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PATTERNS AND CONTROLS OF NITROGEN IN TALLGRASS PRAIRIE STREAMS[1]

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Abstract. A descriptive and experimental approach was used to study patterns of nitrogen concentrations in tallgrass prairie streams in Kansas. Nitrate concentrations varied depending on the year, season, time of day, stream flow conditions, source of water, and location where the sample was taken. Mean nitrate concentrations during the dormant season decreased from 1982 to 1984, corresponding to above-normal precipitation during this same period. Nitrate concentrations decreased from third-order (grass/shrub riparian vegetation) to fourth-order channels (gallery forests). Nitrate, organic N, and total N were higher in a third-order intermittent stream than in a third-order perennial stream. Water from seeps and tributaries had higher nitrate concentrations than stream water; however, streams and tributaries had higher organic N than seeps. Maximum nitrate concentrations during storm flows were directly related to the magnitude of storms and inversely related to the frequency of storm events.

The activity of terrestrial vegetation influenced nitrate concentrations within streams, seeps, and tributaries; nitrate concentrations were always higher during periods of vegetation dormancy. Aquatic biota influenced both spatial patterns (downstream decrease in nitrate concentrations and increase in organic N) and diel patterns of nitrate concentration (night > day). Uptake rates of nitrate by biota were greater during the day than during the night as determined by experimental addition of nitrate.

Nitrogen (N) and/or phosphorus (P) limitations of algal growth were tested experimentally using nutrient-diffusing substrata (clay saucers filled with enriched agar) and enrichment of artificial channels. Addition of N and P in combination increased algal biomass (chlorophyll *a* and ash-free dry mass) over controls or single addition of N or P. Thus, algal biomass was N and P limited; however, individual taxa responded to specific N and/or P concentrations or atomic N:P ratio.

Key words: flooding; intermittent stream; nitrate; nitrogen; nutrient limitation; organic nitrogen; periphyton; phosphorus; tallgrass prairie; stream.

INTRODUCTION

Meyer et al. (1988) summarized recent literature on elemental cycling in stream ecosystems and list the following important reasons for understanding elemental cycling in streams: (1) nutrients regulate ecological processes (e.g., decomposition, primary production) in streams, particularly if the nutrient is limiting; (2) nutrients link terrestrial and aquatic ecosystems (i.e., watershed characteristics determine the nutrient supply to streams); and (3) stream processes (e.g., nutrient uptake and release by biota, denitrification, N fixation, etc.) can alter the timing, magnitude, and form of elemental fluxes to downstream ecosystems and thus nutrient availability to the biological communities downstream.

Prairie streams are of ecological interest because of their unstable hydrologic regime (i.e., annual extremes of flooding and drying) and fluctuations in environmental conditions (Jewell 1927, Gurtz et al. 1982, Mathews 1988). These extreme fluctuations can have a major impact on ecological processes and biota in prai-

rie streams. For example, rates of leaf decomposition in Kansas streams are slower in intermittent than perennial channels (Tate and Gurtz 1986); flood frequency, duration, and timing affect patterns of leaf decomposition in the floodplain (Gurtz and Tate 1988) and retention and storage of organic matter in the stream channel (Gurtz et al. 1988). Duration of flow can influence autotrophic and heterotrophic processes; primary production was not different in Texas intermittent and perennial streams, whereas benthic respiration was reduced 50% in the intermittent stream compared to the perennial stream (Hill and Gardner 1987). Storm flows in prairie streams reduce stream biota, particularly algae (Gurtz et al. 1982, Power and Stewart 1987) and at the same time increase nitrate and phosphate concentrations (McArthur et al. 1985). Since the quantity, type (e.g., algae, detritus, microbes, etc.), and residence time of organic matter in stream channels affects the uptake of nutrients in stream ecosystems (Gregory 1978, Fisher et al. 1982), the variable hydrologic regime can have a major influence on nutrient dynamics in prairie streams.

This study focuses on nitrogen dynamics and factors influencing the nitrogen dynamics in tallgrass prairie

