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Nitrogen limitation in a Sonoran Desert stream

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Abstract. Four nutrient enrichment bioassay experiments were conducted in Sycamore Creek, Arizona, during summer and autumn 1983. In two experiments, nitrogen and phosphorus were added alone and in combination while in the other experiments nitrogen was added singly. In experiments involving enrichment of both nutrient-diffusing substrates (clay flowerpots) and streamwater overlying tile/gravel artificial substrates, nitrogen enrichment significantly enhanced rates of chlorophyll *a* accrual, primary production, and nitrogen uptake. Addition of phosphorus either singly or in combination with nitrogen did not result in significant responses of these parameters; thus ambient concentrations of phosphorus were above limiting levels, even when excess nitrogen was supplied. Nitrogen additions stimulated periphyton growth when background nitrate-N concentrations were ≤0.055 mg/L. We propose that nitrogen limitation is common in the desert Southwest since concentrations lower than this and atomic nitrogen to phosphorus ratios <16 occur in most (82% and 87%, respectively) previously surveyed southwestern streams (n=92). Temporal patterns of chlorophyll *a* accrual suggest that availability of nitrogen limited the rate of algal increase, but not the ultimate periphyton standing crop. If true, this hypothesis predicts that algal recolonization rates should vary depending on nitrogen supply. In desert streams, flood disturbances reduce algal standing crops to near zero, but postflood recovery periods may be quite long. Nitrogen limitation in desert streams thus may exert strong influence on rates and patterns of algal recolonization following floods.

Key words: streams, desert, nutrient limitation, nitrogen, periphyton, primary production, Arizona, succession.

Unidirectional flow is a dominant feature of lotic ecosystems. For many years this caused doubt that stream periphyton could be nutrient limited; continual supply of nutrients from upstream should provide adequate nourishment for growth. Early enrichment bioassays in streams (Patrick 1966, Wuhrmann and Eichenberger 1975) supported this contention and led Wuhrmann (1974) to propose the generalization that nutrients probably do not limit primary productivity in any running waters. Recently, however, several investigators have stimulated periphyton growth with added nitrogen, phosphorus, or both (Elwood et al. 1981, Gregory 1980, Peterson et al. 1983, Stockner and Shortreed 1978, Triska et al. 1983). In heterotrophic, detritus-based streams decomposition also may be nutrient limited (Aumen et al. 1983, Elwood et al. 1981, Howarth and Fisher 1976). Whitford and Schumaker (1961, 1964) showed that mineral uptake is stimulated by currents >15 cm/s. This "physiological richness" arises as current erodes the diffusion shell surrounding attached algal cells. Just as the diffusion gradient is steepened by current, so it may be weakened by microbial films or dead water in algal mats (Elwood et al. 1981) which results in reduced algal access to dissolved nutrients. These empirical observations and theoretical considerations strongly support the contention that nutrients may in fact limit algal growth in flowing waters.

Several investigators have used ratios of nitrogen to phosphorus (N:P) to indicate which of these critical nutrients potentially limits production (Fisher and Grimm 1983, Healey and Hendzel 1979, Redfield 1958, Rhee 1978). Potential nitrogen or phosphorus limitation should be distinguished from actual nutrient limitation as originally defined by Liebig (1855). For example, in an environment in which nitrogen and phosphorus are present at an atomic ratio of 5 when optimal N:P for growth is 15, a relative shortage of nitrogen exists despite an absolute concentration that may be quite high. However, if algae assimilate N and P at a ratio of 15, nitrogen eventually will be depleted to a growth-limiting level while phosphorus will remain relatively abundant. Conversely, if environmental N:P exceeds that ratio required for growth, phosphorus is potentially limiting. Actual phosphorus limitation occurs

TABLE 1. Ambient conditions and design of nutrient enrichment experiments in Sycamore Creek, Arizona, July–November 1983.

Experiment	Type	Treatments	Statistical Tests	Response Parameters[a]	Incubation Time (d)	Ambient Streamwater Concentration (μg/L)			
						NH_4-N	NO_3-N	SRP	N:P
1	clay pot	C, N	*t*-test	CHL	7, 14, 20	8	55	54	2.6
2	clay pot	C, N, P, N+P	ANOVA	CHL, P_n, R	11	14	29	45	2.1
3	channel	C, N, P, N+P	none[b]	CHL, AFDM, P_n, R, UPT	12, 21	11	18	40	1.6
4	channel	C, N	*t*-test	CHL, P_n, R, UPT	10, 21, 35	12	27	47	1.8

[a] CHL = chlorophyll *a*, AFDM = ash-free dry mass, P_n = net primary production, R = community respiration, UPT = nutrient uptake.
[b] See text.

when phosphorus is reduced to limiting levels by uptake.

An extensive survey of 92 streams of arid and semi-arid regions of southwestern USA has shown their mean nitrogen to phosphorus ratio to be 11.4 (SE=7.1) at low flow (Fisher and Grimm 1983). An N:P of 11.4 falls below both the Redfield (1958) ratio of 16 (suggested as the point of transition from N to P limitation in the sea) and the cell composition ratio of 17.1 typical of desert stream periphyton (Grimm 1985). However, cellular N:P may vary widely in algal taxa (DeVries et al. 1983, Rhee 1978, Rhee and Gotham 1980) as may the critical N:P ratio. Schanz and Juon (1983), using an algal growth potential criterion for a river periphyton community, determined that N was limiting at N:P<10, P was limiting at N:P>20, and in the range of N:P=10–20, neither nutrient could be assumed limiting with certainty. This broad range of uncertainty is not surprising because communities consist of many species, each with different optimal N:P requirements. In any event, evidence is strong that a wide spectrum of streams of the American Southwest are potentially nitrogen limited; 87% of those sites surveyed had N:P<16 and 80%<10. The purpose of the work reported here is to test the hypothesis that nitrogen is actually limiting in Sycamore Creek, a typical Sonoran Desert stream in central Arizona. Sycamore Creek has a mean N:P of 2.8 at low flow, strongly suggesting potential N limitation. Actual nitrogen limitation was assessed with in situ nutrient-enrichment bioassays using both nutrient diffusing substrates (Fairchild et al. 1985) and drip-enriched artificial channels located in the natural stream bed. Results from these experiments will be used to determine the nitrogen concentrations that actually limit stream algae and to assess the spatial and temporal (e.g., seasonal) limits of actual nitrogen limitation in desert streams.

