxa present during postflood recovery. (‡ = <0.01).

Taxon	Date: / Day:	13 Aug 1	21 Aug 5	19 Aug 13	7 Sep 22	10 Sep 35	14 Oct 49	18 Oct 63
				Numbers (thousands/m²)				
Baetis quilleri		0.03	0.85	2.6	9.3	6.4	0.9	0
Leptohyphes packeri		0.05	0.02	0.25	2.5	17.3	16.0	29.5
Tricorythodes dimorphus		0	0.07	0.6	0.5	2.5	1.7	3.1
Helicopsyche mexicana		0.03	0.02	0.2	0	0.1	0.03	0.07
Chimarra angustipennis		0	0.04	0.4	0.4	‡	0.3	0.5
Cryptolabis sp.		2.1	13.3	21.3	55.8	32.9	168.7	182.6
Probezzia sp.		0	4.4	3.8	6.9	27.5	27.5	27.9
Corynoneura sp.		1.2	2.9	2.6	11.4	21.6	21.3	11.5
Dicrotendipes sp.		0.4	0.5	0.4	2.8	6.4	3.9	4.8
Cricotopus sp.		‡	0	0.8	3.6	0.4	1.2	1.6
Micropsectra sp.		0	0	0	0	0	0.2	5.6
Pentaneurini sp.		0.1	0.5	0.6	1.8	1.0	0.6	0.25
Oligochaeta		0.03	0.02	0.3	1.9	4.5	12.0	18.1
Total		4.9	22.7	33.7	93.7	120.1	253.7	285.5
Percent of total numbers		99.4	98.7	98.2	98.5	96.6	98.8	99.1
				Biomass (g/m²)				
B. quilleri		‡	0.06	0.2	0.67	0.18	0.03	0
L. packeri		‡	0.01	0.03	0.18	2.03	0.63	0.38
T. dimorphus		0	‡	0.12	0.11	0.14	0.26	0.10
H. mexicana		‡	0.01	0.05	0	0.03	0.01	0.03
C. angustipennis		0	‡	0.05	0.05	‡	0.10	0.08
Cryptolabis sp.		0.15	1.22	4.35	5.63	2.4	5.44	7.68
Probezzia sp.		0.02	0.12	0.12	0.32	0.42	1.0	0.27
Corynoneura sp.		0.03	0.13	0.06	0.24	0.38	0.36	0.26
Dicrotendipes sp.		‡	0.03	0.01	0.06	0.11	0.07	0.11
Cricotopus sp.		‡	0	0.02	‡	0.01	0.02	0.04
Micropsectra sp.		0	0	0	0	0	0.05	0.13
Pentaneurini sp.		‡	0.01	0.05	0.14	0.11	0.01	0.02
Oligochaeta		‡	‡	0.01	0.04	0.09	0.02	0.36
Deronectes nebulosus		0.02	0	0	0.05	0	0	0
Tabanus dorsifer		0	0.23	0.05	0.02	0.1	0.2	0.15
Helichus immsi		0	0.18	0	0	1.03	0.34	0.23
Laccobius sp.		0.01	0.33	0.01	0.66	0.24	0.06	0.05
Total		0.2	2.3	5.1	8.2	7.3	8.8	9.9
Percent of total mass		95.5	97	94	98	93	90	95

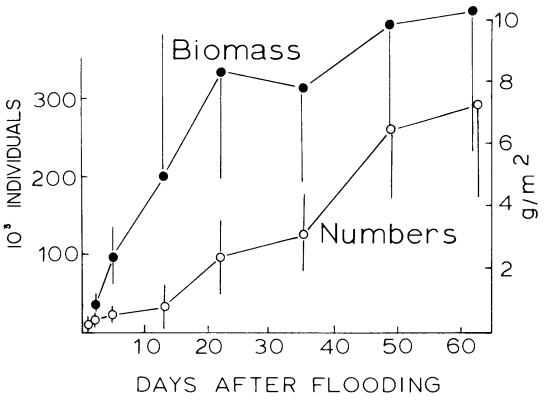

FIG. 6. Changes in mean invertebrate numbers and biomass after flooding. (Vertical bars show 95% CI.)

stream channel and were exposed as discharge decreased. Patch types 1 and 5 tended to be in midchannel and the probability of these types being stranded was correspondingly low. Patch type 2 had a relatively high probability of stranding largely because it was widespread early in the sequence when drying was most rapid.

While biomass and chlorophyll *a* increased in the stream as a whole after flooding, and community structure within the stream generally changed from bare sediment to diatom-dominated assemblages to blue-green algal assemblages, the transition matrix indicates more dynamic changes. Some transitions that frequently occurred within the stream resulted in a decrease in biomass and chlorophyll *a* at those sites. Of those areas with *Cladophora*-epiphyte assemblages that were not stranded (3), the most likely transition was to the diatom-dominated assemblage (2). This transition occurred when *Cladophora* lost attachment to the sediment and drifted downstream, thus exposing sediment which was then colonized by diatoms.