N

N: 59 ± 50.4 μg/L, n=8
P: 11 ± 4.5 μg/L, n=6

U.S.G.S.
GAGE STATION

NORTH BRANCH
N: 13 ± 6.2 μg/L, n=6
P: 6 ± 1.5 μg/L, n=2

N: 7 ± 4.3 μg/L, n=6
P: 8 ± 2.2 μg/L, n=2

N: 9 ± 13.5 μg/L, n=15
P: 4 ± 1.3 μg/L, n=14

N: 9 ± 4.3 μg/L, n=6
P: 5 ± 0.2 μg/L, n=2

P   I

N: 22 ± 27.8 μg/L, n=18
P: 3 ± 1.3 μg/L, n=16

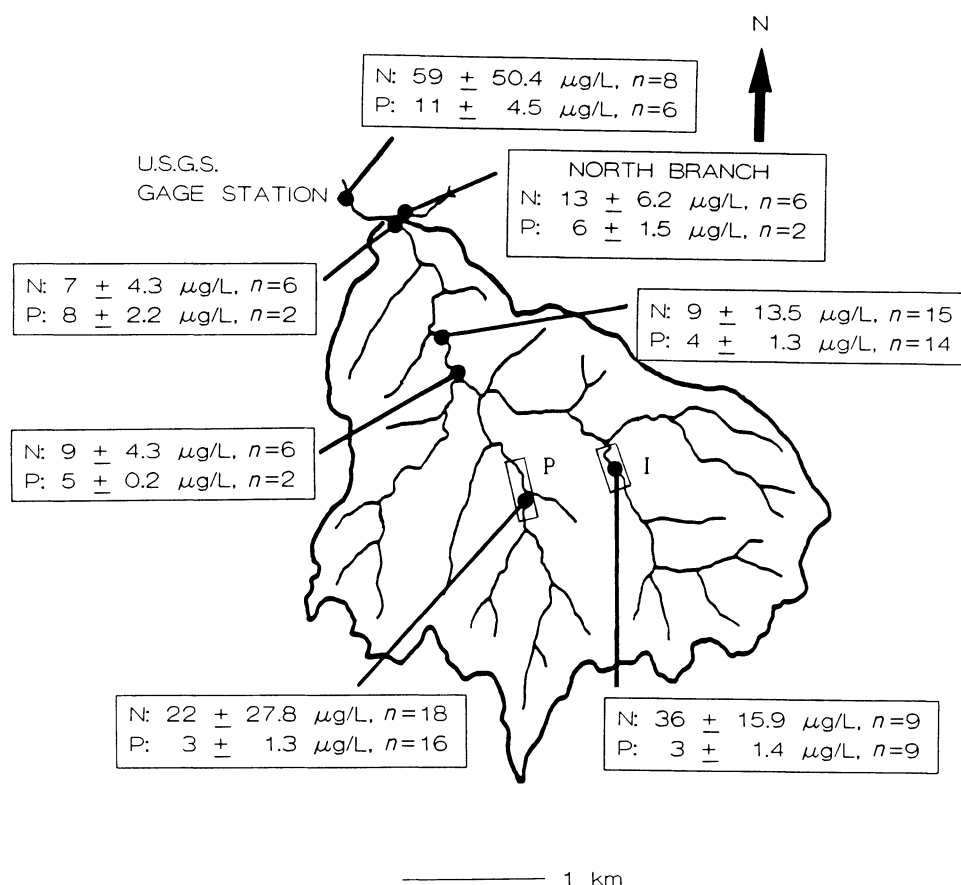N: 36 ± 15.9 μg/L, n=9
P: 3 ± 1.4 μg/L, n=9

1 km

Fig. 1. Mean (±SD) nitrate-N and soluble reactive phosphorus concentrations in the South Branch of Kings Creek, Konza Prairie Research Natural Area, Kansas. P = perennial reach, I = intermittent reach.

streams of the Flint Hills of Kansas. Nitrogen is known to limit plant production in the tallgrass prairie (Risser 1988). My objectives were (1) to describe spatial (stream reach to basin) and temporal (day to years) variation of nitrogen concentrations in tallgrass prairie streams, (2) to determine what hydrologic factors might influence nitrogen variability, (3) to determine whether terrestrial and/or aquatic biota influence nitrogen variability, (4) to measure the influence of algae on nitrate uptake from stream water, and (5) to determine if nitrogen and/or phosphorus limits algal growth during summer.

METHODS

Study site

Kings Creek lies within the 3487-ha Konza Prairie Research Natural Area, a native tallgrass prairie owned by the Nature Conservancy near Manhattan, Kansas. Konza Prairie is representative of the Flint Hills Uplands (a dissected upland of hard chert and flint-bearing limestone layers) and is a part of the United States Geological Survey's (USGS) Hydrologic Benchmark Network (Fig. 1). The South Branch basin has not been grazed by cattle since 1977 or burned since at least

1968 and includes first- to fifth-order stream channels. Three zones of riparian vegetation exist in the watershed: (1) grasses in headwater channels (orders 1–2); (2) mixtures of grasses, shrubs, and small trees in third-order channels; and (3) a gallery forest in fourth- and fifth-order channels (Gurtz et al. 1982). Physical and chemical characteristics are presented in Table 1 (see Gurtz et al. 1988 for a more detailed description).

Annual precipitation averages 835 mm/yr and most occurs as late spring or early thunderstorms. As a result, flow in Kings Creek is spatially and temporally variable. Headwater channels are ephemeral (flow only in response to precipitation) and remaining channels are intermittent (flow 2–10 mo a year); however, perennial pools and flowing reaches can be found within intermittent channels (Gurtz et al. 1982). The magnitude and frequency of storm and intermittent flows vary from year to year. Flow generally ceases by late summer and resumes at any time from October to May.