Methods

Enrichment experiments were conducted in Sycamore Creek, a mid-sized, spatially intermittent desert stream, during summer and autumn 1983. Stream discharge was stable during this period at 0.05–0.06 m^3/s except for three small flash floods (~1 m^3/s) on 8, 9 and 13 August, and one large flash flood (5–8 m^3/s) on 6 October. The latter occurred between experiments and so did not influence algal colonization of experimental substrata. Daily maximum water temperatures were 22–27°C and minima were 18–20°C throughout the period. Monthly means of daily solar radiation at Tempe, Arizona declined from ~30,000 kJ m^{-2} d^{-1} in midsummer to ~20,000 kJ m^{-2} d^{-1} in autumn. None of the sites was shaded during the day. Ambient streamwater nutrient concentrations varied somewhat among the experiments, but N:P was low throughout the study period (Table 1).

Two types of experimental design were used for enrichment (Table 1). Experiments 1 and 4 compared nitrogen enrichment (+N treatment) with unenriched controls; experiments 2 and 3 added a phosphorus (+P treatment) and a combined N+P treatment. Experimental units were sampled from 7 to 35 d after initiation of experiments. Chlorophyll *a*, ash-free dry mass (AFDM), net primary production, community respiration, and N and P uptake were measured (in various combinations) as response variables (Table 1). Scrapings from substrates were examined microscopically to de-

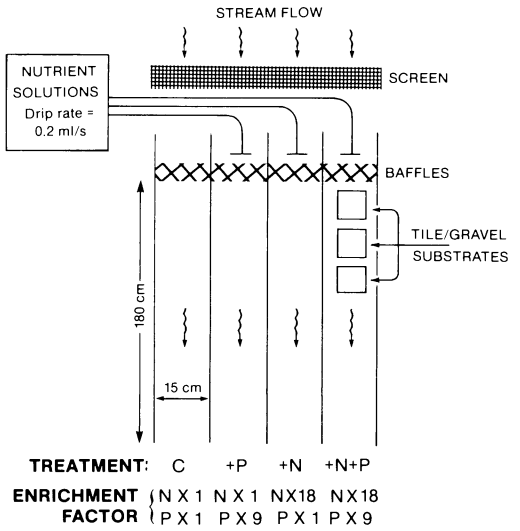

FIG. 1. Diagram of experimental channels, nutrient enrichment experiment 3, Sycamore Creek.

scribe major changes in algal community structure, if any.

Nutrient-diffusing bioassay substrates for experiments 1 and 2 were created from clay flowerpots (diameter = 6 cm, height = 6.5 cm) as described in Fairchild et al. (1985). Concentrations of nitrate-N and orthophosphate in the 2% agar solution used to fill pots were 0.5 and 0.1 M, respectively. Fairchild et al. (1985) found that nutrients at similar concentrations continued to leach through the clay for at least 23 d, and leaching rates were still fairly high (>100 μmol P/d and >3000 μmol N/d) in our experiments after 11 d. We therefore assumed that pots were continuously enriched for the duration of our experiments (≤21 d). Pots were affixed to concrete blocks in sets including one pot per treatment. Ten blocks with one +N and one control treatment each were placed in Sycamore Creek on 19 July 1983 for experiment 1; two blocks each were removed after 7 and 14 d and six blocks were removed after 20 d for analysis of chlorophyll *a*. Six replicates (4 treatments per replicate) were used for experiment 2; all of these were removed on 2 September 1983 after 11 d of colonization, when net primary production, community respiration, and chlorophyll *a* were measured.

In experiment 3 (25 August–14 September 1983), four galvanized steel troughs (channels) (Fig. 1) set on the stream bottom were continuously enriched with sodium nitrate and/or sodium phosphate (1500 mg/L) at 0.2 ml/s from 114-L reservoirs on the stream bank. This yielded treatment concentrations of ~0.32 mg nitrate-N/L (18× ambient) and ~0.34 mg soluble reactive P (SRP)/L (9× ambient) in the channels. Discharge in channels was ~0.001 m^3/s while stream discharge was ~0.05 m^3/s. Velocities in channels (~15–20 cm/s) were comparable to stream velocity. Twenty 58-cm^2 artificial substrates, unglazed clay tiles coated with natural stream substrates (coarse sand), were placed in each channel at day zero. After 12 d of continuous enrichment ten tiles were removed from each channel; four were used to estimate AFDM as described below and six were used for measurement of net primary production, community respiration, and N and P uptake. Chlorophyll *a* was measured on all tiles removed at day 12 and on remaining tiles at day 21. Net primary production was also measured on day 21.

In experiment 4 (11 October–15 November 1983), three channels received ammonium nitrate by dripping to yield concentrations of ~0.11 mg nitrate-N/L and ~0.10 mg ammonium-N/L (4 and 8× ambient, respectively). Channels were stocked with the snail *Physa virgata* at three densities. Three unenriched channels, also stocked with snails at the same densities, served as controls. After 10 d of tile colonization three tiles were removed from each channel for determination of chlorophyll *a*. On day 21 net primary production, community respiration, N and P uptake, and chlorophyll *a* were measured on three tiles from each channel. These measurements were repeated on three tiles per channel on day 35.