Macroinvertebrates

August flooding reduced both macroinvertebrate numbers and biomass by about 98% on an areal basis. Some of this reduction can be attributed to increased stream surface area due to higher discharge after flooding, but even correcting for this rarefaction mechanism, invertebrates were reduced to <4% of preflood levels. Greatest losses occurred among immature nymphs and larvae, with lesser percentage losses among taxa with aquatic adults such as hemipterans and beetles. Recovery occurred rapidly and reached 50% of ultimate (63-d) densities of biomass and numbers in 13 and 35 d, respectively (Fig. 6, Table 4). For this recovery sequence following widespread flooding in the watershed, recolonization occurred primarily via aerial routes. Recolonizers included aquatic adults capable of flight and aerial adults which had emerged prior to flooding, then oviposited upon flood recession. Since summer floods rise and fall so rapidly in desert streams, this "aerial reserve" of insects is scarcely affected and recolonization occurs rapidly by oviposition. When flooding is localized leaving undisturbed upstream reaches, initial recolonization by drift is important for such taxa as *Baetis quilleri* and *Cricotopus* sp.; however, vertical movements from sediments are never significant colonization routes (Gray 1980). Sandy sediments are not a reliable refuge in these streams because of their mobility and attendant depth of scour.

After initial colonization or egg-laying, increased numbers occurred through rapid growth and development. Several groups, including some mayflies and dipterans, develop extremely rapidly (egg to adult in <2 wk) in Sycamore Creek (Gray 1980). While continued immigration probably occurred, no nearby source of colonizers existed since the entire watershed was disturbed, and emigration probably balanced immigration for the stream segment during this recovery

TABLE 5. Trophic structure of macroinvertebrates present during postflood recovery.

Feeding category	Number of species	Percent of numbers	Percent of biomass	Common taxa
Collectors, total	23	87	85	*Cryptolabis* sp. *Baetis quilleri* *Leptohyphes packeri* Chironomidae Tubificid oligochaetes
Filter feeders	3	1	1	*Simulium* sp. *Chimarra angustipennis* *Cheumatopsyche arizonensis*
Scrapers	6	1	5	*Helicopsyche mexicana* *Physa virgata*
Shredders, algal	2	1	1	*Graptocorixa serrulata* *Ochrotrochia* sp.
Predators	17	13	10	Chironomidae *Probezzia* sp. Dytiscid beetles

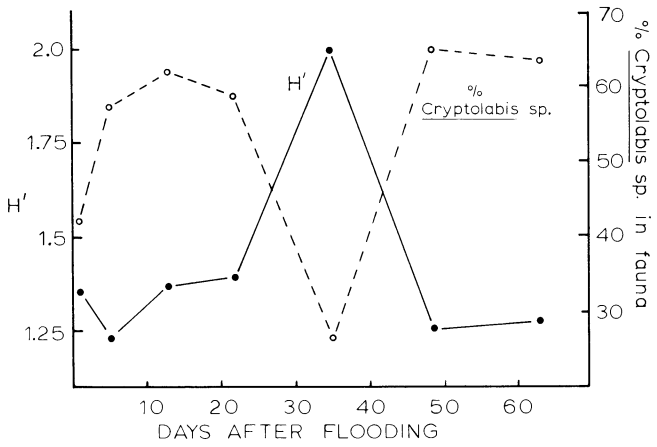

FIG. 7. Invertebrate species diversity (H') and relative proportion of the tipulid *Cryptolabis* sp. in the fauna.

phase. As a result, nearly all population increases after the initial influx period probably occurred from reproduction in situ.

Species diversity

A total of 48 taxa of macroinvertebrates was collected from August to October in Sycamore Creek (Table 4). Flooding caused a net loss of 5 taxa, but all of these eventually reappeared. On any given sampling date, 38–43 taxa were present. Changes in total number of taxa between sampling periods resulted from the sporadic occurrence of rare beetles, such as *Laccophilus* spp.

Species diversity (H') of macroinvertebrates was strongly influenced by the life history of the most common species, *Cryptolabis* sp. (Fig. 7). August flooding had the effect of "synchronizing" the first postflood generation of this tipulid as a result of high flood losses and rapid oviposition by adults that had emerged prior to flooding. Diversity values were low throughout the sequence when *Cryptolabis* sp. density was high, increasing only when density declined as the first generation emerged on day 35.

Macroinvertebrate food habits and trophic structure

The dominant food of invertebrate primary consumers immediately after flooding was allochthonous detritus present as small, dark-colored leaf and wood fragments in guts (Fig. 8). Within 2 wk, diatoms rapidly increased and became the principal invertebrate food. A small peak in consumption of filamentous algae occurred at 5 wk corresponding to initial growths of *Cladophora glomerata,* but this material never comprised >3% of total foods. After filamentous forms appeared, algal detritus, present as light-colored, flocculent material, increased in importance. Overall, the food base of primary consumers was autochthonous production consumed either directly as living algae (diatoms) or indirectly as detritus. In contrast to heterotrophic streams, allochthonous detritus was only important to consumers immediately after flooding.

Throughout the postflood sequence, fast-growing collector-gatherers were the most abundant organisms, comprising >85% of total density and biomass. This is not surprising given that 82–94% of all organic matter present in the system was <100 μm in diameter during the study. Large particles (>1 mm) never comprised >6% of organic matter present after day 1. Predators were the only other common invertebrate group. While no leaf shredders were present, two species, (*Graptocorixa serrulata* and *Ochrotrichia* sp.) were considered algal "shredders" because these were the only invertebrates to consume large filamentous algae as a dominant food (Table 5).