I observed and sampled two third-order reaches, an intermittent (Watershed N1B; Box I, Fig. 1) and a perennial (Watershed N4D; Box P, Fig. 1) reach of Kings Creek from October 1983 to October 1984. The intermittent reach drained a 116-ha watershed, was 263

TABLE 1.   Physical characteristics of South Branch of Kings Creek and chemical characteristics of water at the USGS gaging station of Kings Creek, Konza Prairie Research Natural Area, Kansas.

Watershed area* (ha)	660
Maximum elevation* (m)	430
Minimum elevation* (m)	338
Main channel length* (km)	5.38
Main channel gradient* (m/km)	17.0
Maximum discharge for study period† (m³/s)	128
Range of pH†	7.4–8.2
Concentrations (mean ± SD)	
Hardness† (mg/L as CaCO₃)	283 ± 21.9
Alkalinity† (mg/L as CaCO₃)	257 ± 23.1
Calcium† (mg/L as Ca)	86 ± 6.9
Magnesium† (mg/L as Mg)	17 ± 1.2
Sodium† (mg/L as Na)	5.4 ± 0.98
Potassium† (mg/L as K)	1.2 ± 0.59
Sulfate† (mg/L as SO₄)	36 ± 6.8
Chloride† (mg/L as Cl)	2.3 ± 0.91
Dissolved organic carbon‡ (mg/L as C)	1.3 ± 0.56

* Data from Gurtz et al. 1988.
† Data from United States Geological Survey 1981, 1982, 1983, 1984, 1985. $n = 18$.
‡ Data from Gurtz et al. 1982. $n = 6$; samples from South Branch near confluence with North Branch of Kings Creek.

m long, averaged 1.7 m in width, had a channel area of 466 m², a pool-to-riffle ratio of 1.8 based on area, a cobble substrate, and mean baseflow discharge of 18 L/s. The perennial reach drained a 129-ha watershed, was 578.3 m long, averaged 1.6 m in width, had a channel area of 619 m², a pool-to-riffle ratio of 0.9, a bedrock/cobble substrate and a mean baseflow discharge of 19 L/s. Riparian vegetation consisted of mixed grasses and small American elms (*Ulmus americana*) in both reaches.

Spatial and temporal variation in N and P

Water samples were collected on several spatial (i.e., basin and reach) and temporal (i.e., year, season, day) scales within the South Branch of Kings Creek. Spatial variation within the basin was measured by periodically collecting water samples along the entire South Branch during the 1982 water year (October–September) and analyzing for nitrate and occasionally for soluble reactive phosphorus (SRP) (sites in Fig. 1). Year-to-year variation in nitrate was examined by collecting water samples approximately monthly during 1982 and 1983 and weekly during 1984 water years at sites P and I (Fig. 1).

During the 1984 water year, seasonal and within-reach variation in nitrate, total N, and organic N concentrations were measured. Duplicate baseflow water samples were collected weekly from 10 stations located between a groundwater source and 263 m below the source in the intermittent reach (Box I, Fig. 1), and at 12 stations located between the source and 578.3 m below the source in the perennial reach (Box P, Fig. 1). The upstream intermittent reach, three adjacent
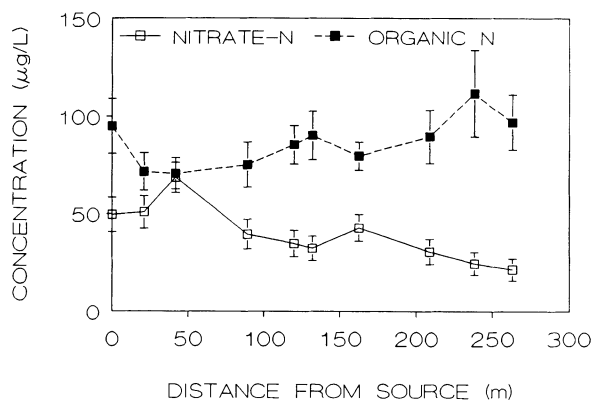

FIG. 2.   Organic and nitrate nitrogen concentrations downstream from the source in the intermittent stream of South Branch of Kings Creek for the 1984 water year (means ±SE).

groundwater seeps, and two tributaries flowing into the perennial reach were also sampled. Seasonal variation in SRP was measured by collecting water samples at a single site (P, Fig. 1) in a perennial reach.

Diel variation in nitrate was measured one day a month in May and June in the intermittent reach and from May to October in the perennial reach. Water samples were collected hourly by automatic samplers for 28 h and preserved with 1 mg/L phenylmercuric acetate. Uptake rates of nitrate at ambient concentrations were measured by placing a second automatic sampler 30 m downstream during the diel sampling in May and June in the intermittent reach and July to September in the perennial reach. Uptake rates were calculated using the formula of Grimm et al. (1981).