Experiments 3 and 4 were set up as one- and two-way analysis of variance designs, respectively; however, if experimental units are considered to be channels receiving (or not) nutrients, rather than tiles, then treatments were pseudoreplicated (Hurlbert 1984). Inferential statistics thus are not presented for experiment 3. Results of the grazer manipulation in experiment 4 were not conclusive (Grimm 1985) and are not discussed here. However, the manipulation provided a source of replication for the nutrient enrichment experiment. Statistical inferences for experiment 4 are therefore derived from comparison of means of the three means of combined enriched vs. unenriched channels

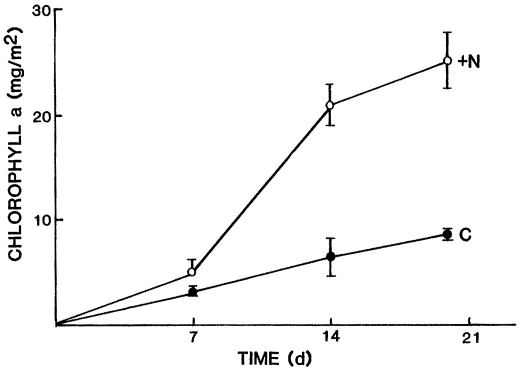

FIG. 2. Response of periphyton chlorophyll *a* standing crop (mean ± standard error) to nitrogen enrichment during experiment 1, Sycamore Creek, Arizona. C—control, +N—nitrogen added.

(*t*-test), disregarding the different snail densities. Since any grazer effect would increase the variance of nutrient treatments, demonstration of significant differences between them is more difficult.

Chlorophyll *a* was determined on all artificial substrates by extraction of the entire substrate in methanol (Tett et al. 1977). Ash-free dry mass (AFDM), measured only in experiment 3 (day 12), was calculated from chlorophyll to AFDM ratios determined on four tiles reserved for this purpose. These tiles were thoroughly brushed into a pan and the scraped material was collected on a filter (Whatman® GF/F, 0.7 μm pore size). Chlorophyll *a* was extracted from half the filter and AFDM, as weight loss of dried filters (60°C, 48 hr) on ignition (550°C, 2 hr), was determined on the other half. Material remaining on brushed tiles was extracted in methanol and small remaining amounts of chlorophyll *a* were added to the chlorophyll *a* estimates from extracted filters. Mean chlorophyll to AFDM ratio from each channel was used to calculate AFDM of all tiles.

Metabolism was measured using closed-bottom, cylindrical Plexiglas® chambers (10.7 cm diameter) as described by Grimm and Fisher (1984). Tiles or clay pots were first cleared of invertebrates, agar was removed from pots, and substrates were placed in chambers containing 750 ml stream or channel water. Respiration was measured as oxygen change in motor-stirred chambers darkened with aluminum foil, and net primary production as oxygen change during a subsequent light incubation. Oxygen was analyzed using a modified micro-Winkler technique (Busch and Fisher 1981).

Following measurement of metabolism, water in chambers was replaced and N and P uptake were calculated from concentration changes during a light incubation (experiments 3 and 4 only). Water was stored and transported at 4°C and filtered (Whatman® GF/F filters) prior to analysis within 24 hr. Nitrate was determined after reduction to nitrite in cadmium-copper columns (Wood et al. 1967). Nitrite thus formed was measured by a diazotization technique (Strickland and Parsons 1972). Ammonium was measured with the phenolhypochlorite method of Solorzano (1969), and SRP was measured colorimetrically (after Murphy and Riley 1962).

Results

Experiment 1

After one week no significant difference in chlorophyll *a* was observed between N-enriched and control clay pots, but by day 14, differences were significant ($t=5.15$, 2 df, $p<0.05$). Higher chlorophyll *a* standing crops of +N treatments persisted at 20 d ($t=5.47$, 10 df, $p<0.001$), although rate of chlorophyll accrual between days 14 and 20 on enriched pots was slightly reduced compared to days 7 to 14 (Fig. 2).

Experiment 2

Marked response of chlorophyll *a* standing crop to N enrichment was observed by day 11 with both +N and +N+P treatments in experiment 2 (Fig. 3; $F=84.08$, 3,20 df, $p<0.0001$). Net primary production also was significantly higher on flowerpots enriched with N than on control or +P pots ($F=12.66$, 3,20 df, $p=0.0001$), while community respiration did not differ significantly among treatments ($F=0.33$, 3,12 df, $p=0.80$). Chlorophyll and net primary production responses to combined N and P enrichment were not significantly different from responses to N alone, but both were significantly higher than control and +P treatments (Tukey's multiple comparison test, $p<0.05$).

Experiment 3

Chlorophyll *a* increased rapidly in 12 d to 97.7 and 116.4 mg/m² in +N and +N+P channels, but reached just 35.2 and 39.4 mg/m² in

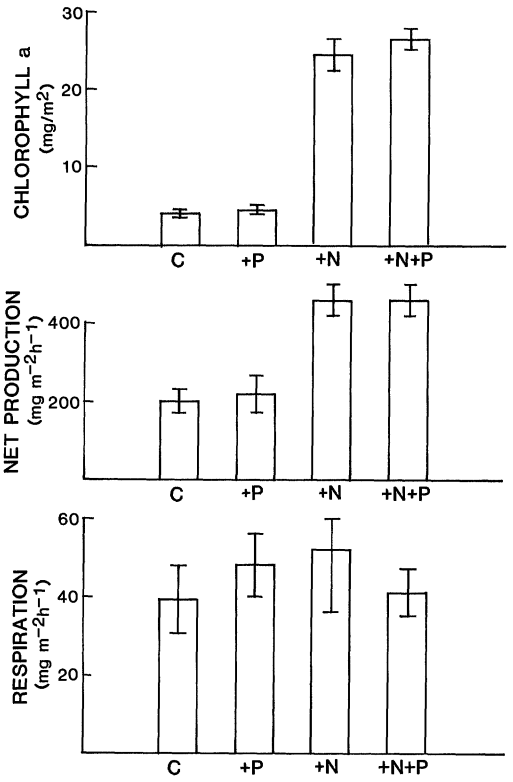

FIG. 3. Responses of periphyton chlorophyll *a* standing crop and oxygen metabolism (mean ± standard error) to nutrient enrichment after 11 d in experiment 2. C—control, +P—phosphorus added, +N—nitrogen added, +N+P—nitrogen and phosphorus added.

control and +P channels (Fig. 4). Net primary production was also higher in both N-enriched channels than in control and P-enriched channels (Fig. 4). In no case was there evidence of an additive effect of P enrichment. Responses to combined enrichment were similar to responses to N enrichment alone.

