

SPATIAL HETEROGENEITY OF STREAM WATER NUTRIENT CONCENTRATIONS OVER SUCCESSIONAL TIME

C. LISA DENT AND NANCY B. GRIMM

Department of Biology, Arizona State University, Tempe, Arizona 85287-1501 USA

Abstract. Nutrient availability in ecosystems is patchy both in space and in time. Whereas temporal trends have often been studied, less information exists on spatial patterns of nutrient availability, particularly in aquatic ecosystems. The goals of this study were (1) to describe and quantify patterns of nutrient concentration in surface waters of an arid land stream and (2) to compare spatial patterns of nutrient availability across nutrients and over a successional sequence.

We describe changes in the spatial pattern of stream water nutrient concentrations over successional time (between floods) using quantitative measures of heterogeneity. Samples were collected from the middle of the channel every 25 m over a 10-km section of a Sonoran Desert stream during three periods: early succession (2 wk post-flood), middle succession (2 mo post-flood), and late succession (9 mo post-flood). Nutrient concentrations were extremely variable in space (coefficients of variations as high as 145%). Coefficients of variation increased over successional time and were consistently greater for nitrate-nitrogen than for soluble reactive phosphorus. Semi-variogram analysis showed that nutrient concentrations were spatially dependent on all dates, but to different degrees and over different distances. The distance over which nutrient concentrations were spatially dependent, as measured by the semi-variogram range, tended to decrease with successional time. The strength of spatial dependence, as measured by the slope of the ascending limb of the semi-variogram, increased with successional time. The limiting nutrient, nitrogen, was consistently more spatially heterogeneous than phosphorus or conductivity, both in terms of patch size (range) and strength of spatial dependence.

In streams, downstream transport combined with nutrient transformation produces patches of similar nutrient concentrations that are elongated compared with nutrient patches in terrestrial soils. Variation in nutrient concentration is likely to affect the spatial distribution of organisms and rates of ecosystem processes.

Key words: *desert streams; geostatistics; heterogeneity; nitrogen; nutrients; patch; scale; spatial variability; succession; variograms.*

INTRODUCTION

Concentrations of available nutrients vary in space in both terrestrial and aquatic ecosystems. At regional or continental scales, variation in soil fertility generally coincides with patterns of climate and vegetation (Jenny 1980, Post et al. 1985, Schlesinger 1991, Vitousek and Howarth 1991), whereas variation in aquatic nutrient loading is related to catchment geology, vegetation, land use, and atmospheric inputs (Hynes 1975, Meybeck 1982, Howarth and Cole 1985, Meyer et al. 1988, Billen et al. 1991, Vitousek and Howarth 1991). Variation in nutrient concentrations has been observed at smaller scales in both terrestrial and aquatic systems (Beckett and Webster 1971, Lehman and Scavia 1982, Schimel et al. 1985, Boerner and Koslowsky 1989, Palmer 1990) but is less well studied, despite the fact that variation at these scales is likely to affect the local abundance and distribution of organisms (Tilman 1982, Pringle 1990) as well as rates of microbial activity and

primary production (Nadelhoffer et al. 1983, Plymale et al. 1987).

This lack of understanding is partly due to a lack of appropriate quantitative methods for describing spatial variability (Robertson and Gross 1994, Li and Reynolds 1995, Cooper et al. 1997). Cooper et al. (1997) identified three components of spatial variability: overall variation, gradients or periodicities, and patterns of spatial dependence. Overall variation refers to the dispersion of sample values around the mean, and can be quantified by indices such as the standard deviation or coefficient of variation. Gradients or periodicities can be examined using regression, gradient analysis, or spectral analysis. Spatial dependence, the focus of our study, refers to the extent to which a parameter value at one location is related to values at other spatial locations. Ecologists have recently begun to quantify spatial dependence, using methods originally developed in geology such as spatial autocorrelation and semi-variogram analyses (Journal and Huijbregts 1978, Isaaks and Srivastava 1989). These geostatistical methods allow the rigorous description of the spatial heteroge-

neity of ecological properties and can support hypotheses about potential causes and consequences of spatial patterns (Legendre and Fortin 1989, Rossi et al. 1992).

Geostatistics have been used to describe variation in nutrient concentrations in agricultural fields (Robertson et al. 1993, 1997), desert shrubland and grassland (Schlesinger et al. 1996), forests (Palmer 1990, Lechowicz and Bell 1991), and lakes (Harris 1986), but not in running waters. Streams are extremely heterogeneous systems, varying both temporally and spatially in many properties, including flow rate, temperature, light, substrate, and resource availability. Spatial variation in nutrient concentrations has often been observed (Grimm et al. 1981, Tate 1990, Valett et al. 1990), but most work has focused on temporal variation. As interest in the causes and consequences of spatial variation in streams increases (Pringle et al. 1988, Downes et al. 1993, Cooper et al. 1997, Palmer and Poff 1997, Valett et al. 1997), there is growing recognition of the need for more spatially explicit data sets and for quantitative analyses of these data (Cooper et al. 1997).

Streams are characterized by the continuous flow of water in a downstream direction. Nutrients and other materials in the water are therefore transported downstream, but may also be retained or transformed by physical, chemical, or biological processes. The combination of downstream transport with nutrient cycling led to the concept of nutrient spiraling, which is used as a framework for understanding nutrient dynamics in streams (Elwood et al. 1983, Newbold et al. 1983). Patterns of spatial variability in nutrient concentrations produced by nutrient spiraling are likely to differ from those produced by in place nutrient cycling.

We report here the results of a study examining and quantifying spatial heterogeneity in nutrient concentrations in the surface waters of a desert stream. Streams in arid lands are subject to frequent, intense disturbances by flash floods that remove the instream biota. Biomass returns rapidly to predisturbance levels following a fairly predictable successional pattern (Fisher et al. 1982, Grimm and Fisher 1989). Nutrient concentrations in stream water also change over successional time; flood waters tend to be high in nutrients and, as the biota return, nutrient concentrations decline. Late in succession, concentrations may increase due to decomposition or, for nitrogen, N_2 fixation.

We measured the spatial heterogeneity of nutrient concentrations at three different times in succession: early succession (2 wk post-flood), middle succession (2 mo post-flood) and late succession (9 mo post-flood), over a 10-km stretch of a desert stream. Due to the unidirectional flow of water, we decided to sample concentrations along a one-dimensional longitudinal transect. We were interested in the following questions: How spatially variable are stream water nutrient concentrations at this scale? Which nutrient (N or P) is

more variable? How does the spatial variation in nutrient concentrations change over successional time?

We used geostatistical methods to describe the spatial dependence of nutrient concentrations in stream water. These techniques quantify the strength, pattern, and extent of spatial dependence; that is, they examine how site values covary as a function of the distance between them. Most often, values from sites close together are more similar than values from sites far apart. The h -scatterplot is a basic geostatistical tool that portrays spatial dependence at some separation distance h , known as the lag, by a plot of all possible pairs of values that are separated by that distance (Isaaks and Srivastava 1989). (For one-dimensional transect data, this is sufficient; for two-dimensional data sets, h -scatterplots can be made for any particular direction, or for all directions combined.) For example, a 25-m scatterplot for nitrate-nitrogen plots all nitrate-nitrogen values against nitrate-nitrogen values 25 m away (Fig. 1). The closer the plotted points are to the line $x = y$ (a 45 degree line passing through the origin), the more similar are data values at locations 25 m apart. As the lag is increased, we expect that points will be more scattered, as illustrated by the 125-m scatterplot for nitrate-nitrogen (Fig. 1).