Relative abundance of algae was measured in each 30-m reach during diel sampling by a line intercept method (Smith 1974). Transects were measured at 5-m intervals and the presence of filamentous algae, blue-green/diatom mixture, macrophytes, or bare sediment categories was counted at 0.1-m increments across the channel. Percent occurrence was calculated as the sum of 0.1-m points in a category, divided by the sum of all 0.1-m points, times 100%.

Hydrologic influence on nitrate concentrations

To examine if hydrologic history influenced patterns of nitrate concentrations, seasonal variation in precipitation and nitrate concentrations were compared. Precipitation data (1982 to 1984 water years) obtained from the Konza Prairie weather station (data set APT011, Konza Prairie LTER data bank) were compared to normal precipitation amounts for Manhattan, Kansas (data from Kansas Agricultural Experiment Station Weather Data Library).

Duplicate water samples were collected below the USGS gaging station during storm flows in the spring and early summer 1984 to observe the effect of changing flow on nitrate concentrations. Peak discharge val-

ues were taken from the USGS gaging station records (United States Geological Survey 1985).

Algae and nitrate uptake

Experimental addition of nitrate to the perennial reach was conducted on 25 August 1984 during the day (1217) and at night (2107) to test if photosynthetic activity of algae influenced nitrate uptake rates. A concentrate made from KNO_3 (NO_3-N: 5.5 mg/L) and NaCl (Cl: 5250 mg/L) was dripped (2 mL/min) into the stream for 1 h, raising mean ($\pm$SD) nitrate-N concentrations in stream water to 100 ± 24.3 µg/L ($n = 10$). Duplicate water samples were collected at 0 and 30 m below the point of enrichment at 0, 1, 5, 15, 30, 45, and 60 min after enrichment began and 0, 1, 5, 15, 30, 45, and 60 min after enrichment ended. Cl was used as an inert tracer to evaluate dilution effects. Uptake rates were calculated using the formulas of Sloane (1979). Mean uptake rate was calculated using samples collected during periods when Cl concentrations were the same at upstream and downstream sites.

Algal cover was measured as previously described. To estimate algal biomass, three core samples were taken of filamentous algae (area = 4.9 cm²) and bare sediment (area = 3.8 cm²). Cores were placed into 100 mL of water, mixed, and subsampled for chlorophyll a (20 mL) and ash-free dry mass (AFDM, 10 mL).

Nutrient limitation experiments

Two methods, nutrient-diffusing artificial substrata (Fairchild et al. 1985) and enrichment of artificial channels, were used to test nutrient limitation of algal growth in the perennial stream during the summer.

Nutrient-diffusing artificial substrata (clay saucers) were constructed out of 10.2 cm diameter clay flowerpot saucers glued to a 12 × 12 cm plexiglass plate. Clay saucers were filled with 225 mL of 1.8% agar solution containing: 0.5 mol/L $NaNO_3$ (+N), 0.1 mol/L KH_2PO_4 (+P), 0.5 mol/L $NaNO_3$ plus 0.1 mol/L KH_2PO_4 (N + P), or no nutrients, as controls (C). Drainage holes were closed with Number 00 rubber stoppers. Nine sets of pots were placed in a bedrock reach (25 m long, 1.28 m wide) on 6 July 1984. Each set of saucers was attached to 60-cm metal bars arranged in a diamond shape with a C saucer placed upstream, +N and +P saucers placed side by side downstream from C, and an N + P saucer at the downstream end, to minimize contamination among treatments. Three sets of saucers were collected on day 14 and six sets on day 21. Algae were scraped from a known area (71.1 cm²) of each saucer's surface, scrapings were mixed and subsampled for chlorophyll (20 mL), AFDM (10 mL), and algal composition (25 mL).

During the clay saucer experiment, discharge in the stream channel decreased from 17.2 to 3.2 L/s, current velocity decreased from 18 to 6.7 cm/s, nitrate increased from 1 to 7 µg/L (mean = 4 µg/L) and SRP ranged from 1 to 3 µg/L (mean = 2 µg/L). Atomic N:P ratio of water increased from 2 to 10 (mean = 4) and temperature ranged from 16° to 23°C.

Leaching rates of nutrients for three sets of saucers were monitored on day 1 and 2 and then every 4 d until day 21. Saucers were taken from the stream, placed in a plastic jug containing 1 L of distilled water for 1 h, removed, and replaced in the stream channel. Nitrate and SRP in the water were analyzed. Release rates of nitrate and SRP from the saucers declined exponentially through time. Nitrate-N (5.2 mg/h on day 1 to 0.4 mg/h on day 21) and SRP (236 µg/h on day 1 to 5 µg/h on day 21) leached more slowly from the N + P treatment than either N from the +N (5.1 mg/h on day 1 to 0.6 mg/h on day 21) or P from the +P (632 µg/h on day 1 to 10 µg/h on day 21) treatments. Biota were not removed from the saucers; thus, differences in release rates may reflect biotic uptake of nutrients. Differences in release rate from saucers caused atomic N:P ratios to vary during the experiment. Checks made to determine if leaching of nutrients from saucers enriched stream water proved negative (i.e., comparison of stream water chemistry upstream and downstream of saucers, Student's t test, $P > .05$).