Chlorophyll to AFDM ratios differed among channels; +N+P channel tiles had the highest ratio (4.16 mg/g) while control tiles were lowest (1.36 mg/g). Ratios of +N and +P tiles were intermediate, at 2.94 mg/g and 2.24 mg/g, respectively. Differences in AFDM among channels were less striking than those for chlorophyll *a* (Fig. 4). Community respiration was only slightly higher in both N-enriched channels than in control and +P channels (Fig. 4). Because community respiration includes respiration not only of autotrophic organisms but also of microorganisms colonizing detritus, AFDM and community respiration responded similarly to enrichment.

Uptake of nitrate-N and TDN by the N-enriched community greatly exceeded uptake in control and +P channels (Table 2). Incubation times were kept short (<30 min) so that uptake would not deplete the nutrient supply in enclosed chambers; however, a few control and +P tiles completely removed nitrate and uptake was therefore underestimated. SRP uptake did not differ among treatments, indicating luxury P uptake by N-limited periphyton.

Temporal patterns of chlorophyll *a* accrual and net primary production during experiment 3 suggest that N-enriched channel tiles reached a maximum chlorophyll *a* level dictated by some factor other than nitrogen supply (Fig. 5). Chlorophyll *a* accrual in control and +P channels was slower than in the two N-enriched channels, but accrual rate was constant throughout the experiment and by day 21, chlorophyll *a* standing crop was approaching N-enriched channel levels.

Experiment 4

Accrual of chlorophyll *a* through time followed a pattern in experiment 4 similar to that observed in experiment 3. Chlorophyll *a* in enriched channels approached an apparent asymptote while it increased continuously until day 35 in unenriched channels (Fig. 6). Differences between treatments therefore were most pronounced on days 10 and 21; standing crops of chlorophyll *a* and rates of net and gross primary production and community respiration in N-enriched channels were significantly higher than in control channels on those days (Table 3).

Both nitrate-N and ammonium-N in approximately equal concentration were added to enriched channels as the N source, but ammonium-N was taken up preferentially by the periphyton. Rates of nitrate-N uptake on day 21 by N-enriched tiles were higher than uptake by controls, but were substantially lower than uptake rates observed during experiment 3 (Table 3 vs. Table 2). Ammonium-N uptake rates of N-enriched channels on day 21 were near nitrate-N uptake rates of experiment 3 and greatly exceeded control channel rates (Table 3). SRP uptake was low in both nutrient treat-

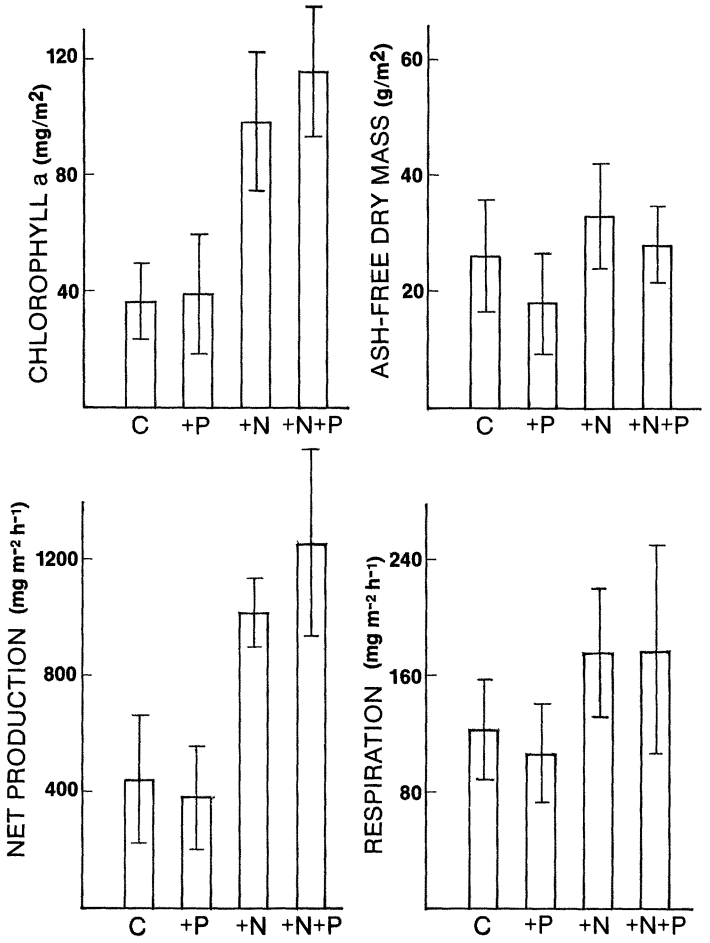

FIG. 4. Responses of periphyton chlorophyll *a* standing crop and oxygen metabolism (mean ± standard deviation) to nutrient enrichment after 12 d in experiment 3. Symbols as in Figure 3.

ments. In fact, SRP was released by control channel periphyton communities on day 21 (Table 3).

By day 35 nutrient treatment effects were not significant (Table 3) except that chlorophyll *a* remained higher in the N-enriched group than in the control, and SRP uptake was higher in the control treatment. Other measured differences were much less pronounced than earlier in the experiment.

Community structure was not assessed quantitatively; however, no clear differences in proportional representation of major taxa among treatments were detected by microscopic examination. Diatoms, the chlorophytes *Oedogonium* sp., *Stigeoclonium* sp., and *Cladophora glomerata*, and the bluegreens *Calothrix* sp. and *Schizothrix* sp. dominated periphyton communities of all treatment substrata of experiments 2, 3, and 4. Further, microscopic examination of treatment vs. stream substrata revealed that major taxa colonizing treatment substrata also

TABLE 2. Uptake of nitrogen and phosphorus by channel tile periphyton on day 12 of experiment 3. Parenthetical values are standard deviations, $n=6$.