Semi-variograms are used to summarize the information contained in many h -scatterplots, showing how differences between data points change with increasing lag. A semi-variogram plots half the average, squared difference between pairs of points against separation distance (Isaaks and Srivastava 1989, Rossi et al. 1992). As for h -scatterplots, only one variogram need be computed for one-dimensional transect data, but for two-dimensional data, variograms can be computed either for one particular direction or over a range of directions. For data that are spatially independent, semi-variance (γ) will not increase with increasing lag distance and the semi-variogram will be relatively flat (Fig. 2, Random Model; pure "nugget" behavior). For most data that are spatially dependent, points closer together will tend to be more similar, causing semi-variance to increase with separation distance. Semi-variance may increase for all lags, indicating that points further apart become continuously more different (Fig. 2, Linear Model). Alternatively, semi-variance may eventually level off to an asymptote, called the "sill" (Fig. 2, Spherical Model). At the lag distance of the sill, called the "range," values are no longer spatially dependent. The range therefore indicates the distance over which values are spatially correlated (Rossi et al. 1992), a distance which may also be interpreted as average patch size. Here we use the term "patch" to denote a region that differs from its surroundings, but is not necessarily internally homogeneous (Kotliar and Wiens 1990, Fisher et al. 1998a). The y -intercept of the semi-variogram often appears to be greater than zero, although theoretically its value should always be zero since it compares the amount of variability of a

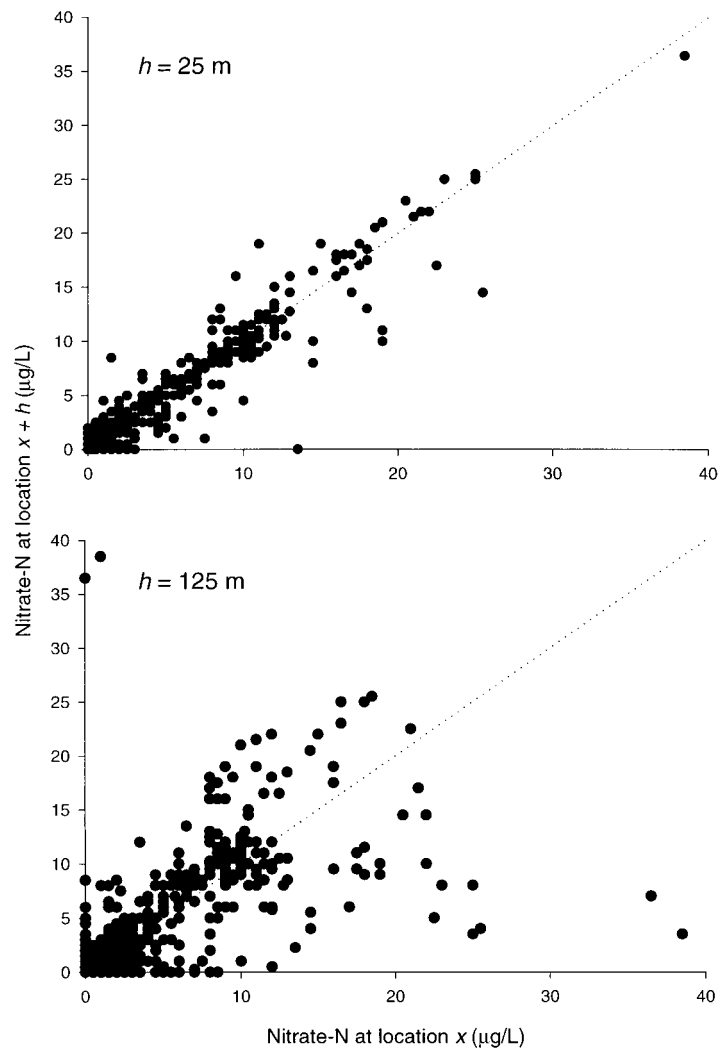


FIG. 1. Two h -scatterplots, for separation distances of 25 meters ($r = 95\%$) and 125 meters ($r = 60\%$) between pairs of nitrate-N values sampled in middle succession. For the larger separation distance, the similarity between pairs of values is less and the points are more scattered.

point with itself. The apparent y -intercept, called the “nugget,” represents either measurement error or variability occurring at scales smaller than the sampling grain (Rossi et al. 1992). The difference between the sill and the nugget represents the amount of variance attributed to spatial dependence. If this difference is divided by the sill, it gives a measure of the proportion of total variation attributable to autocorrelation (or structural variation) (Li and Reynolds 1995). The values of the sill, range, and nugget parameters come from fitting a model to the observed semi-variogram (Webster 1985, Isaaks and Srivastava 1989). Another index of spatial heterogeneity is the strength of spatial dependence over the range. It can be measured by calculating the slope of the ascending limb of the semi-variogram (Cooper et al. 1997).

We examined stream water nutrient concentrations at points separated by 25 m in a downstream direction over a 10-km stretch of Sycamore Creek, Arizona. Sycamore Creek is a tributary of the Verde River, 32 km

northeast of Phoenix, Arizona. The stream drains a catchment of 505 km² that ranges in elevation from 427 m to 2164 m. The study site is a 10-km stretch of stream ranging from 600 m to 700 m in elevation. Stream substrata consist primarily of coarse sand and gravel which can be several meters deep. Riparian vegetation in this lower Sonoran Desert scrub life zone consists of cottonwood (*Populus fremontii*), willow (*Salix goodingii*), walnut (*Juglans major*), sycamore (*Platanus wrightii*), and ash (*Fraxinus arizonensis*). Although these trees achieve considerable size, they are sparsely distributed along an active stream channel that is generally >20 m wide. The stream bed thus receives full sunlight during much of the day. Annual precipitation ranges from 39 cm/yr at a rain gauge station located at 510 m to 51 cm/yr at 1040 m, and peaks bimodally in winter and summer. Pan evaporation in the area is 313 cm/yr; thus, the stream is frequently intermittent, especially in summer. Sycamore Creek is characterized by moderately hard, calcium and magnesium bicar-

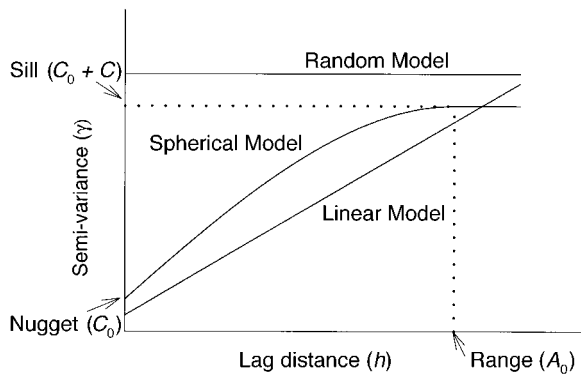


FIG. 2. Theoretical semi-variograms, showing the semi-variance (γ) found at increasing separation distances of paired samples (lag distances). When variable values are randomly distributed in space, semi-variance does not increase with lag (Random Model). Continuously increasing semi-variance indicates a large-scale gradient in variable values. Variates are spatially dependent, but there is no local pattern within the scale sampled (Linear Model). When variates are spatially dependent over lags less than the range and independent beyond that distance, semi-variance increases to a maximum and then levels off (Spherical Model). In this case the maximum semi-variance is known as the sill, and variation at a scale smaller than the sampling grain is the nugget.

bonate water with average conductance values of 500 $\mu\text{S}/\text{cm}$ and total alkalinity (as CaCO_3) near 250 mg/L. Nitrate-nitrogen concentrations are generally 15–150 $\mu\text{gN}/\text{L}$, ammonium-nitrogen 0–25 $\mu\text{gN}/\text{L}$, soluble reactive phosphorus 40–80 $\mu\text{gP}/\text{L}$ (Grimm 1987), and dissolved organic carbon 3.4–7.4 mgC/L (Jones et al. 1996). Nitrogen limits primary production during base-flow when hydrologic conditions allow algal growth (Grimm and Fisher 1986); phosphorus limitation has not been demonstrated. We predicted that nutrient concentrations would be more heterogeneous for the limiting nutrient, nitrogen, than for phosphorus. We also predicted that spatial heterogeneity would increase later in succession when stream discharge was lower and the biological community was more patchy.