Artificial channels were placed below a waterfall ≈25 m downstream from the substrata enrichment site. Stream water was piped into a fiberglass header box (0.5 × 2.1 × 0.5 m) and flowed into 12 troughs (5 cm × 3 m) through 90°-elbows, all made from polyvinyl chloride pipe. Plexiglass baffles in the upper 40 cm of each channel aided in mixing nutrients with stream water. Mean ($\pm$SD) discharge in channels was 1.3 ± 0.15 L/min ($n = 119$) and velocity averaged 4.4 ± 0.82 cm/s ($n = 12$), similar to stream water velocity (4–6 cm/s).

Three channels were selected for each of four nutrient treatments: control (C), nitrate (+N), phosphate (+P), and nitrate plus phosphate (N + P). Channels were continuously enriched for 12 d with a concentrate of $NaNO_3$ (N, 5.5 mg/L) and/or KH_2PO_4 (P, 2.0 mg/L) at a mean ($\pm$SD) rate of 16 ± 2.3 mL/s from a 121-L reservoir placed on the stream bank. Nitrate decreased from 5 µg/L to undetectable levels and SRP decreased from 3 to 1 µg/L in the C channels during the experiment. Nitrate averaged 62 ± 1.8 µg/L ($\bar{X} \pm$ SE, $n = 60$) for +N and N + P channels and SRP averaged 17 ± 1.2 µg/L ($n = 60$) for +P and N + P channels. Atomic N:P ratios of water averaged 3.8 ± 4.66 ($\bar{X} \pm$ SE, $n = 30$) for C, 101.8 ± 11.32 ($n = 30$) for +N, 0.5 ± 0.21 ($n = 30$) for +P and 10.9 ± 0.98 ($n = 30$) for N + P channels. Water temperatures ranged from 17° to 32°.

Twenty-seven (2.54 × 2.54 × 0.25 cm) acid-washed ceramic tiles were placed 5 cm apart in each channel on 16 August 1984. Nine tiles (total area = 139 cm²) from each trough were collected 12 d later and algae were scraped into 100 mL of water and subsampled for chlorophyll a (10 mL), AFDM (10 mL), and algal composition (25 mL). Checks made to determine if

measurable amounts of SRP or nitrate leached from acid-cleaned tiles proved negative.

Analysis

Subsamples for algal composition were preserved in a modified Lugol's preservative (Meyer 1971). Algae were identified to genus and counted at 400×. Filamentous algae were counted using a sedimentation chamber method (Wetzel and Likens 1979). Diatoms and smaller algae were counted by placing 0.025 mL on a glass slide and counting the entire slide. Chlorophyll a samples were filtered (Whatman GF/C filters), ground in 9 mL buffered acetone and analyzed spectrophotometrically using the trichromatic method (Strickland and Parsons 1968). AFDM samples were dried (100°) for 24 h, weighed, ashed (450°) for 4 h, rehydrated with water, dried for 24 h and reweighed.

Water samples were filtered (Gelman A/E filters) in the field and analyzed within 6 h of collection or frozen. SRP was analyzed by the method of Murphy and Riley (1962). (Nitrate + nitrite) was analyzed from November 1981 to December 1983 using the Cu–Cd reduction method of Strickland and Parsons (1968) and from January to October 1984 using Technicon (1973) procedures. Nitrite and ammonia were not analyzed routinely because concentrations were below detection limit. Total nitrogen (TN) was analyzed as nitrate (Technicon 1973) after an alkaline persulfate digestion using a modified method of D'Elia et al. (1977; R. Edwards, *personal communication*). Organic N was calculated by subtracting nitrate values from TN values since ammonia concentrations were negligible. Cl was analyzed by Technicon (1974) procedures.

Nutrient concentration data were divided into two seasonal categories for statistical analyses, growing (April through August) and dormant (September through March), based on terrestrial vegetation on Konza Prairie. The growing season is normally April through September (Seastedt 1985); however, a drought during September 1984 caused the grasses to be functionally dormant (M. Abrams, *personal communication*). Nutrient concentrations between streams, within streams, and between seasons were compared for descriptive purposes only because treatment effects cannot be separated from site effects (Hurlbert 1984). ANOVA was used to compare log-transformed chlorophyll a, and AFDM and arcsine square-root transformed percent of total diatoms, among treatments using the general linear model procedure of SAS82 (SAS 1982).