Channel	Uptake (mg m^{-2} h^{-1})		
	Nitrate-N	TDN	SRP
Control	2.59 (0.58)	6.35 (4.64)	8.82 (6.11)
+P	2.31 (0.67)	3.69 (2.37)	4.14 (5.71)
+N	28.05 (8.08)	29.46 (10.33)	4.87 (1.14)
+N+P	39.16 (9.62)	36.00 (6.16)	5.06 (3.07)

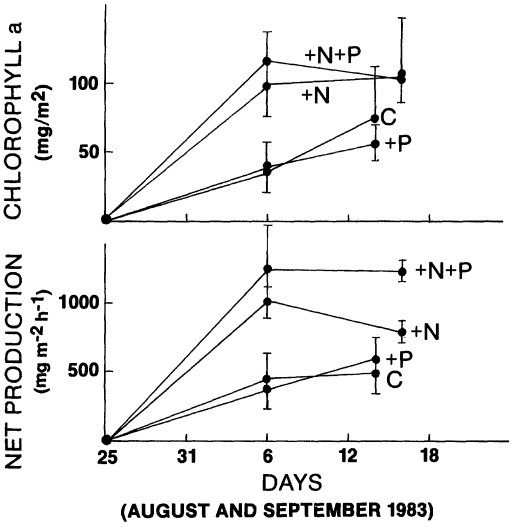

FIG. 5. Temporal pattern of chlorophyll *a* accrual (top panel) and net primary production (oxygen units, bottom panel) (mean ± standard deviation) in nutrient treatment channels, experiment 3. Symbols as in Figure 3.

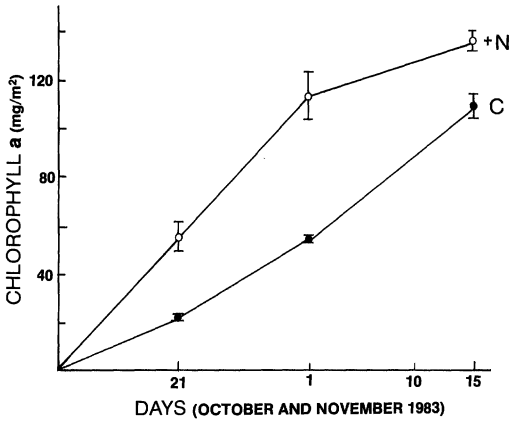

FIG. 6. Temporal pattern of chlorophyll *a* accrual (mean ± standard error) in nitrogen enriched and control channels, experiment 4. Symbols as in Figure 1.

predominated in the stream. Taxonomic shifts in response to enrichment at the level of diatom species may have occurred, but this was not determined.

Discussion

Our experiments clearly demonstrated stimulation of chlorophyll *a* accrual, primary production, and nutrient utilization by nitrogen additions. Experiments 2 and 3 showed that phosphorus in Sycamore Creek is above limiting concentration even when nitrogen is supplied in abundance. We conclude that nitrogen was the limiting nutrient and that phosphorus was not secondarily limiting.

Single nutrient enrichments (as in experiments 1 and 4) have demonstrated both N and P limitation in other streams. P availability limited decomposition rate, leaf disc respiration, and periphyton chlorophyll *a* and AFDM standing stocks in a Tennessee woodland stream (Elwood et al. 1981). A later enrichment of the same stream with ammonium produced no stimulation of periphyton growth (Newbold et al. 1983). N was identified as the limiting nutrient in three studies in Pacific Northwest forest streams (Busch 1978, Gregory 1980, Triska et al. 1983). Although light is the primary limiting factor in these heavily shaded streams, removal of shading or experimental increase in lighting resulted in significant responses to N enrichment over lighted, unenriched controls.

Other studies demonstrating nutrient limitation employed experimental designs similar to our experiments 2 and 3. A Pennsylvania stream was N-limited, but showed an additive effect of P enrichment (Crawford 1979), while Vancouver rainforest (Stockner and Shortreed, 1978), Alaskan tundra (Peterson et al. 1983), and Michigan woodland streams (Pringle and Bowers 1984) were primarily P limited, with additive N effects. An additive effect occurs when N and P are both at low concentration so that when the primary limiting nutrient is supplied the secondary nutrient is rapidly depleted and becomes limiting. No additive effect of P enrichment was observed in Sycamore Creek. P concentration is ample to support elevated growth of N-enriched periphyton.

Nitrogen limitation in the desert Southwest

Ratios of nitrogen to phosphorus (ammonium + nitrate-N/SRP) and concentrations of these nutrients in lotic ecosystems of the American Southwest, when considered in light of results reported here, indicate that nitrogen limitation is common regionally. Mean N:P for stream sites (n=92) sampled by Fisher and Grimm (1983) was 11.4, and 87% of these sites had N:P<16. In Sycamore Creek N:P is <16,

TABLE 3. Results of *t*-tests for nitrogen enrichment effects, experiment 4. Treatment means were calculated disregarding grazer densities; $n=3$. Means marked * significantly higher than means of the other treatment ($p<0.05$).