METHODS

Field sampling and laboratory analysis

Stream nutrient concentrations were surveyed on 22 May 1995, 2.5 mo after a 6 March 1995 flood, on 7 December 1995, 9 mo after the same flood, and on 17 March 1997, 2 wk after a 28 February 1997 flood. These dates were representative of middle, late, and early successional conditions in the stream, respectively. Maximum flood discharge and daily average discharge throughout the study period were obtained from a U.S. Geological Survey monitoring station on Sycamore Creek at Fort McDowell, ~ 5 km downstream from our study site. Discharge, algal cover, chlorophyll, and ash-free dry mass (AFDM) were measured before and after each survey in a 400-m baseline reach (N. B. Grimm, unpublished data). On each date, duplicate

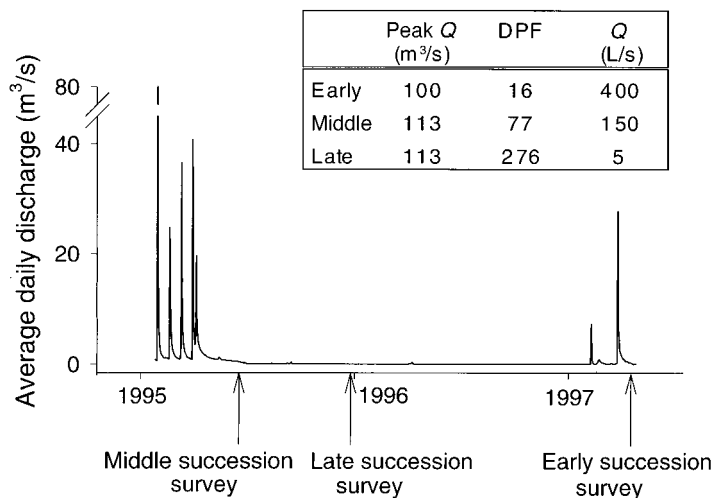
samples of surface water were collected in 60-mL bottles from the stream's thalweg. Samples were taken at points longitudinally separated by 25 m, and were collected as simultaneously as possible by 10–14 different people arrayed along the 10-km stream segment. Each person walked upstream as they collected samples over ~ 800 m. All samples were collected within three hours. Locations at each 800 m overlap were sampled both at the beginning and end of the collection period to check for diel variation in nutrient concentrations. On the late succession date when the stream was intermittent, samples were taken only where flowing water was present (not in stagnant pools).

On return to the laboratory, water samples were analyzed for nitrate-nitrogen (nitrate-N), soluble reactive phosphorus (SRP), and conductivity. Nitrate-N and SRP were analyzed within 24 hr of collection. Due to the large number of samples (~ 800), ammonium-nitrogen (ammonium-N) was not measured. Previous studies generally have found very low ammonium-N concentrations in Sycamore Creek (Fisher et al. 1982, Grimm and Fisher 1986, Holmes et al. 1996). Nitrate-N was determined by colorimetric analysis following reduction to nitrite (Wood et al. 1967), on a Bran & Luebbe TRAACS 800 autoanalyzer (Bran & Luebbe, Norderstedt, Germany). Molybdate-antimony analysis was used to determine SRP concentrations (Murphy and Riley 1962), and conductivity was measured with a VWR Scientific conductivity meter (VWR Scientific, West Chester, Pennsylvania, USA). Some nitrate-N values were below the detection limit (1 $\mu\text{g}/\text{L}$); these were set to 0.5 $\mu\text{g}/\text{L}$. Analytic variability was low, with standard deviations for replicate samples usually $< 10\%$ of mean values. Inspection of value frequency distributions revealed no obvious non-normality in most cases, so to facilitate comparison across parameters, the data were not transformed. Exploratory semi-variogram analyses on transformed and untransformed data produced similar results.

Statistical analysis

Spatial heterogeneity is a multifaceted concept that requires a number of different quantitative measures, each of which captures a different aspect of spatial pattern (Li and Reynolds 1995). We used four different measures to describe heterogeneity in nutrient concentrations. The coefficient of variation (CV) (standard deviation divided by the mean), was used as a standardized measure of overall variation, without reference to spatial patterns. CV has been criticized because it decreases systematically with sample mean (Downing 1991), so we were particularly interested in large differences and in patterns that go against this trend. The semi-variogram range, or distance over which variates are spatially dependent, was used to describe average patch size. The proportion of structural variation (as opposed to random variation) was calculated by subtracting the semi-variogram nugget from the sill and

FIG. 3. Average daily discharge in Sycamore Creek, Arizona, throughout the study period, as measured at a U.S. Geological Survey monitoring station on Sycamore Creek at Fort McDowell, ~5 km downstream of the bottom of the study section. For each survey, the inset shows peak discharge of the flood that initiated the successional sequence (Peak Q), days post-flood (DPF), and discharge (Q) in the baseline monitoring reach.



dividing by the sill (Li and Reynolds 1995). Finally, the slope of the ascending limb of the standardized semi-variogram was used as a measure of the strength of spatial dependence within the range.

Semi-variograms were calculated using GS+ software (Gamma Design 1995). Downstream trends in nutrient concentration over the entire reach were first removed by linear regression (Legendre and Fortin 1989, Cooper et al. 1997). The results of the regressions are not reported, as trends were weak and there were no systematic relationships with successional time. All subsequent analyses used the residuals from these regressions. We used a lag interval of 25 m (since this was the smallest distance between samples), and extended our analysis to a lag of up to 3000 m, 30% of the maximum lag interval. As lag distance increases, the number of pairs used to calculate semi-variance decreases, reducing the accuracy of the results (Journal and Huijbregts 1978, Webster and Oliver 1993). Because fewer samples were collected in the late succession survey than in the other two surveys, we used a maximum lag of 1500 m for late succession and 3000 m for early and middle succession. This resulted in a maximum of 391 and a minimum of 66 data pairs per lag.

To determine the values of the range, sill and nugget, spherical models were fit to the semi-variograms using weighted least-squares analysis (Cressie 1985, Gamma Design 1995). Several different models can be used in semi-variogram analysis (Webster 1985); we chose to use spherical models because they rigorously define a sill and range (Fig. 2), which provide a quantitative measure of patch size, and because they are commonly used for soil nutrient semi-variograms (Webster 1985, Schlesinger et al. 1996, Robertson et al. 1997). In the spherical model, if $h < A_0$, then $\gamma(h) = C_0 + C[1.5(h/A_0) - 0.5(h/A_0)^3]$, where h is the lag interval, A_0 is the range, $\gamma(h)$ is the semi-variance at lag h , C_0

is the nugget variance, and C is the structural variance. If $h \geq A_0$, $\gamma(h) = C_0 + C$.

In cases where a linear model (Fig. 2) fit the observed semi-variogram better than a spherical model, the range and sill were not calculated. A spherical model fit to such data will have a range larger than the maximum extent of the variogram, which is not meaningful for describing spatial heterogeneity at the scale of the study.

The strength of spatial dependence was measured by calculating the slope of the ascending limb of the semi-variogram, after standardizing semi-variance by dividing through by its maximum value. Maximum semi-variance is already addressed by the index of overall variability, cv . By standardizing semi-variance before calculating the slope, we obtained an index that depends on only the range and the nugget (y -intercept). For semi-variograms with defined ranges, the ascending limb ended at the range. For semi-variograms with no defined range, slopes were fairly consistent across all distance classes, so we used the slope to lag 400 as a measure of the strength of spatial dependence.

RESULTS

The early succession survey was done on 17 March 1997, 2 wk after a flood of 100 m^3/s maximum discharge. Surface flow was present throughout the study section and discharge was relatively high at ~400 L/s (Fig. 3). In the baseline reach, algal cover was dominated by diatoms, typical of early succession (Fig. 4). On 11 March, 71% of the stream bottom was bare or colonized by a light diatom cover, whereas by 20 March there were no bare substrata and heavy diatoms (88%) and flocculent material (10%) predominated. Mean algal biomass for the reach (as chlorophyll a) increased from 14.75 ± 3.98 (SE) to 30.36 ± 2.09 mg/m^2 during this time, and sediment ash-free dry mass (AFDM) increased from 85.07 ± 23.62 to 107.28 ± 14.46 g/m^2 .