RESULTS

Spatial and temporal variability in nitrogen concentrations

Nitrogen (N) concentrations in the South Branch of Kings Creek exhibit spatial and temporal variability on several scales. Spatial variation in nitrate concentrations occurs within drainage basins, between stream

TABLE 2. Annual and seasonal mean nitrogen (μg/L) concentrations averaged for all sites in an intermittent stream, and in seeps, tributaries, and stream of a perennial reach of Kings Creek.*

	n	Nitrate N Mean	Nitrate N SE	Organic N Mean	Organic N SE	Total N Mean	Total N SE
		1984 Water year					
Intermittent	228	41	2.4	85	3.8	126	4.6
Perennial							
Stream	562	12[a]	0.5	73[a]	1.9	84[a]	2.0
Seeps	127	46[b]	3.7	53[b]	3.0	98[b]	4.4
Tributaries	78	31[c]	3.1	72[a]	5.7	103[b]	6.7
		Growing season†					
Intermittent	147	21	1.2	81	4.7	102	4.7
Perennial							
Stream	258	7[a]	0.5	81[a]	5.3	87[a]	3.4
Seeps	59	26[b]	3.5	58[b]	3.3	84[a]	6.6
Tributaries	38	12[a]	2.3	78[a]	7.3	90[a]	8.2
		Dormant season†					
Intermittent	80	77	3.9	94	6.6	171	7.8
Perennial							
Stream	304	16[a]	0.7	66[a]	2.0	82[a]	2.1
Seeps	68	63[b]	5.5	48[b]	3.3	111[b]	5.6
Tributaries	40	48[b]	4.0	66[a]	8.7	115[b]	10.6

* Means with different superscript letters within a column are significantly different from others within the same year or season (Duncan's multiple range test, $P < .05$).

† Growing (April–August) and dormant (September–March) seasons refer to terrestrial vegetation.

reaches, and within stream reaches. Within the Kings Creek basin, nitrate concentrations decreased downstream from third-order reaches (sites I, P, Fig. 1) to confluence of North and South Branch of Kings Creek and increased (presumably due to groundwater input) at the USGS gaging station during the 1982 water year. During the 1984 water year, annual mean nitrate-N, organic N, and total N concentrations varied among stream reaches; higher concentrations were found in the intermittent stream than in the perennial stream (Table 2). Nitrate-N concentrations in intermittent streams varied fourfold from high (e.g., intermittent stream, Table 2) to low (e.g., intermittent reach upstream of the perennial reach; mean $\pm$ SE $= 9 \pm 2.0$ μg/L, $n = 34$). Within a stream, annual mean nitrate-N concentrations decreased and mean organic N concentrations increased downstream from the source in the intermittent stream (Fig. 2). Nitrate-N concentrations also decreased downstream from the source in the perennial reach, although the magnitude of the decrease varied temporally (Fig. 3). Local inputs from seeps and tributaries influenced nitrate concentrations within a stream reach (Fig. 3) and nitrate-N concentrations varied among seeps and tributaries (Table 2). Not all seeps have high nitrate concentrations; the seep located 25 m below the source of the perennial reach had lower mean annual nitrate-N concentrations (11 μg/L) than other seeps (Table 2).

Temporal variation in nitrate-N concentrations occurred among years (Fig. 4) and seasons (Table 2). Over
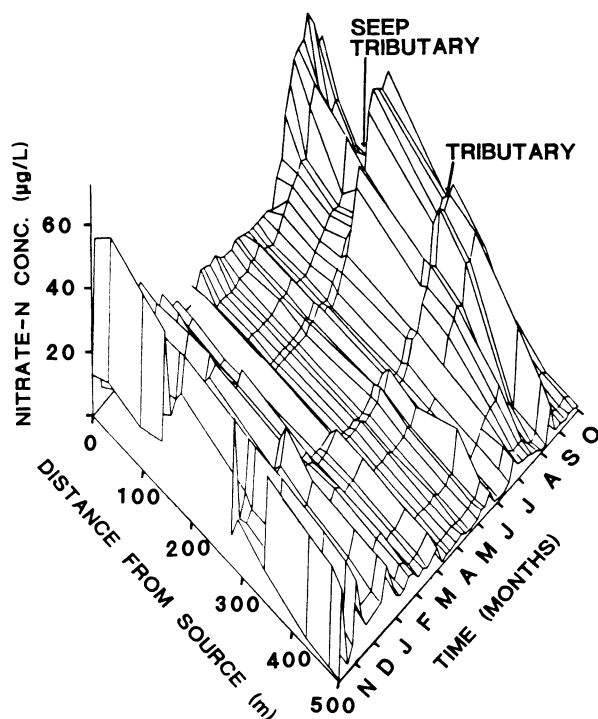
FIG. 3. Nitrate concentrations measured downstream from a groundwater source in the perennial stream of South Branch of Kings Creek from November 1983 to October 1984.