Parameter	Treatment Mean (Std. Error)	
	Control	Enriched
Day 10		
Chlorophyll *a* (mg m^{-2})	20.7 (1.26)	55.6 (6.07)*
Day 21		
Chlorophyll *a* (mg m^{-2})	54.5 (1.64)	113.5 (9.60)*
Net production (mg O_2 m^{-2} h^{-1})	240.8 (21.87)	436.3 (17.00)*
Respiration (mg O_2 m^{-2} h^{-1})	132.5 (11.48)	175.7 (4.02)*
Gross production (mg O_2 m^{-2} h^{-1})	373.4 (32.68)	612.0 (18.77)*
Nitrate-N uptake (mg m^{-2} h^{-1})	1.93 (0.20)	9.22 (0.45)*
Ammonium-N uptake (mg m^{-2} h^{-1})	0.55 (0.25)	24.72 (0.54)*
TDN uptake (mg m^{-2} h^{-1})	0.78 (1.58)	17.09 (0.71)*
SRP uptake (mg m^{-2} h^{-1})	−6.64 (1.23)	1.54 (0.44)*
Day 35		
Chlorophyll *a* (mg m^{-2})	109.2 (3.60)	137.1 (3.39)*
Net production (mg O_2 m^{-2} h^{-1})	677.3 (16.20)	737.1 (101.9)
Respiration (mg O_2 m^{-2} h^{-1})	141.7 (2.15)	134.5 (24.90)
Gross production (mg O_2 m^{-2} h^{-1})	819.0 (17.20)	871.5 (124.4)
Nitrate-N uptake (mg m^{-2} h^{-1})	3.09 (0.47)	1.97 (0.87)
Ammonium-N uptake (mg m^{-2} h^{-1})	2.58 (0.47)	10.43 (2.81)
TDN uptake (mg m^{-2} h^{-1})	1.41 (3.81)	2.18 (3.05)
SRP uptake (mg m^{-2} h^{-1})	3.35 (0.16)*	0.85 (0.26)

indicating potential nitrogen limitation, much of the time (Fig. 7). Actual N limitation was demonstrated by our experiments when N:P was 1.6–2.6 and nitrate-N concentration was 0.018–0.055 mg/L (Table 1). Periphyton growth was nitrogen-limited at all ambient nitrate-N concentrations tested up to 0.055 mg/L. Further experimentation would be necessary to determine if nitrogen limits production at concentrations higher than this. If 0.055 mg nitrate-N/L is taken as a conservative estimate of limiting concentration (assuming adequate P), then N limitation is probably quite common in Sycamore Creek, at least during summer (Fig. 7). If this criterion for N limitation is extended to southwestern streams surveyed by Fisher and Grimm (1983), 75 (82%) had nitrate-N concentrations <0.055 mg/L (Fig. 8) and were therefore presumed nitrogen-limited during low-flow periods.

Water in spatially intermittent desert stream channels often originates from discrete in-channel springs, or sources, which are fed by vast interstitial reservoirs of water stored from floods or high-elevation runoff. Such springs, and the precipitation and floodwaters feeding them, are usually rich in nitrate-N and have N:P>16 (Fisher and Grimm 1983, Fisher and Minckley 1978, Grimm et al. 1981). Why then does nitrogen limitation occur downstream of sources when uptake should deplete phosphorus before nitrogen declines to limiting concentration? The answer may be that phosphorus concentration in southwestern streams is physicochemically mediated, e.g., by adsorption/desorption equilibrium of water and sediments or by solubility control of P concentration by abundant calcium phosphate minerals of these waters. Phosphorus concentration is also high in Sycamore Creek and in many southwestern streams relative to lakes and streams elsewhere (Fisher and Grimm 1983, Grimm et al. 1981). Streams throughout the region drain watersheds of volcanic origin where waters are often rich in phosphorus (Dillon and Kirchner 1975, Golterman 1975). In a study of N:P of Washington's surface waters, Thut and Haydu (1971) concluded that over half the sur-