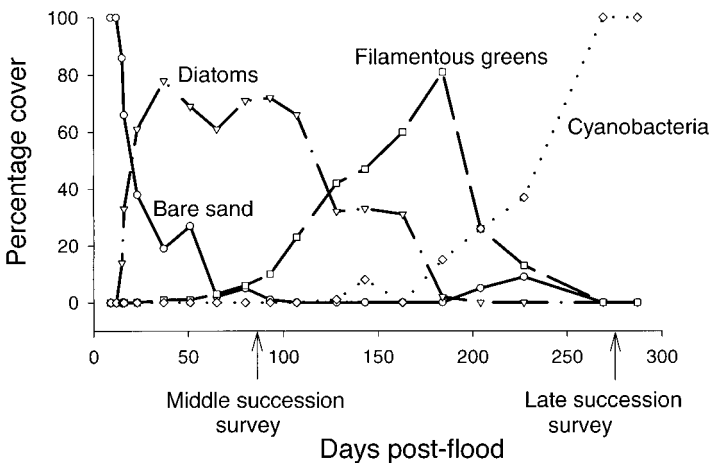


FIG. 4. Changes in the percentage cover of four patch types after the 6 March 1995 flash flood in Sycamore Creek, Arizona, illustrating the successional sequence of algal cover and the timing of the middle and late succession surveys. The early succession survey (not shown) was done during a different successional sequence when diatoms dominated and before the appearance of filamentous green algae (i.e., similar to days 10–50 in this figure). Patch cover was sampled over a 400-m baseline monitoring reach at ~2-wk intervals. On the last two sampling dates, the reach was dry except for a single transect dominated by an epilithic cyanobacterial species (*Calothrix*).

On the day of the survey, water was being pumped from a gravel pit beside the stream into the stream channel at a location in the middle of the study section. The water in the gravel pit was from a shallow aquifer directly connected to the stream and was being removed to lower the water table in the pit. The chemistry of the pumped water differed significantly from the stream water at that point (Table 1). This input was not present during the other two surveys, which were completed before the gravel pit was established.

The middle and late successional surveys were conducted during 1995 and were part of the same successional sequence, initiated by a flood of 113 m³/s maximum discharge on 6 March 1995. The stream did not flood again until 22 August 1996. Discharge on 22 May 1995, the day of the middle successional survey was typical for baseflow conditions (150 L/s; Fig. 3). By 5 December 1995, the day of the late succession survey, large stretches of the 10-km section had no surface water. Nine distinct stretches of surface flow were present, separated by dry channel reaches with lengths ranging from 25 m to 2550 m. Surface flow of about 5 L/s (Fig. 3) covered 65% of the length of the entire study section. A successional context for these two surveys is provided by changes in algal cover and biomass in the baseline reach throughout the first 290 d of this long successional sequence, until the reach dried in late December 1995 (Fig. 4). Typical of many successional sequences following large winter floods in Sycamore Creek (Fisher et al. 1982), bare substrata were colonized by a diatom assemblage that was dom-

inant from 3 wk until 4 mo post-flood. Filamentous green algae increased in abundance from 2 mo post-flood until late summer, when they occupied 80% of the baseline reach. Thereafter, filamentous green algae abruptly crashed and were replaced by flocculent material and cyanobacterial mats. During the early succession survey, done during a different successional sequence, diatoms were dominant (conditions similar to days 10–50 in Fig. 4). The middle succession survey was done while filamentous greens were increasing in abundance, whereas the late succession survey occurred after these algae had been replaced by cyanobacteria and flocculent material (Fig. 4). Algal biomass (as chlorophyll *a*) increased from <10 mg/m² in early succession, to ~250 mg/m² in late May, to >400 mg/m² at the time of the December survey, while AFDM at the baseline reach increased from ~50 to 90 to 130 g/m² over the same interval.

Diel variation

Daytime depression of nitrate-N concentrations due to autotrophic uptake often occurs in Sycamore Creek (Grimm 1987). Because samples were collected in the morning, we were concerned that nutrient concentrations would decrease over the sampling period, obscuring spatial patterns. Therefore, we had each person take their last sample from the same location as the first sample taken by the person just upstream, giving us a number of paired samples to check for diel variation. Fewer paired samples were taken for the late succession survey because much of the stream was dry.

TABLE 1. Water chemistry characteristics on 17 March 1997 in a gravel pit and in Sycamore Creek upstream and downstream from the gravel pit. Values at each location are based on two analytical replicates.

Characteristic	Unit	Stream water		
		25 m above input	Gravel pit input	25 m below input
Nitrate-N	μg/L	91	1065	513
SRP	μg/L	4	49	28
Conductivity	μS/cm	361	362	366

TABLE 2. Changes in water chemistry characteristics over time, from the start to the end of each survey, at selected points within the 10-km stretch of Sycamore Creek. Values are calculated for *n* sample locations; values at each sample location are based on two analytical replicates.

Characteristic	Unit	<i>n</i> (pairs)	Pre-sampling concentration	Post-sampling concentration	Average change	Percentage of range
Early succession (2 wk post-flood)						
Nitrate-N	μg/L	11	258	236	-22*	4
SRP	μg/L	11	18	18	0	0
Conductivity	μS/cm	11	385	381	-4*	7
Middle succession (2 mo post-flood)						
Nitrate-N	μg/L	11	7.8	7.3	-0.5	1
SRP	μg/L	11	27	28	1	4
Conductivity	μS/cm	11	402	400	-2*	2
Late succession (9 mo post-flood)						
Nitrate-N	μg/L	5	10	7	-3	1
SRP	μg/L	5	23	25	2	4
Conductivity	μS/cm	5	475	469	-6*	3

* Indicates the change is significant at the 0.05 level in a paired sample *t* test.

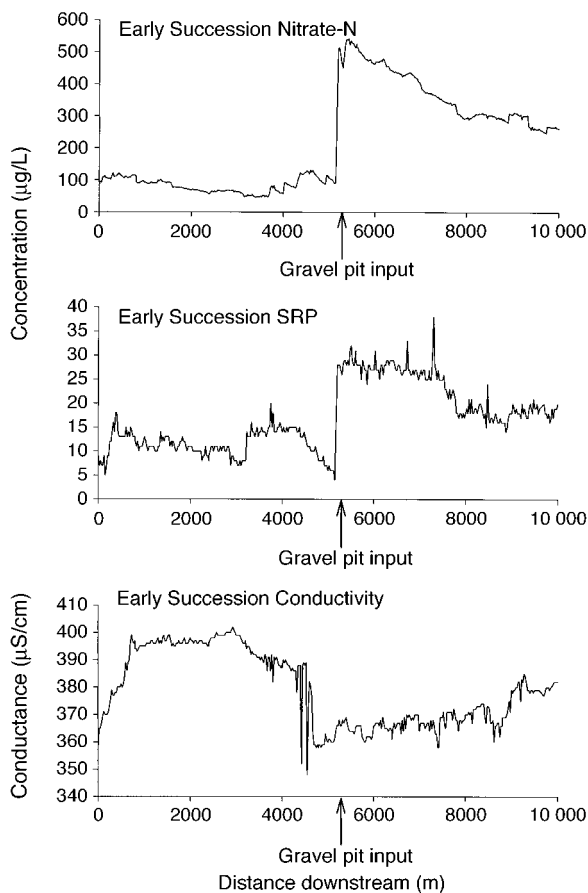


FIG. 5. Spatial variation in nitrate-nitrogen, soluble reactive phosphorus (SRP), and conductivity over a 10-km stretch of Sycamore Creek, Arizona, in early succession (2 wk post-flood). Arrow indicates location of a pipe bringing water into the stream from a gravel pit operation.

We found that nitrate-N concentrations dropped significantly (according to a paired *t* test) between the start and end of the early succession survey, and that conductivity dropped significantly between the start and end of all three surveys (Table 2). However, the magnitude of diel change was at most 7% of the total range of concentrations observed, so we felt confident that the spatial patterns we observed were not overwhelmed by diel variation. We attribute the drop in conductivity to a reduction in bicarbonate concentrations due to photosynthesis.