the 3-yr period from 1982 to 1984, higher mean nitrate concentrations were found in the perennial stream when terrestrial vegetation was dormant than during the growing season. Nitrate-N concentrations in seeps and tributaries showed similar seasonal patterns as observed in the perennial stream (Fig. 4); higher nitrate-N concentrations were found during dormant than growing season in seeps and tributaries (ANOVA, $P < .05$, Table 2). Nitrate-N and TN concentrations in the intermittent reach were higher during dormant season than growing season (ANOVA, $P < .001$), and there was no seasonal pattern in organic N (Table 2). In the perennial stream, nitrate-N was higher and organic N lower during dormant than growing season (ANOVA, $P < .001$) and there was no seasonal pattern in TN concentrations (Table 2).

Spatial and temporal variability in phosphate concentrations and N:P ratios

In contrast to N, soluble reactive phosphorus (SRP) increased downstream from the third-order to fifth-order streams during the 1982 water year (Fig. 1). SRP concentrations did not vary seasonally but did show year-to-year variation with mean ($\pm$SE) SRP concentrations greater in the 1982 water year (3 ± 0.4 μg/L, $n = 22$) than in 1984 (1 ± 0.1 μg/L, $n = 32$). Mean ($\pm$ SD) atomic N:P ratios were lower during growing season (7 ± 5.1, $n = 9$ in 1982; 15 ± 10.9, $n = 18$ in 1984)

than during the dormant season (39 ± 31.0, $n = 12$ in 1982; 48 ± 36.7, $n = 14$ in 1984).

Hydrologic influence on nitrogen concentrations

Seasonal drying of stream channels influenced nitrate concentrations. Nitrate concentrations were higher when the intermittent stream began to flow, then decreased as flow continued (Fig. 4).

Previous hydrologic history can influence nitrate concentrations. For example, water year 1982 was preceded by two dry years. In Kings Creek flow occurred during the dormant season for 26 d during 1980 and 0 d during 1981. From 1982 to 1984, longer flow periods occurred during the dormant season because precipitation amounts during this time were higher than normal (1982: 36.3% higher; 1983: 7.5%; 1984: 70.6%). Consequently, mean ($\pm$SE) nitrate-N concentrations during the dormant season were highest in 1982 (67 ± 25.2 μg/L, $n = 15$) and then decreased from 1983 (48 ± 17.2 μg/L, $n = 6$) to 1984 (20 ± 2.3 μg/L, $n = 32$) at the perennial site (same site as Fig. 4).

Highest nitrate concentrations occurred during storm flows. Water samples collected during a series of storms
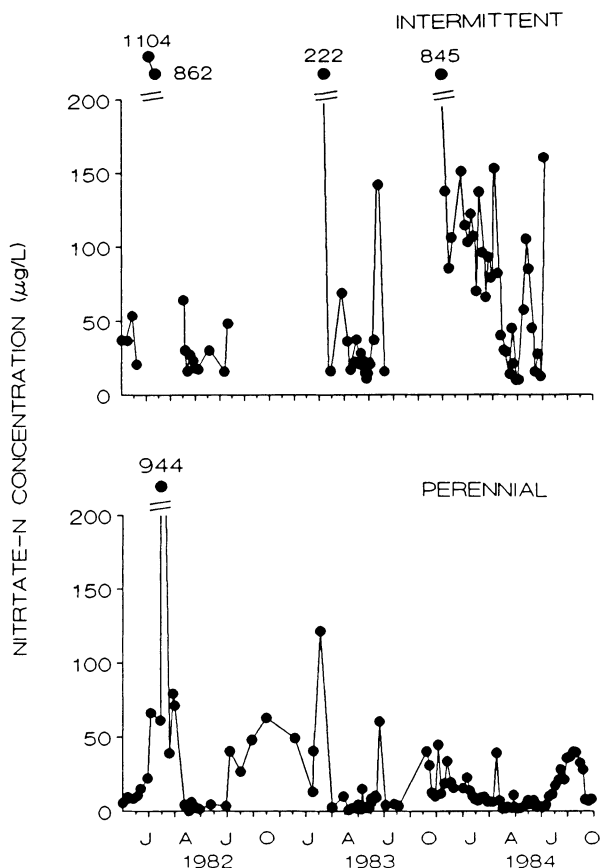

FIG. 4. Nitrate concentrations in the intermittent and perennial reaches of South Branch of Kings Creek from November 1981 to October 1984. Lines not connected during dry periods in the intermittent stream. J = January or July, A = April, O = October.

TABLE 3.   Relations among biotic uptake rate, nutrient availability, and types of benthic algae in two Kansas stream reaches during diel sampling in 1984.