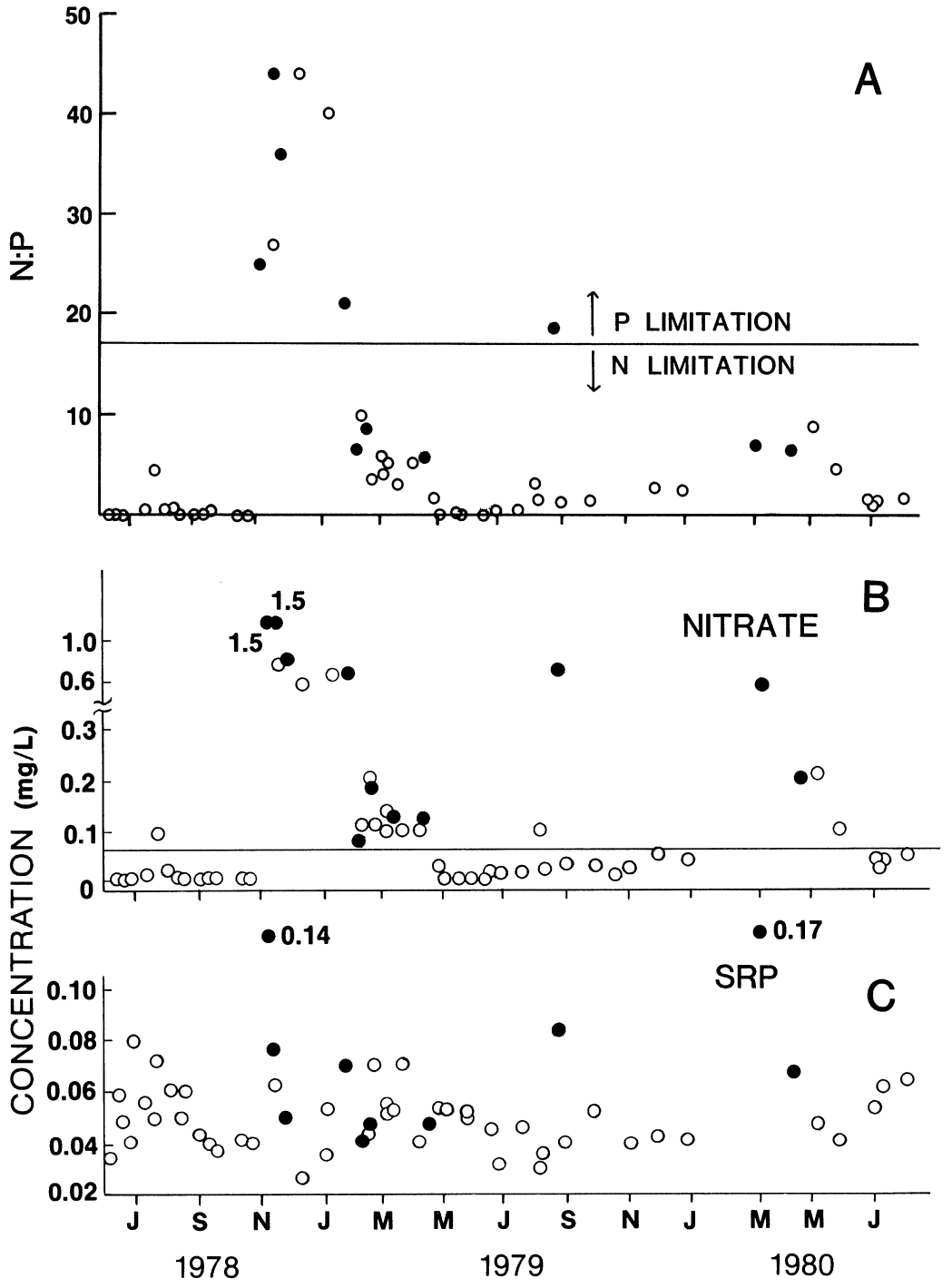

FIG. 7. Atomic ratios of nitrate-nitrogen to soluble reactive phosphorus (SRP) (A), nitrate-N concentration (B), and SRP concentration (C) in Sycamore Creek, Arizona, 1978–1980. Floods are denoted by closed circles, non-flood flows by open circles. Horizontal line in A (N:P=17) indicates point of transition from potential nitrogen to phosphorus limitation (based on periphyton cell composition ratio), horizontal line in B indicates minimum estimate of limiting nitrate-N concentration (see text).

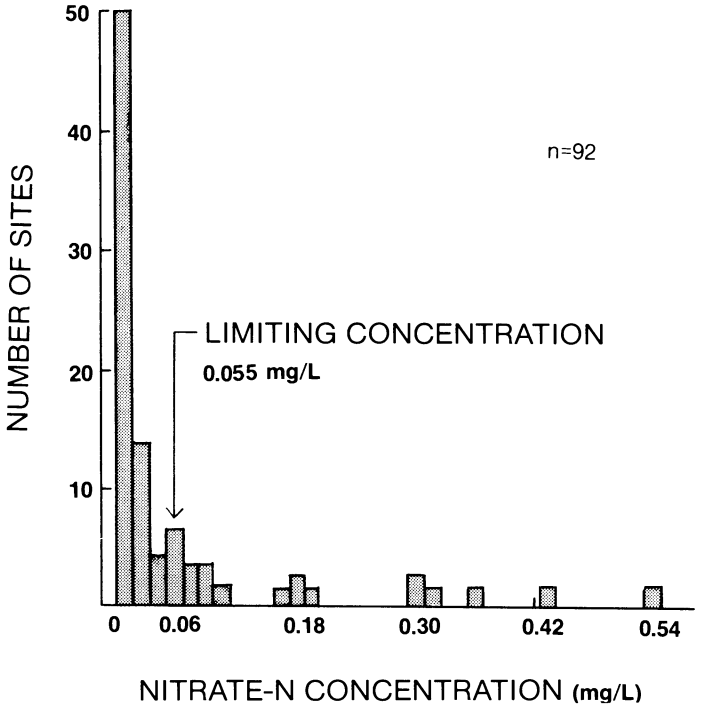

FIG. 8. Frequency histogram of nitrate-N concentration for 92 southwestern stream sites sampled during summer and autumn low flows (from Fisher and Grimm, 1983).

face waters of that state were potentially N-limited (N:P<10). Many of these originated in volcanic regions, while potentially P-limited streams drained watersheds of glacial or granitic parent material. Early emphasis on phosphorus as the limiting nutrient in freshwater ecosystems (Likens 1972, Schindler 1977) may have been the result of restricted geographical scope of such investigations.

Effects of N limitation on desert stream periphyton communities

Discussions of nutrient limitation too often fail to identify precisely which ecosystem component or process is limited by nutrient availability. Many investigators have simply compared standing crop in enriched and nutrient-limited waters to assess nutrient limitation. Others have measured rates of standing crop accrual or of primary production as response criteria. We found both structural (e.g., chlorophyll *a* standing crop) and dynamic (e.g., primary production) differences between N-enriched and unenriched periphyton communities. Structural differences, however, are products of dynamic processes, the properties most immediately affected by nutrient availability. For example, chlorophyll *a* standing crop in experiments 1, 3, and 4 approached asymptotes under enriched conditions, but increased more linearly when N was limiting. If experiments had been terminated after 3 months rather than 3–5 weeks, chlorophyll *a* may not have differed between treatments. If N-limited communities do eventually reach the same maximum standing crop as N-enriched periphyton but at a slower rate, the rate of primary production, not standing crop, would be the nutrient-limited property. Maximum standing crops would be determined by some other factor or combination of factors such as light limitation, sloughing, or grazing (McIntire 1968, 1973).

Another structural attribute influenced by N availability was the chlorophyll to AFDM ratio. N-enriched periphyton was characterized by higher chlorophyll to AFDM ratios than N-limited periphyton in Sycamore Creek (experiment 3). Triska et al. (1983) similarly found no