Ecosystem metabolism

Gross primary production and ecosystem respiration were estimated with the model described earlier (Busch and Fisher 1981). Macroinvertebrate standing crop measured as dry mass was 2 g/m^2, during model development, but varied from near zero to almost 10 g/m^2 during postflood recovery. Ecosystem respiration rates predicted by the model were adjusted to reflect the respiration of invertebrates present after flooding. A specific respiration rate in milligrams O_2 per gram dry mass per hour of 5 mg$\cdot$g$^{-1}\cdot$h^{-1} was used for insects in Sycamore Creek. This value was derived from our preliminary work with *Baetis quilleri* and chironomids at 22° C and agrees well with literature data on small mayflies and dipterans (Trama 1972, Harp and Campbell 1973, McCullough et al. 1979), taxa which comprise the bulk of invertebrate standing crop at Sycamore Creek.

Estimated gross primary production and ecosystem respiration increased rapidly after flood recession (Fig. 9). After 13 d, rates of P_g and R were nearly 80% of

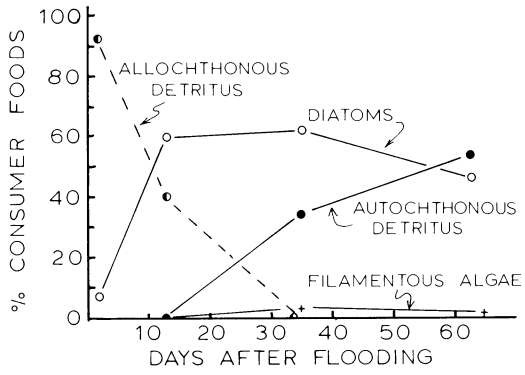

FIG. 8. Proportion of foods in invertebrates' guts following flooding. Data are based on nine species comprising 85% of the invertebrate biomass present and are weighted by the percent of total biomass represented by each of those species.

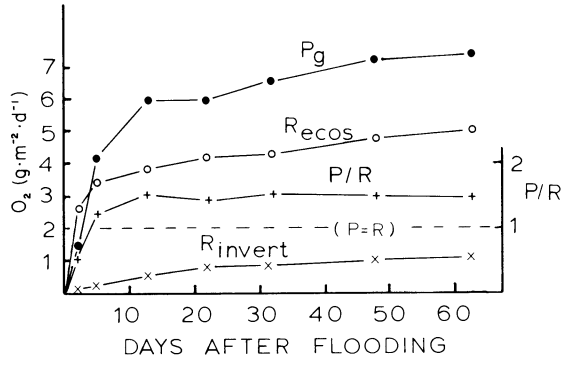

FIG. 9. Patterns of gross primary production (P_g), ecosystem respiration (R_{ecos}), macroinvertebrate respiration (R_{invert}), and P/R after flooding.

ultimate maxima. By day 5, and for the remainder of the recovery period, P_g exceeded respiration and P_g/R averaged 1.46, indicating system autotrophy. After day 5, macroinvertebrate respiration accounted for 14–22% of total respiration.

The ratio of gross primary production to biomass (P_g/B) rose rapidly until day 15 and gradually declined thereafter (Fig. 10). Low early values of P_g/B occurred because detritus dominated "biomass" early in the sequence and production was thus low. The ratio of gross production to chlorophyll *a*, which eliminates the detritus effect, declined steadily through the 63-d period of study (Fig. 10).

Net primary production (P_n), applied iteratively through time, should produce a curve representative of biomass in the ecosystem. The rate of biomass increase (net biomass increment; NBI) is not predicted well by P_n. Biomass accrued much more rapidly during the 1st 2 wk of recovery, and more slowly during the last 6 wk, than P_n predicts (Fig. 11a). Early accrual was 7 g·m^{-2}·d^{-1} between days 2 and 5. Algae were largely responsible for this increase, and if a chlorophyll *a* : biomass ratio typical of later stages is applied to early rates of chlorophyll increase, net production of algae during this period would have to be 14 g·m^{-2}·d^{-1} to account for the observed increase in biomass. Gross production would of course be higher than this. We suggest that this rate, effected by the same type of algal assemblage present later, and requiring a doubling time of ≈12 h, is beyond reason for this system. We thus attribute the observed biomass increase early in succession to import of algae. While we have no measurements of drift of algae into the section, we consider this vector unlikely since the entire watershed had been flooded and no "seed source" existed upstream. Rather we suggest immigration of algae from sediments. Floods thoroughly scour, mix, and redeposit sediments upon recession. Viable algal cells could thus be trapped in these sandy sediments and subsequently move to the surface. Shallow stream sediments after flooding contain ≈0.1% organic matter which, based upon chlorophyll content, is up to 16% algal biomass. To generate the algal increase observed, migration of algae from only 6.3 cm of sediment would be required. Round and Palmer (1966) documented diel vertical migration encompassing several millimetres by *Euglena obtusa* and several diatom species in River Avon tidal muds.

Movement of algae to the sediment surface could have both active and passive components. Most forms present early in recovery are motile and could move to the surface actively (e.g., *Chlamydomonas globosus*, several diatoms). Movement of water through porous sediments could also passively transport algae to the surface by elutriation (Bruns and Minckley 1980); however, this mechanism alone is unlikely to have accounted for the observed increase in chlorophyll *a* : biomass as detrital organic matter in the same size range would have been similarly elutriated.