Means and overall variability

In early succession, both nutrient concentrations and conductivity were homogeneously distributed in space with the exception of values just downstream of the gravel pit input, which dramatically increased nitrate-N and SRP concentrations (Fig. 5). The increase in concentration caused by the gravel pit input was followed by a gradual decline over several kilometers. In order to compare nutrient variability in this survey, which had the gravel pit input, with the other two surveys, which did not have this input, we calculated all indices for the early succession survey in three ways: using only data from upstream of the gravel pit input, using only data from downstream of the input, and using all the data (Table 3). In all three cases the pattern of overall variation (CV) was the same; highest for nitrate-N, followed by SRP, and lowest for conductivity. However, the small differences between coefficients of variation for nitrate-N and SRP upstream and downstream of the gravel pit suggest that without the gravel pit input, overall variation in nitrate-N and SRP would be similar. Note that the CV for conductivity was consistently lower than for nitrate-N, even downstream of the gravel pit where the mean values were comparable. N:P ratios ranged from a low of 7, well below the ratio at which N becomes potentially limiting to algal growth, to a high of 50, well above the ratio at which P becomes

TABLE 3. Water chemistry characteristics for the early succession survey on 17 March 1997 over three reaches of Sycamore Creek: upstream of the gravel pit input, downstream of the gravel pit input, and over the entire 10-km section. All values are calculated on the basis of n sample locations; values at each sample location are based on two analytical replicates.

Characteristic	Unit	n	Mean	SD	Minimum	Maximum	CV (%)
Early succession, upstream of the gravel pit input							
Nitrate-N	$\mu\text{g/L}$	213	84	22	46	131	27
SRP	$\mu\text{g/L}$	213	11	3	4	20	24
Conductivity	$\mu\text{S/cm}$	213	388	13	348	402	3
N:P		213	17	7	7	50	
Early succession, downstream of the gravel pit input							
Nitrate-N	$\mu\text{g/L}$	185	376	84	249	543	22
SRP	$\mu\text{g/L}$	185	23	5	14	38	21
Conductivity	$\mu\text{S/cm}$	183	369	5	358	385	2
N:P		185	36	4	21	47	
Early succession, over entire 10-km section							
Nitrate-N	$\mu\text{g/L}$	398	219	158	46	543	72
SRP	$\mu\text{g/L}$	398	17	7	4	38	42
Conductivity	$\mu\text{S/cm}$	396	379	14	348	402	4
N:P		398	26	11	7	50	

potentially limiting to algal growth (Redfield 1958, Grimm and Fisher 1986). Concentrations of both nitrate-N and SRP were relatively high, however, so actual nutrient limitation is unlikely.

In middle succession, both nutrients and conductiv-

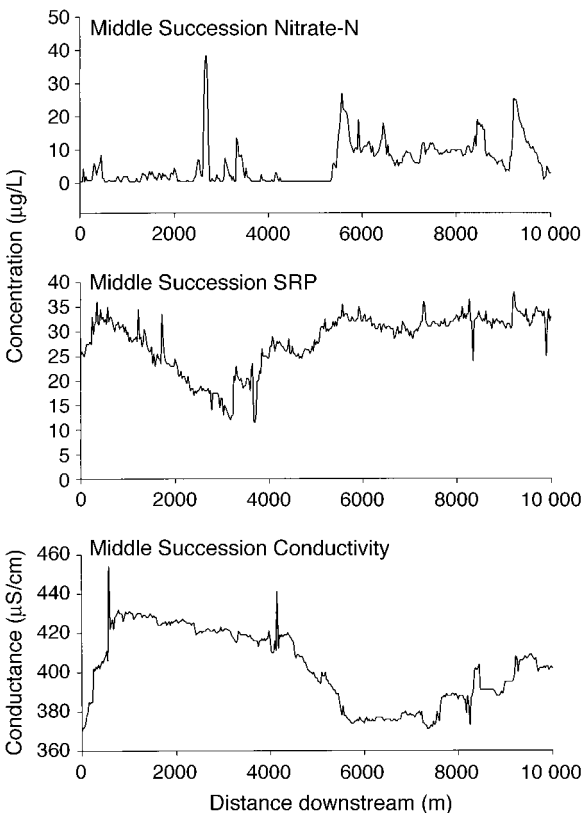


FIG. 6. Spatial variation in nitrate-nitrogen, soluble reactive phosphorous (SRP), and conductivity over a 10-km stretch of Sycamore Creek, Arizona, in middle succession (2 mo post-flood).

ity varied considerably in space (Fig. 6). The survey was completed before construction of the gravel pit, yet concentration of nitrate-N increased at approximately the same location as the first survey, though to a lesser degree. We believe this increase was due to a large upwelling at this location that brings nitrate-rich subsurface water to the surface. The amount of variation was greatest for nitrate-N ($CV = 104\%$), followed by SRP ($CV = 20\%$) and conductivity ($CV = 5\%$) (Table 4). Nitrate-N concentrations were consistently below concentrations where actual nitrogen limitation has been demonstrated in Sycamore Creek (Grimm and Fisher 1986). Because the lowest SRP concentrations coincided with low nitrate-N, the N:P ratio was always below 5, again indicating the potential for nitrogen limitation.

Nutrient concentrations in surface water were even more variable in late succession (Fig. 7). Overall variation was again highest for nitrate ($CV = 145\%$), followed by SRP ($CV = 44\%$) and conductivity ($CV = 14\%$) (Table 4). Both the CV and the mean of nitrate concentrations increased dramatically relative to middle succession. For SRP concentrations, the CV also increased, but the mean remained about the same as in middle succession. Conductivity increased both in CV and in mean value. N:P ratios were generally below 16, indicating the potential for N limitation (Grimm and Fisher 1986), but reached almost 30 over one 100-m stretch of stream (Table 4). This shows that P limitation of algal growth is possible in restricted spatial areas.

Geostatistics

In early succession, semi-variance rose continuously with separation distance for nitrate-N, SRP, and conductivity (Fig. 8), resembling the pattern for a linear model (Fig. 2). The shapes of the semi-variograms were not affected by the gravel pit input; semi-variograms

TABLE 4. Water chemistry characteristics over the 10-km stretch of Sycamore Creek. All values are calculated on the basis of *n* sample locations; values at each sample location are based on two analytical replicates.

Characteristic	Unit	<i>n</i>	Mean	SD	Minimum	Maximum	CV (%)
Early succession (2 wk post-flood)							
Nitrate-N	μg/L	398	219	158	46	543	72
SRP	μg/L	398	17	7	4	38	42
Conductivity	μS/cm	396	379	14	348	402	4
N:P		398	26	11	7	50	
Middle succession (2 mo post-flood)							
Nitrate-N	μg/L	399	6	6	bdl	39	104
SRP	μg/L	399	28	6	12	38	20
Conductivity	μS/cm	399	402	19	370	454	5
N:P		399	0.5	0.5	bdl	5	
Late succession (9 mo post-flood)							
Nitrate-N	μg/L	260	35	51	bdl	279	145
SRP	μg/L	260	28	13	2	59	44
Conductivity	μS/cm	260	488	68	416	633	14
N:P		260	3	4	bdl	29	

Note: In the "Minimum" column, an entry of "bdl" indicates that the value was below detection limits.

calculated using data only above and only below the input also increased linearly. Continuously increasing semi-variance indicated that all three variates showed spatial dependence, and that there was no local patchiness within the scale of the survey. Although there appeared to be some decrease in semi-variogram slope as lag approached 3000 m, especially in the SRP semi-

variogram, it was not sufficient to fit a spherical model with range <3000 m. Therefore no spherical model parameters were obtained (Table 5). The strength of spatial dependence was estimated by calculating the initial slope of the semi-variograms between lag 25 and