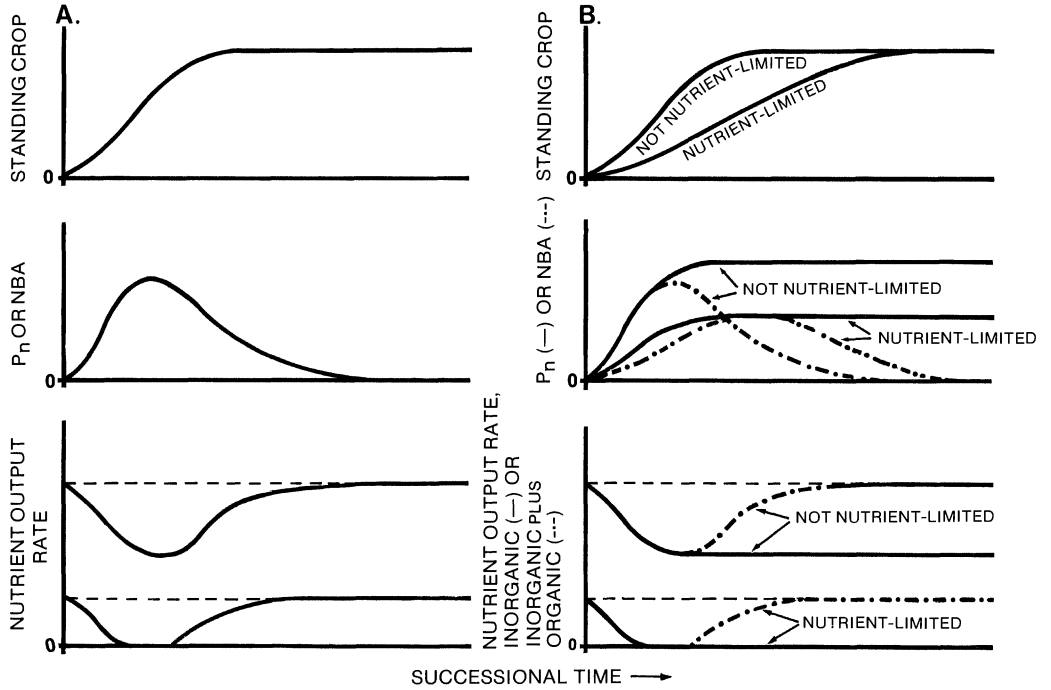

FIG. 9. Models of nutrient dynamics during succession. A) Changes in standing crop, net primary production (P_n) and net biomass accrual (NBA), and nutrient input/output balance during forest succession (after Vitousek and Reiners 1975). B) Changes in standing crop, P_n and NBA, and nutrient input/output balance during stream succession for nutrient limited and non-limited stream periphyton. Nutrient input rates are shown as horizontal dashed lines in bottom panels.

differences in AFDM between N-enriched and control treatments despite large differences in chlorophyll *a* because of higher chlorophyll to AFDM ratios of enriched periphyton. There are several possible explanations for this phenomenon. First, algal growth is slow when N-limited, and colonization of bare substrates proceeds less rapidly than in enriched conditions. Detritus settling on bare sand may be trapped in interstices and become incorporated into periphytal matrices. All tiles developed a thick layer of organic material that eventually formed a smooth mat over the rough tile/sand surface. The mat on N-enriched tiles, however, was distinctly greener in color and relatively smaller amounts of detritus were incorporated into the growing algal communities. Algae grew rapidly and filled interstitial spaces which limited detrital accumulation. A second explanation is that much of the AFDM of N-limited tile periphyton consisted of dead algal cells. Since N was at limiting concentration, N may have been depleted by "upperstory" algae, depriving adnate cells of N. Chlorophyll *a* rapidly degrades upon death of algal cells. Finally, chlorophyll *a* synthesis often is reduced or ceases in N-deficient algal cells and such cells tend to accumulate carbon storage compounds (Healey 1973). For this reason Healey and Hendzel (1979) found chlorophyll to biomass ratio a reasonably good indicator of N deficiency for several algal species.

Although N availability may or may not limit maximum standing crop attained at steady state, it clearly can limit the rate of synthesis of new organic material. Maximum standing crop in terrestrial and intertidal ecosystems is determined by organism size and longevity and available space (canopy and attachment space in forest and intertidal systems, respectively) whereas in streams the upper limit of algal biomass may be set by current or light. Vitousek and Reiners (1975) presented a conceptual model of nutrient utilization and production

dynamics during forest succession. Input of essential or limiting nutrients initially exceeds output as standing crop and net primary production increase. As maximum biomass is approached, net primary production declines to zero, gross primary production is balanced by ecosystem respiration and nutrient input is balanced by output (Fig. 9). In streams, steady state standing crop is achieved when the sum of gross primary production and organic matter import balance the sum of ecosystem respiration and organic matter export (Fisher and Likens 1973). The pattern of net primary production through successional time therefore differs from the pattern of forest succession. In forests, net primary production equals net biomass accrual (NBA) since export is essentially zero. In streams net primary production may be positive while standing crop remains constant (steady state) or while NBA declines to zero if excess production is exported (Fig. 9; Busch and Fisher 1981, Fisher et al. 1982). The rate of net primary production in streams which are not light-limited is set by the input rate of the limiting nutrient as it is in forests. However, in streams inorganic nutrient output may remain at a low level as long as net primary production is positive. Nutrient input is balanced by output only when organic and particulate forms of the nutrient are included in outputs (Fig. 9).

This simplified model leads to the hypothesis that nutrient availability does not ultimately limit standing crop, but does influence rates of primary production, maximum accrual rate of standing crop and time required for accumulation of maximum standing crop (Fig. 9). Since desert streams, like most lotic ecosystems, are frequently "reset" by flooding (Fisher 1983, Fisher et al. 1982), this hypothesis would predict that nutrient availability strongly influences rates and patterns of postflood ecosystem recovery, but not steady state standing crop.

Results of our experiments fit this scheme. Chlorophyll *a* of unenriched and enriched treatments began to converge late in the experiments (Figs. 2, 5, and 6). In other words, net chlorophyll *a* accrual rates of N-enriched periphyton were greater than those of control or P-enriched periphyton early in experiments but later declined to near zero (Figs. 2, 5, and 6). Longer term experiments should provide better resolution of the degree to which recolonization by desert stream periphyton follows predictions of our hypothesis (Fig. 9). Specific predictions are that nutrient-limited periphyton should exhibit lower maximal rates of net primary production, but maximum standing crop similar to non-limited periphyton. Periphyton communities grown in an enriched N environment should maintain maximum standing crops even if the enrichment source is removed with a return to ambient N concentration, although rate of organic matter production would be reduced. These predictions would be expected to hold only in the absence of significant grazing pressure or other factors that reduce maximum possible standing crop. Our model should be applicable to any lotic system, although in more heavily shaded streams light limitation imposes primary control on rates of algal recolonization after disturbance.

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