Later in the recovery sequence (after day 13), P_n exceeded NBI indicating system losses of organic matter in excess of respiration. We attribute this loss to export downstream. An organic matter budget for the 63-d recovery period is presented in Table 6. Gross primary production was the predominant input to the system and respiration was the major output; however, gross inputs and outputs in stream water transport are not known. Net import and output, computed from differences in P_n and NBI curves (Fig. 11b), comprised 10% and 14% of total input and output, respectively. Export of organic matter to peripheral stream banks by drying accounted for an additional 6% of organic matter output. From day 13 to day 63 when the system was in the export mode, 56% of net production was exported and only 44% contributed to increased standing crops on the site.

While export estimates based on difference calculations should be regarded with caution, it is important to note that autotrophic ecosystems must either con-

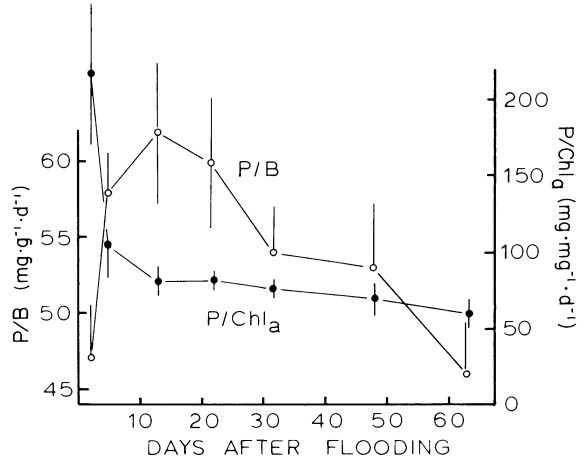

FIG. 10. Mean ratios of gross primary production (as O_2) to ash-free dry biomass (P/B) and chlorophyll a (P/Chl a) after flooding. (Vertical bars show ±1 SE.)

tinually grow (by increased standing crops) or export organic matter. Since there is an eventual limit to organic matter storage capacity in streams, autotrophic streams at steady state must export organic matter equivalent to net production. This is in marked contrast to geographically widespread heterotrophic streams which are always net importers of organic matter (Fisher and Likens 1973, Fisher 1977).

While Sycamore Creek did not reach steady state with respect to organic matter during this recovery period, the export mode was reached rapidly (2 wk); thus, even nonsteady state, autotrophic desert streams are exporters. The fate of exported (thus excess) production is an exceedingly important question in the ecology of desert drainages. As we have seen, lateral export during drying accounts for a portion of loss, but the bulk of export is to downstream reaches. Net

TABLE 6. Organic matter budget for the 500-m study section of Sycamore Creek during the 63-d recovery period.

	Total for period (kg)	g·m^{-2}·d^{-1}
Inputs:		
P_g	1060	5.43
Import, net (days 0–13)	119	0.61
Total input	1179	6.04
Outputs:		
Respiration, ecosystem	728	3.73
(R, macroinverts)	(138)	(0.71)
(R, algae, microorgs)	(590)	(3.02)
Export, lateral	54	0.28
Export, net downstream (days 13–63)	122	0.63
Total output	904	4.64
Δ *Storage* (Computed)	275	1.40
Δ *Storage* (Observed)	278	

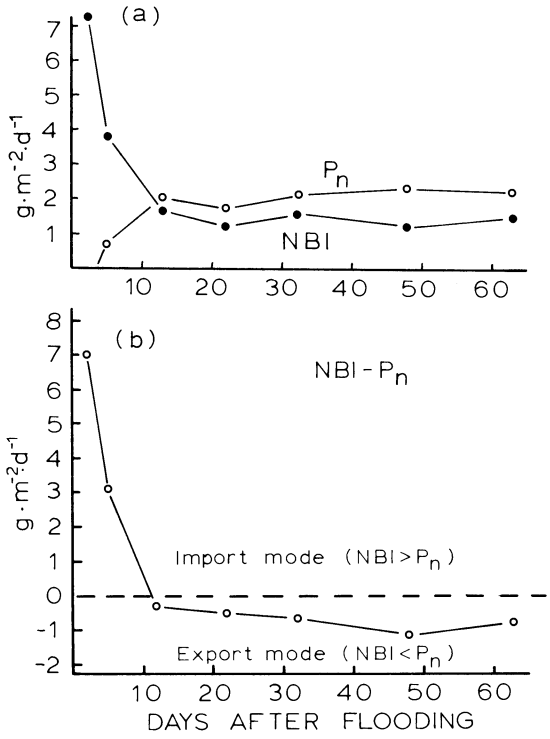

FIG. 11. (a) Net primary production (P_n) and net biomass increment (NBI) during postflood recovery. P_n is estimated from the production model and NBI reflects observed rates of organic matter accretion on the site. (b) Difference between net biomass increment (NBI) and net production (P_n) after flooding. If NBI > P_n, net import of organic matter (OM) is occurring, while net export obtains when NBI < P_n.

export downstream cannot occur without attendant organic matter loading of downstream reaches. In desert drainages, gradual drying proceeds laterally and longitudinally, eventually breaking the stream into spatially discontinuous and continually shrinking segments. Thus, ultimately, all exported organic matter is subject to stranding and drying, and is subsequently accessible to terrestrial consumers such as ants and termites. This is an interesting and important reversal of the pattern in mesic streams where drying is less pronounced and the net flow of organic matter is from terrestrial to aquatic ecosystems. The utility to terrestrial consumers of this material exported from stream to dry land is dependent in part on the length of the dry period, for with the next flash flood, this material is entrained and exported long distances downstream. In most desert drainages today, this usually means to man-made impoundments, but historically this material entered large desert rivers such as the Salt, Gila, Verde, and Colorado.