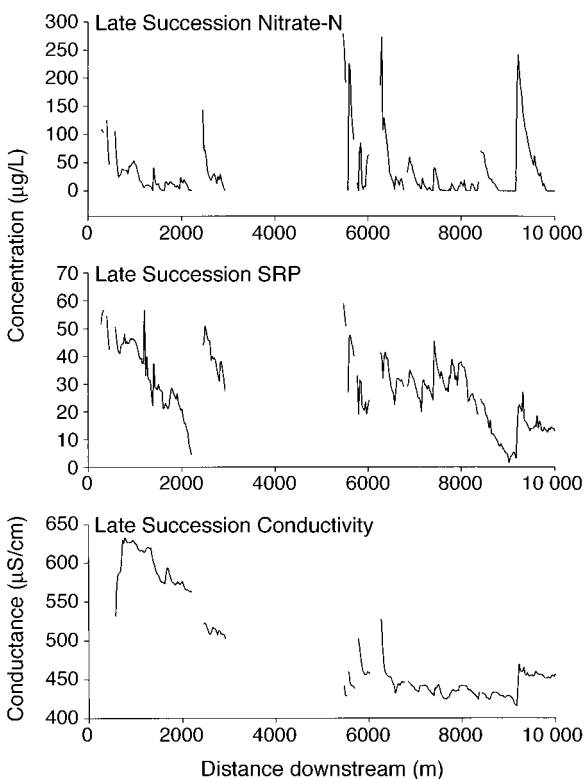


FIG. 7. Spatial variation in nitrate-nitrogen, soluble reactive phosphorous (SRP), and conductivity over a 10-km stretch of Sycamore Creek, Arizona, in late succession (9 mo post-flood). Gaps indicate no surface water at those locations.

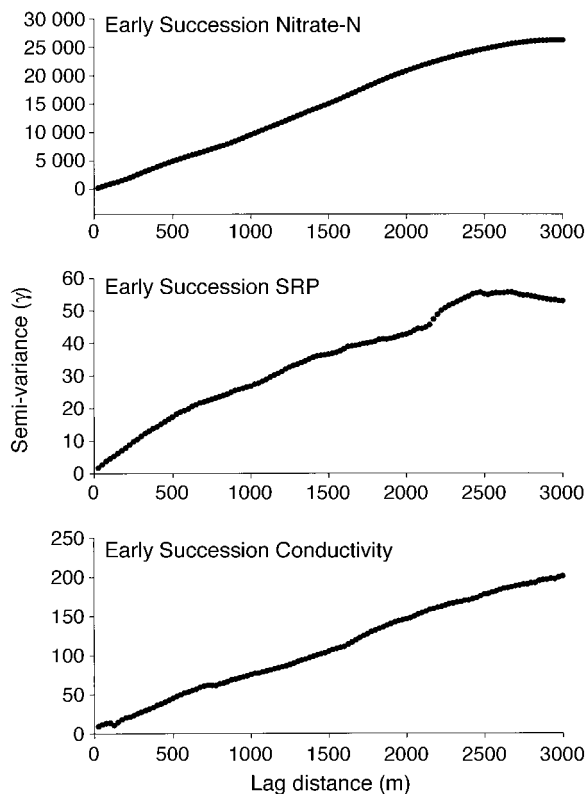


FIG. 8. Semi-variograms for regression residuals of stream water nutrient concentrations and conductivity in early succession (2 wk post-flood). Spherical models were not fit to any semi-variogram. Indices of spatial heterogeneity are given in Table 5.

TABLE 5. Indices of spatial heterogeneity and spherical model parameters for nutrient concentrations and conductivity over 10-km of Sycamore Creek, Arizona.

Element	R^2	Nugget (C_0)	Sill ($C_0 + C_1$)	Structural variance ($C/C_0 + C_1$)	Range (m)	Initial slope†	CV (%)
Early succession (2 wk post-flood)							
Nitrate-N	>3000	0.038	72
SRP	>3000	0.034	42
Conductivity	>3000	0.036	4
Middle succession (2 mo post-flood)							
Nitrate-N	0.51	4.7	31.5	0.85	401	0.161	104
SRP	>3000	0.031	20
Conductivity	>3000	0.040	5
Late succession (9 mo post-flood)							
Nitrate-N	0.60	195	2265	0.91	359	0.219	145
SRP	0.98	9.5	120	0.92	1068	0.086	44
Conductivity	0.94	1.0	973	1.00	1025	0.075	14

Notes: Ellipses indicate that the spherical model did not level off to an asymptote less than the maximum lag. For fitted models, the goodness of fit (R^2), nugget variance, sill variance, proportion of total variance that is structural, and range (patch size) are given. Initial slope indicates the strength of spatial dependence.

†Slope from 25 m to the semi-variogram range (if available) or to 400 m.

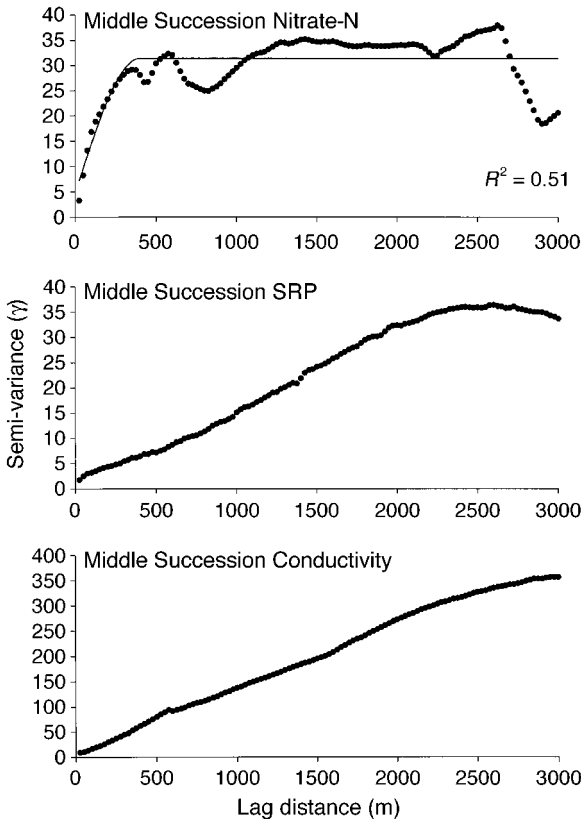


FIG. 9. Semi-variograms for regression residuals of stream water nutrient concentrations and conductivity in middle succession (2 mo post-flood). The solid thin line in the top plot (for nitrate-N) shows the fitted spherical semi-variogram model. Spherical models were not fit to SRP or conductivity. Indices of spatial heterogeneity are given in Table 5.

400, after standardizing by dividing by maximum semi-variance. In early succession, the strength of spatial dependence was fairly similar for all response variables (Table 5).

In middle succession, all variates were again spatially dependent at local scales (semi-variance increased), but nitrate-N semi-variance leveled off, showing that concentrations became spatially independent within the scale of the survey (Fig. 9). Spatial dependence, as measured by semi-variogram slope, was stronger for nitrate-N than for SRP and conductivity (Table 5). SRP and conductivity semi-variograms could not be fit to a spherical model with range <3000 m. The middle succession nitrate-N semi-variogram, however, was fit to a spherical model with a range of 401 m (Table 5). This indicates that patches of similar nitrate-N concentrations were smaller and more differentiated from their surroundings than were patches of similar phosphate concentrations or conductivity. The high proportion of structural variance (85%) for nitrate-N indicates that most of the variation in this middle succession spatial pattern occurred at scales >25 m.