Nutrient dynamics

Compared to streams elsewhere, nitrate-N in Sonoran Desert streams is relatively low and variable

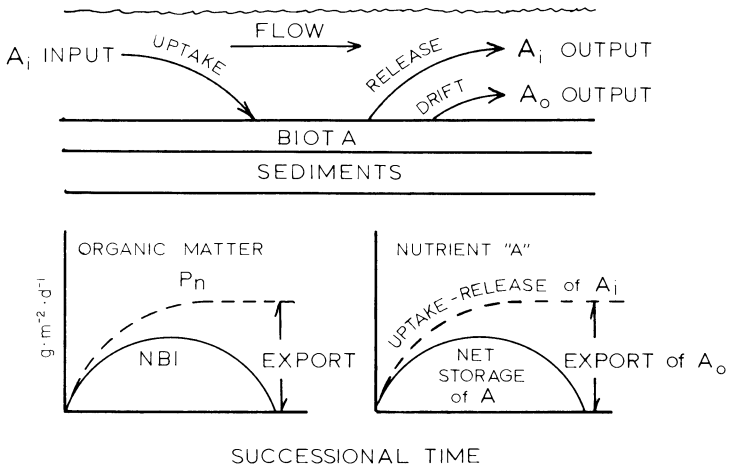

FIG. 12. Simplified model of hypothetical nutrient A in a stream ecosystem. Inorganic, readily utilizable forms of the element (A_i) are taken up and released by biotic processes. Drift or other losses of element A in organic form (A_o) also contribute to total output from the ecosystem. In successional time, the net change in A_i (uptake-release of A_i) is proportional to net primary production (P_n) and storage of A is proportional to net biomass increment (NBI). Net uptake of A_i which is not stored in situ is exported as A_o; therefore at steady state, the total net uptake of A_i is exported as A_o, just as all of P_n is exported.

and soluble reactive phosporus (SRP) is high and more stable. Both average near 50 μg/L. Two exceptions to this generally low N:P ratio are floodwaters and stream sources where water first emerges from alluvial sediments or deep aquifers. Here nitrate-N may range from 500 to several thousand μg/L and averages 700 μg/L, while SRP averages 65 μg/L (Grimm 1980). Such a source is located 200 m upstream from our study section, and while it is diluted greatly by channel flow at this time, water entering the study section is higher in nitrate than streamwater upstream of this source.

As water flows through the study reach nitrogen and phosphorus (and other essential nutrients) are subject to uptake as biomass is synthesized. Thus we predict declining nutrient concentrations as water moves through the reach. Of those nutrients examined by us, only nitrate and SRP exhibited detectable downstream changes in concentration during this study.

Vitousek and Reiners (1975) presented a simple model of nutrient input-ouput budgets for terrestrial watersheds during succession which we have adapted to stream ecosystems (Fig. 12). The model predicts that rate of uptake of essential nutrients is proportional to rate of organic matter accretion in the system. In successional time, early stages will show little uptake, middle stages of high biomass accretion will exhibit high uptake rates, and later, steady-state systems will again exhibit zero net uptake as inputs and outputs of essential elements balance. This model applies only when fluxes of all forms of a given nutrient are reckoned. That is, nitrate may decline longitudinally even at steady state if nitrate uptake is balanced by net export of, for example, particulate organic nitrogen (Fig. 12).

This model was tested during postflood recovery at Sycamore Creek for nitrogen and phosphorus. During the study, nitrate in water entering the 500-m study section declined from 436 μg/L early to near 70 μg/L later in the sequence, while phosphorus (SRP) input concentration varied from 54 to 94 μg/L. These temporal changes in nutrients at site 1 probably reflect upstream activities but are of no consequence to the model. What is germane are N and P declines through the study reach which occur at increasing rates through time (Figs. 13 and 14).

Changes in concentration were converted to areal uptake based on stream surface area (A, square metres) and discharge (Q, cubic metres per hour):

TABLE 7. Fluxes of carbon, nitrogen and phosphorus in Sycamore Creek during postflood recovery. P_n is estimated from the Busch-Fisher (1981) model. N and P uptake are computed from downstream change in concentrations (Figs. 13–14) using the equation presented in the text. Regressions of distance on concentration not significant.

		mmol·m^{-2}·d^{-1}			
Day	Time	P_n (C)	Uptake of N	Uptake of P	C:N:P
2	1130	9.9	0.47	0.47	21:1:1
5	1000	19.2	3.67	0.59	32:6:1
13	1100	55.9	16.7	0.86	64:19:1
22	0900	48.1	13.5	1.08	45:13:1
32	1230	60.3	11.5	0.64	94:18:1
44	1130	64.2	13.4	0.31	207:43:1
63	1030	62.5	17.2	1.01	65:17:1
1–63 (mol·m^{-2}·63 d^{-1})		3.28	0.80	0.043	76:18:1

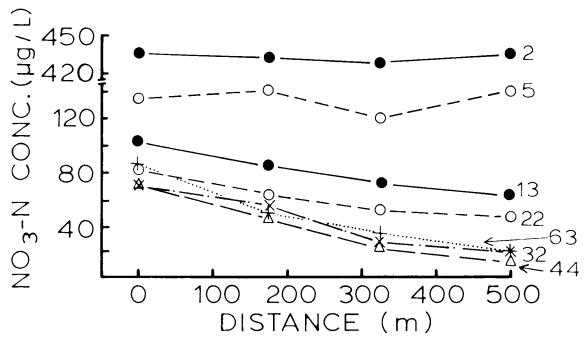

FIG. 13. Change in concentration of NO_3-N in streamwater as it flows through the study reach. Numeric label on each line indicates days since flooding.

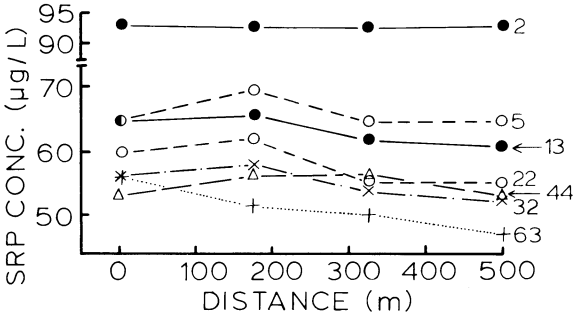

FIG. 14. Change in concentration of soluble reactive phosphorus (SRP) in streamwater as it flows through the study reach. Numeric labels on each line indicates days since flooding.

Nutrient Uptake (milligrams per square metre per hour) $= \frac{m \cdot l \cdot Q}{A}$

where m = rate of nutrient decline downstream (milligrams per cubic metre per metre) and l = length of study reach (500 m). Simple concentration changes between the 0 and 500-m sites were used when r^2 for regressions of distance on concentration were not significant (days 2 and 5). Uptake of both nitrate and SRP increased rapidly early in the recovery sequence and remained positive throughout the 63-d period (Table 7). Low rates of uptake for both nitrate and SRP during days 1–5 when biomass was accruing rapidly on the site lend further support to the hypothesis that early, rapid increases in biomass (and chlorophyll) were due to import rather than in situ production.

The N:P ratio in uptake over the 63-d study period at Sycamore Creek was 18:1. If a PQ of 1.2 is assumed for net primary production estimated in oxygen units (Westlake 1974), C:N:P of nutrient uptake is 76:18:1. This ratio is lower in carbon than Redfield's (1958) suggested C:N:P of 106:16:1 for oceanic plankton, which suggests that either P_n was underestimated in our study or that nitrogen and phosphorus are removed from the water column in part by mechanisms other than biomass accretion attending photosynthesis (e.g., denitrification, adsorption of phosphorus to sediments), or both. It should be emphasized that biomass accretion is only one of several processes potentially responsible for the disparity in nutrient inputs and outputs of ecosystems (Gorham et al. 1979).

Our nutrient uptake model (Fig. 12) is supported in that carbon, nitrogen, and phosphorus uptake increase rapidly after flooding and do so in proportions which are reasonable for biomass accretion; however, the recovery sequence was interrupted by a flood before steady-state biomass was achieved and thus later stage nutrient dynamics cannot be assessed.

Samples upon which these computations were based were taken at midmorning. On 6–7 September (days 21 and 22) uptake computed on a diel basis indicated uptake of both nitrogen and phosphorus in light and dark with no discernible diel pattern. While nutrient concentrations may fluctuate on a diel basis, we have been unable to show diel variation in uptake rates at this or other sites on Sycamore Creek (Grimm 1980).

SYNTHESIS

E. P. Odum tabulated attributes of successional and mature ecosystems in his classic 1969 paper. Several of these attributes were evaluated during succession in Sycamore Creek, and are compared with the predictions of Odum (Table 8). Both Odum's trends and ours are asymptotic; however, later successional stages may be marked by patterns which are cyclical, stepwise, or regressive (Crocker and Major 1955, Reiners et al. 1971, Loucks 1970, Connell 1978). Deviation from the asymptotic pattern may occur in Sycamore Creek after 63 days, a possibility addressed later; however, comparisons are restricted to the asymptotic 1st 2 mo. In the text which follows, reference to the numbered attributes in Table 8 is made parenthetically.

Gross primary production and ecosystem respiration rapidly increase after flooding and P_g/R exceeds 1 by day 5. P_g/R does not approach unity as predicted by Odum (1), nor would we expect this to occur in autotrophic ecosystems with several export vectors. Similarly, net primary production (yield) increases asymptotically in variance with Odum's prediction (4). This is a case where criteria derived from relatively closed ecosystems (Odum 1960, Beyers 1963, Cooke 1967, Gordon et al. 1969) are inadequate to describe succession in open systems such as streams. Both net-importing heterotrophic and net-exporting autotrophic systems can maintain steady-state function and exhibit features of maturity with P_g/R considerably greater or less than one (Fisher and Likens 1973). Although less than half of net production remains in the system, organic matter accrues (6) and by inference, inorganic nutrients are increasingly intrabiotic (7) as predicted.

Production per unit biomass (P_g/B) is hypothesized

TABLE 8. Comparison of trends in postflood recovery of Sycamore Creek with those predicted by Odum (1969).