In late succession, the shapes of all three semi-variograms were similar (Fig. 10). Spherical models (Fig. 2) were fit to observed semi-variograms for nitrate-N, SRP, and conductivity, indicating that all three showed spatial patchiness within the scale of the survey on this date (Fig. 10 and Table 5). The range where nitrate-N concentrations became spatially independent (359 m) was about the same as in middle succession (Table 5). Phosphate and conductivity were also patchy, with ranges (1068 m and 1025 m respectively) much smaller than in middle succession, but larger than for late succession nitrate-N. Structural variance was a very high proportion of overall variance for all response variables

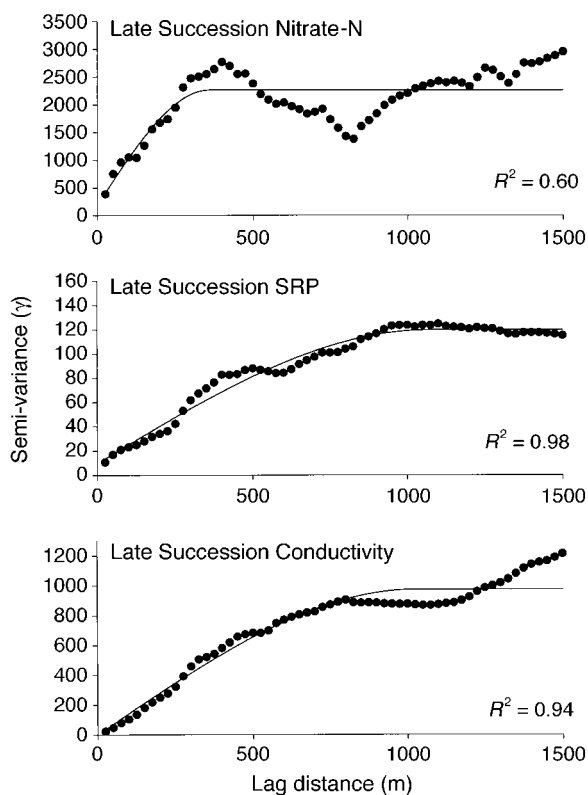


FIG. 10. Semi-variograms for regression residuals of stream water nutrient concentrations and conductivity in late succession (9 mo post-flood). Solid lines show fitted spherical semi-variogram models. Indices of spatial heterogeneity are given in Table 5.

(Table 5). The initial slope of the semi-variograms was steepest for nitrate-N, followed by SRP and then conductivity.

Overall variance (as indicated by the coefficient of variation) and spatial heterogeneity indices (range and slope) differed between parameters and over successional time (Table 5). In early succession, nitrate-N and SRP were more variable than conductivity (higher coefficients of variation), but did not show spatial structure at the scale of the survey. In middle succession, nitrate-N concentrations were more variable than SRP concentrations or conductivity, were spatially dependent over a smaller distance, and were more strongly spatially dependent within this distance. SRP concentrations were more variable than conductivity, but had a lower initial semi-variogram slope. In late succession, nitrate-N remained the most variable and spatially heterogeneous nutrient, followed by SRP and conductivity. Thus the limiting nutrient, nitrogen, was consistently more variable and more patchy than phosphorus or conductivity. Over successional time, variability in nitrate-N increased and spatial patchiness, as indicated by semi-variogram range and slope, also increased. For SRP, overall variation showed no successional pattern, perhaps due to an inflation of early succession cv by

the gravel pit input. Spatial heterogeneity, however, was greatest in late succession. Conductivity became more variable and more spatially heterogeneous with successional time, though to a lesser degree than nitrate-N.

DISCUSSION

How spatially variable are stream water nutrient concentrations at this scale?

We were surprised by the amount of longitudinal variation present in the nutrient concentrations of this stream. We have monitored surface water nutrient concentrations in Sycamore Creek at a single location for 18 yr, and over that time the total amount of variation in nitrate-N concentration was only twice what we found over 10-km in middle succession (cv over 18 yr = 201% for 416 samples, cv over 10 km = 104% for 399 samples). If we had taken water samples from sections of the stream that were less well mixed than the thalweg (e.g., edges, backwaters, etc.), spatial variation would probably have been even higher. This is contrary to conventional wisdom in stream ecology and may be a neglected but important consideration in stream water monitoring programs.

Although the distances over which chemical parameters were spatially dependent differed between nutrients and among dates, all variates were spatially dependent at small scales; in all cases, semi-variance increased with separation distance (Figs. 8–10). No variate had a semi-variogram pattern indicating unpatterned, or random, data. Given the unidirectional flow of stream water, it is not surprising that nutrient concentrations at nearby locations were correlated. The fact that patches were present at certain times, however, shows that nutrient transformations affected patterns of nutrient concentrations, creating “hot spots” and “cold spots” (Fisher et al. 1998a). Spatial dependence can be problematic for ecological studies that use classical statistical tests, because observations are not independent when samples are taken close together (Legendre and Fortin 1989). To ensure that samples are independent, they should be taken from locations separated at least by a distance equal to the semi-variogram range, the distance at which values are no longer spatially dependent. From our study, samples of nitrate-N should be collected at least 400 m apart to be independent in middle and late succession.

The proportion of variance that was not spatially structured (nugget variance) was low in our semi-variogram models. Nugget variance can be attributed to either measurement error or to spatial dependence at scales smaller than those measured (Isaaks and Srivastava 1989). Therefore our small nugget variances suggest that stream water nutrient concentrations vary little at scales <25 m. Again, this is true only for samples taken in the thalweg, and we expect that samples

taken in lateral areas, especially back channels and side pools, would be heterogeneous at much smaller scales.

Although no other studies have quantified the spatial pattern of nutrients in streams, considerable work has been done on terrestrial soil properties. Spatial dependence in soil properties typically occurs over much shorter distances than we found for stream water. In forest soils, most elements showed spatial dependence of 2–5 m (Palmer 1990, Lechowicz and Bell 1991); in desert shrublands, ranges went up to 7 m (Schlesinger et al. 1996); and in agricultural fields, soil nutrients were spatially dependent over distances of up to 100 m (Robertson et al. 1997). Larger patch sizes may also exist for these soils, as the maximum extent of these studies was 1200 m, and most covered 20 m or less. Processes occurring in soils are similar to those occurring in streams: organic matter enters the system as litter or new production, is consumed by microbes and fauna, and decomposition products are released back to the system. It has been suggested that soil ecologists and stream ecologists have different perspectives because the spatial scales over which processes occur in soils are so much smaller than for streams (millimeters vs. meters or even kilometers) (Wagener et al. 1998). Our results are consistent with this view. Downstream transport of nutrients lengthens the distance over which nutrient concentrations are spatially dependent. It also separates different nutrient transformations spatially, by carrying products away from where they are formed (Wagener et al. 1998). This makes individual transformations more readily observable in stream systems than in soils. The small spatial scale of soil processes, on the other hand, make them easier to study in entirety. We agree with Wagener et al. (1998) that soil and stream ecologists have much to learn from each other.

Which nutrient (N or P) is more variable?

Total variation in our study was much lower for SRP than for nitrate-N, especially in middle and late succession. Spatial dependence of SRP occurred over fairly large distances and resembled conductivity more than nitrate-N. This is consistent with prior work in Sycamore Creek suggesting that SRP is not limiting in this system and is controlled by physical factors, such as adsorption to sediments or solubility of calcium phosphate minerals, rather than by biological factors (Grimm and Fisher 1986). However, the longitudinal patterns of SRP concentration in late succession (Fig. 7) as well as N:P ratios raise the possibility that P may decline to limiting levels in highly localized regions. The mechanisms that produced these patterns are unknown, but we speculate that P limitation could arise in locations where N₂ fixation provides a new source of N, driving P to low levels.

How does spatial variation change over successional time?

Classic predictions about changes in nutrient dynamics over successional time do not address changes in

spatial patterns (Odum 1969, Vitousek and Reiners 1975). We found that spatial heterogeneity in nutrient concentrations increased markedly from early to middle to late succession. Although we studied only three representative dates in detail, smaller surveys done between middle and late succession corroborate the idea that increases in nutrient heterogeneity were continuous over successional time (Fig. 11). We were unable to perform geostatistical analyses on these smaller surveys due to low sample sizes. Although few other studies have examined changes in nutrient heterogeneity over time, Robertson et al. (1993) used semi-variograms to compare spatial variability in soil resources in relatively undisturbed and frequently disturbed fields. The distance over which samples were spatially dependent was generally greater for the frequently disturbed field than for the undisturbed field, indicating that the undisturbed field was more spatially heterogeneous. They suggested that field cultivation homogenizes soil properties, which then become more heterogeneous over time due to the effects of individual plants.

Nutrient spiraling

The nutrient spiraling concept is used by stream ecologists as a framework for understanding stream nutrient retention. The spiraling parameter that is most often measured is uptake length, defined as the average downstream distance traveled by a nutrient in dissolved form before being removed from the water column. Downstream declines in nutrient concentration such as those observed in our study can be used to estimate “net” uptake length (Martí et al. 1998). Shorter uptake lengths result from steeper declines, which also produce smaller patch sizes (distances over which concentrations are spatially dependent). Therefore patch size is at least partly related to uptake length. Several studies have found that uptake lengths in streams are shorter for limiting nutrients than for nonlimiting nutrients (Munn and Meyer 1990, Martí and Sabater 1996, Martí et al. 1998). Limiting nutrients are retained more efficiently, leading to smaller patch sizes. Limiting nutrients have also been found to have smaller patch sizes than other nutrients in desert shrublands (Schlesinger et al. 1996). Another important factor affecting nutrient uptake length is disturbance by flooding. Floods remove instream biota, increasing uptake length. Uptake lengths become shorter over successional time due to regrowth of algae and declines in discharge that increase water residence time (Martí et al. 1998). Again this is consistent with our results that patch size decreases with successional time.

Factors affecting uptake length, such as algal species and biomass (Martí et al. 1998), organic matter inputs (Mulholland et al. 1985), or channel morphology (Munn and Meyer 1990, Martí and Sabater 1996) likely also affect spatial patterns in nutrient concentrations. However, processes affecting uptake length can explain

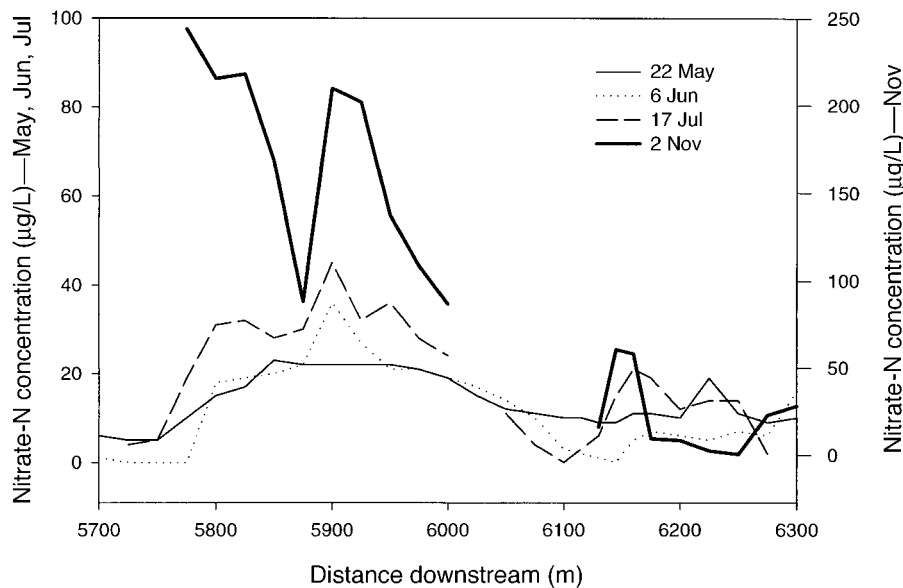


FIG. 11. Spatial variation in nitrate-N over 600 m of Sycamore Creek, Arizona, on four dates from middle (22 May 1995) to late succession (2 November 1995), illustrating how increases and decreases in concentration became more pronounced over time. Gaps indicate no surface water at those locations.

only part of the spatial patterns we observed. Nutrient spiraling models assume a uniform reach without any inputs (Newbold et al. 1981, Elwood et al. 1983), and therefore only address declines in nutrient concentration, not increases. A recent elaboration of nutrient spiraling, the telescoping ecosystem model (Fisher et al. 1998b), takes a broader view. This model expands nutrient spiraling to incorporate multiple subsystems, each of which has an associated "processing length." Processing length can be negative, if the subsystem is a source of nutrients, or positive, if the subsystem is a nutrient sink. Hydrologic connections between subsystems, such as subsurface sediments and the surface water, can result in increases in surface water nutrient concentration.

Spatial variability in stream water nitrate concentrations: a hypothesis

We suggest that in streams, flooding homogenizes nutrient concentrations by removing the instream biota and by turbulent mixing of sediments and water. Over time, nutrient concentrations become more spatially heterogeneous due to successional changes in microbial and algal processes accentuated by reductions in flow. In Sycamore Creek, microbial activity increases the concentration of nutrients in subsurface sediments compared to surface water (Valett et al. 1990, Holmes et al. 1994, Jones et al. 1995), causing enrichment of surface water at localized "upwelling" zones where subsurface water enters the surface stream (Valett et al. 1994, Fisher et al. 1998a). As succession proceeds, surface discharge declines in proportion to subsurface discharge, enhancing the effect of surface enrichment

by upwellings (see also Stanley and Valett 1992). At the same time, uptake of nutrients causes downstream declines in nutrient concentrations (Grimm 1987, Mulholland and Rosemond 1992), particularly for limiting nutrients, and these declines become more pronounced over successional time as algal biomass increases and discharge decreases. Longer hydraulic residence times and a reduced ratio of water to biota (e.g., algal mats) increase interactions between materials transported by water and biota attached to benthic surfaces and sediments (see also Valett et al. 1996). The combination of these processes could produce nutrient patches at upwelling zones that become smaller and more differentiated over successional time (Fig. 11). Other factors are also likely to contribute to spatial patterns in nutrient concentrations, including N_2 fixation, denitrification, and sorption to sediments.

We plan to test one aspect of this scenario by comparing the spatial locations of upwelling zones with the locations of observed increases in nitrate-N concentration. Upwelling of subsurface water into the surface stream is controlled to a large extent by physical geomorphology. Upwellings occur at different spatial scales: water emerges from the downstream end of gravel bars (10s-of-meters scale), at the upstream end of runs where channel slope changes from steep to shallow (100s-of-meters scale) (Harvey and Bencala 1993), and where wide valleys narrow into canyons (1000s-of-meters scale). Given the scale of our surveys and the average nitrate-N patch size of 400 m, we predict that the increases in nitrate-N we observed should be associated with slope changes and possibly valley width.

A better understanding of the processes that influence spatial patterns in nutrient concentrations will involve a model of the stream as an ordered series of subsystems, or patches, each with its own processing length specific to the nutrient in question (Fisher et al. 1998*b*). There are also feedbacks involved: spatial variation in nutrient concentrations causes variation in the distribution of primary producers and in rates of ecosystem processes (Palmer 1990, Lechowicz and Bell 1991, Schlesinger et al. 1996). Elevated stream nutrient concentrations at upwelling zones increase algal biomass and speed recovery of algae in these zones (Valett et al. 1994), whereas low concentrations of stream nitrate-N are associated with N-fixing cyanobacteria (Grimm and Petrone 1997). Finally, spatial patterns and the processes that affect them occur at multiple scales and can be organized into a hierarchy (Wu and Loucks 1995, D'Angelo et al. 1997, Fisher et al. 1998*a*). A complete understanding of controls on spatial patterns of nutrient concentrations must consider flow regime, geomorphology, response to disturbance, and the spatial configuration of subsystems at multiple scales.

CONCLUSIONS

This study shows that nutrient concentrations in stream water can be extremely variable in space. In a nitrogen-limited, desert stream, concentrations of nitrate-N were generally more spatially variable than those of SRP and conductivity. Overall variation and spatial heterogeneity increased over successional time for both nutrients and for conductivity, with the limiting nutrient, nitrogen, changing most dramatically. Geostatistical analysis allowed us to quantify different aspects of spatial patterns in nutrient concentrations and to compare the heterogeneity of stream nutrients with that of soil nutrients.

The spatial distribution of available nutrients can have important implications for population dynamics (Pacala 1987, Hastings 1990), community composition (Caldwell and Percy 1994) and biogeochemical fluxes (Matson et al. 1989), in both terrestrial and aquatic ecosystems. Thus, quantification of the spatial heterogeneity of resources may significantly enhance our understanding of controls on population, community and ecosystem-level processes (Robertson et al. 1993). In addition, the description of spatial patterns of available nutrients gives valuable information about the spatial configuration of the processes that generate such patterns, and as such, is an essential component of a patch dynamics perspective of ecosystem functioning.

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