Attribute	Odum 1969	Sycamore Creek	Agreement?
(1) *P/R*	approaches 1	rises from <1 to >1	no
(2) *P/B*	decreases	increases rapidly, then declines	yes
(3) *P*/Chlorophyll *a*	not considered	decreases	...
(4) P_n (yield)	decreases	increases	no
(5) Food chains	grazing → detritus	detritus → grazing → detritus	yes
(6) Total organic matter	increases	increases	yes
(7) Inorganic nutrients	increasingly intrabiotic	increasingly intrabiotic	yes
(8) Species diversity	increases	depends upon group	
Algae, *H'*	...	relatively stable	no
Invertebrates, *H'*	...	fluctuating	no
Invertebrates, richness	...	relatively stable	no
(9) Biochemical diversity ($O.D._{480}/O.D._{666}$)	increases	stable	no
(10) Size of organisms	increases	depends upon group	
Algae	...	increases	yes
Invertebrates	...	remains small	no
(11) Life cycles	increasing length and complexity	stable (short, simple)	no
(12) Role of detritus in nutrient regeneration	increasingly important	increasingly important	yes
(13) Nutrient conservation	improves	improves	yes
(14) Resistance to perturbation	improves	remains low	no

to decrease during terrestrial succession (2), largely due to temporal accretion of metabolically less active supportive tissues (e.g., wood). In Sycamore Creek less active detritus is abundant early in succession before autotrophs develop, and P_g/B rises early, then gradually declines. The decline in P_g/B after 2 wk probably results from accretion of autochthonous (algae-derived) detritus. Gross production per unit chlorophyll *a*, an index which eliminates the detritus effect, drops rapidly during the 1st 2 wk and gradually, but not significantly, thereafter (Fig. 10). With allowance for this effect, these observations agree with Odum.

Odum predicts that early successional food chains are supported by autotrophs via grazing and that detritus assumes greater importance in mature systems (5). With the exception of the 1st wk of recovery when residual allochthonous detritus is an important food, Sycamore Creek invertebrates utilize increasing amounts of detritus with time (Fig. 8), supporting Odum's contention and lending circumstantial support to his prediction of an increasing role of detritus in nutrient regeneration (12).

Species diversity increases during succession according to Odum (8). In Sycamore Creek the only significant increase in autotroph species diversity (Shannon-Weaver Index, *H'*) occurred in the 1st wk of recovery. *H'* then remained remarkably constant until the end of the sequence. Despite Margalef's (1968) contention that species diversities of disparate components of the same ecosystem are correlated, the pattern of macroinvertebrate species diversity was quite different from that of algae. Species richness changed little and *H'* fluctuated in response to abundance of a single taxon (*Cryptolabis* sp.) through the equitability component. We suspect this pattern will recur in a system where organisms are small, life cycles are rapid and asynchronous, and competition for resources is low. Our observations do not support Odum's prediction and suggest that patterns of diversity depend upon the taxonomic group from which diversity is computed.

Through succession we found no significant increase in biochemical diversity measured as the carotenoid: chlorophyll *a* pigment ratio, though an increase was predicted by Odum (9). We suggest that this criterion, proposed by Margalef (1966), be abandoned unless accompanied by a biologically meaningful rationale for continued use. Attempts to evaluate this parameter in a successional context have been singularly unsuccessful (e.g., Motten and Hall 1972, Winner 1972).

Odum predicts that early successional communities will be dominated by small organisms with rapid, simple life cycles (11) and that larger organisms with more complex life cycles will characterize later stages. Algae in Sycamore Creek fit this pattern in the transition from diatoms and unicellular greens to larger filamentous greens and blue-greens. Size of invertebrates remains small and development times remain short at all times of year and all stages of succession (Gray 1980). These life history attributes are adaptations to flooding and drying—hazards that no degree of biotic modification can ameliorate. We thus cannot support the contention that a more mature Sycamore Creek ecosystem is more stable than earlier stages when resistance to perturbation (by flooding) is the criterion for stability (14). We have no other data which can be used to assess "overall homeostasis" criteria proposed by Odum.

As Vitousek and Reiners (1975) have aptly demon-

strated, the successional trends in nutrient cycling proposed by Odum require revision (see also Gorham et al. 1979). Our data show that rates of nitrogen and phosphorus uptake from the medium are proportional to net primary production. Vitousek and Reiners (1975) correctly argue that net uptake cannot occur indefinitely and later steady-state systems exhibit equal uptake and release rates. However, if readily available nutrient species (NO_3-N, SRP) are considered separately, input can exceed output at steady state. Excess input is fixed in organic matter and exported. Continued uptake of available nutrients can thus occur indefinitely, just as can P_n, without violating the Vitousek-Reiners model. In the sense that available nutrients are removed from the medium more effectively and completely in late succession, nutrient conservation "improves" with time as Odum predicts (13).

Our findings at Sycamore Creek agree only partially with the predictions of Odum (1969). Greatest disparity is in features unique to or accentuated in open, frequently disturbed ecosystems such as streams (P_g/R, P_n, diversity and life history attributes). While trends in Sycamore Creek make biological sense, appreciable modification is required to reconcile these observations with Odum's framework. We thus agree with Drury and Nisbet (1973) who doubt the attainability of a general theory of succession, applicable to all ecosystems.

An important aspect of successional theory should be sought at the organismal level and firmly grounded in evolutionary principles (Pickett 1976). However, the problem of describing patterns of succession within algal patches of Sycamore Creek at the same level of resolution as within patches of trees in forests is intractable.

A second approach to succession, more closely attuned to that of Odum (1969), considers collective properties of populations and communities and is more appropriate to resolution of temporal change in ecosystems such as streams, where spatial relationships are fluid and organisms turn over rapidly. This approach is descriptive, generalizations arise by induction, and explanation lies in physiology of aggregates, not in evolution of populations.

We described postflood recovery of Sycamore Creek in this latter context and find Odum's list of attributes useful. We have tried to avoid implications of successional "progress" and the attendant view that organisms of early stages are somehow less well adapted than those which occur later. We have made no attempt to reconcile these two approaches in a hybrid theory of succession, too often attempted without success in the literature. To do this successfully one must invoke mechanisms (such as selection at the group and community levels) which are biologically untenable.

Long-term succession at Sycamore Creek

While the sequence we detailed ended at 63 d, we have made several observations of considerably older systems. Biomass attained at day 63 (159 g/m^2) is near the low end of a range of biomass values determined for Sycamore Creek in late summer 1978, several months after flooding (100–400 g/m^2). At high biomass levels of 400 g/m^2, gross primary production measured as O_2 is near 23 g·m^{-2}·d^{-1}, community respiration (as O_2) is 6.5 g·m^{-2}·d^{-1}, and P/R is 3.5 (Busch and Fisher 1981); thus, at these high standing crop levels, typical of late succession, the system maintains its autotrophic habit. Community structure in these late stages is similar to that late in our 63-d period. Macroinvertebrate communities continue to be dominated by small mayflies, chironomids, and beetles at the approximate standing crop levels observed on day 63 (Gray 1980). Filamentous algae, particularly *Cladophora*, continue to dominate floral communities (Busch 1979) and macrophytes are abundant only during years of modest flow. Pattern is patchy, drifting algae are common and patches are continually opened as algal mats break loose from the substrate. This pattern of localized, patchy disturbance, established just 30 d after flooding, is analogous to small-scale patch disturbance described for terrestrial forests and coral reefs (Connell and Slatyer 1977).

Two exceptions to this highly productive, autotrophic, high pattern-diversity state occur. The first results when the stream dries and ecosystem boundaries rapidly collapse. The second happens when nutrients limit primary production. Shrinking systems strand autotrophs and concentrate mobile consumers such as insects and fish. Insects can and do emerge and emigrate from drying stream segments; however, fish are trapped. *Agosia chrysogaster* (longfin dace), the principal fish species present in Sycamore Creek, is an omnivorous cyprinid which consumes large quantities of algae (Fisher et al. 1981). Late in the drying sequence consumption exceeds primary production and the stream ecosystem eventually consists of fish, fish feces, and a few piscivorous belastomatid hemipterans. Likens (1970) discusses morphometric exigencies which dictate changes in community structure and function of lakes undergoing eutrophication. Deterioration of desert stream communities during drying is similarly dictated by severe morphometric constraints.

Grimm (1980) has shown that nitrogen is the nutrient most likely to limit primary production in streams of the arid Southwest. This results when nitrogen input at stream sources is insufficient to support potential production of downstream autotrophs. On several occasions we have observed spontaneous deterioration of filamentous green algal assemblages long after resetting floods. This crash is always associated with low (<0.03 mg/L) or undetectable nitrate levels, and

is often accompanied by an ascension of blue-greens, particularly heterocystous *Anabaena variabilis*, a nitrogen fixer. This blue-green assemblage thus represents an edaphic "climax" for this system. Under conditions of ample nutrient supply, however, the typical summer community of Sycamore Creek is the *Cladophora*-chironomid-ephemeroptera community which we observed on day 63.

All of the changes we described occur during interflood periods shorter than a year. Floods of 1 m^3/s reset the system and initiate another successional sequence. Less frequent floods of greater magnitude may also influence succession by, for example, removing vascular hydrophytes or temporarily extirpating macroinvertebrate taxa such as selected caddisflies (Gray 1980). Floods of this magnitude may occur only once in several years. Studies of streams in northwestern United States emphasize the need to examine cyclic processes in heterotrophic forest streams over a variety of time scales. Stream channel detrital accumulations exhibit turnover rates on the order of tens or hundreds of years (Keller and Tally 1979, Naiman and Sedell 1980). Stochastic flooding events of similar frequency may scour streams of coniferous forests to bedrock and reset accumulation sequences (Swanson and Lienkaemper 1978). While free-flowing desert streams currently appear to exhibit shorter pulse-reset periods, this may not have been the case historically. Extensive cienegas or riparian marshes were prevalent in many desert drainages in Arizona, including Sycamore Creek, until the turn of this century when a combination of overgrazing and intense flooding led to their demise (Hastings 1959). Today only remnants remain. These systems probably have a life span on the order of a hundred years and only floods with this recurrence frequency are capable of cutting and draining them (Schumm and Hadley 1957). Cienega building, characterized by organic matter accumulation, is slow and requires low gradient sites and several years without intense flooding to begin. On this longer time scale, cienegas may be considered the archetypal desert stream climax community. In this context, sequences such as that we studied represent often-interrupted, pioneer stages of a long-term successional sequence culminating in the desert cienega. This perpective supports Margalef's (1960) view that the true climax stream community is the terrestrial climax for that geographic region. The terrestrial climax for continually wet sites in the arid Southwest is the cienega.

The patterns we have described for Sycamore Creek are accentuated but are by no means unique to desert streams. All free-flowing streams flood, yet desert streams flood less often. Flooding reduces the biota in all streams, but to a greater degree in desert streams with unstable substrates. Postflood recovery of biota occurs in all streams, but more rapidly in warm, well-lighted streams of arid regions. We thus suggest that a successional perspective is useful and relevant to stream studies everywhere and urge stream ecologists to incorporate this perspective, if only to include recent flooding history among other physical, chemical, and biologic descriptors.

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