	Daytime NO_3-N uptake rate ($\mu g \cdot m^{-2} \cdot min^{-1}$)			Nighttime NO_3-N uptake rate ($\mu g \cdot m^{-2} \cdot min^{-1}$)			Nitrate-N concn. ($\mu g/L$)			Water temp. (°C)	Frequency of occurrence of patch type (%)			
											Fila-men-tous algae	Bare sedi-ment	Blue–green diatom mix	Macro-phyte
Date	Mean	SE	n	Mean	SE	n	Mean	SE	n					
							Intermittent reach							
16 May	114	6.2	17	94	4.4	10*	20	2.4	28	12.9	76.3	18.6	1.7	5.1
27 June	28	5.4	14	19	4.6	11	12	0.8	27	14.0	3.3	32.8	50.0	13.9
							Perennial reach							
26 July	3	0.8	15	7	0.7	11*	7	2.2	26	16.4	35.6	63.3	⋯	1.1
23 August	5	0.6	13	4	0.5	13	8	2.4	25	18.4	71.9	28.1	⋯	⋯
21 September	2	0.3	17	1	0.5	10	4	1.9	28	13.8	51.1	46.8	⋯	2.1

* = day and night uptake rates significantly different for this date (Student's t test, $P < .05$).

in Spring 1984 found that maximum nitrate concentrations generally occurred just before or during peak discharge at the USGS gaging station. The magnitude of maximum nitrate concentrations during storm flows was directly related to the magnitude (i.e., peak discharge) of the storm and inversely related to the frequency (i.e., days since last storm) of the storm events. Eight storm flows occurred frequently (i.e., every 2–9 d) in March and April and were of low magnitude (0.5–2.3 m^3/s). Maximum nitrate concentrations during this time decreased from 138 to 48 $\mu g/L$. Peak nitrate-N concentrations were highest during the highest magnitude storms of 29 April (245 $\mu g/L$, 4.05 m^3/s) and 15 June (237 $\mu g/L$, 4.53 m^3/s). In contrast, a 9 June storm was preceded by 42 dry days and was approximately equal in magnitude (1.54 m^3/s) to storms occurring in March, but nitrate-N concentrations were higher (162 $\mu g/L$).

Influence of biota on nitrogen concentrations

Biotic uptake of nitrate by algae, heterotrophs, and possibly riparian vegetation may be an important mechanism for the downstream decrease of nitrate found in prairie streams (Figs. 2 and 3). Diel variation in nitrate concentrations and uptake was used as an indicator of algal influence on nitrate removal. Lower nitrate-N concentrations (mean ± SE, $n = 13$) during the day vs. the night for some days in the intermittent (16 May: 13 ± 0.3 $\mu g/L$ for night, 9 ± 0.2 $\mu g/L$ for day; 27 June: 12 ± 0.3 $\mu g/L$ for night, 10 ± 0.2 $\mu g/L$ for day) and perennial (26 July: 9 ± 0.3 $\mu g/L$, $n = 11$ for night, 5 ± 0.4 $\mu g/L$, $n = 15$ for day) streams (Student's t test, $P < .05$) corresponded to the timing of uptake of nitrate during algal photosynthesis. No diel differences in nitrate-N concentration were found during May, August, September, and October in the perennial reach. Mean daily uptake rates were greater than nightly uptake rates in May in the intermittent reach when nitrate concentrations were higher and filamentous algae were abundant; the opposite trend was

found in July in the perennial reach (Table 3). Mean uptake rates in the intermittent stream were approximately 4–20× greater than in the perennial reach. Low nitrate concentrations in the perennial reach made diel differences in nitrate concentrations and uptake difficult to measure; algal abundance also had little influence on nitrate uptake at low concentrations (Table 3).

Although there was no diel difference in nitrate uptake in the perennial reach at ambient nitrate concentrations in August (Table 3), experimental addition of nitrate found mean (±SE) uptake rates of nitrate-N during the daytime enrichment (57 ± 2.9 $\mu g \cdot m^{-2} \cdot min^{-1}$, $n = 5$) were higher than during the nighttime enrichment (45 ± 7.9 $\mu g \cdot m^{-2} \cdot min^{-1}$, $n = 5$) (Student's t test, $P < .01$). Filamentous algae covered 52.3% (19.7 m^2) and bare sediment covered 47.7% (18.0 m^2) of the stream bottom on the day of experimental addition; chlorophyll a was 131.6 mg/m^2 and ash-free dry mass (AFDM, including algae and detritus) was 58.6 g/m^2. Nitrate-N concentrations during the addition were 12× higher (100 $\mu g/L$) than ambient (8 $\mu g/L$); however, concentrations were not atypical of concentrations obtained during storm flows. Higher uptake rates during the day than night for the diel study in the intermittent stream and experimental addition of nitrate in the perennial stream suggest algal uptake was an important mechanism of nitrate removal.

Influence of nutrients on algal growth and taxa

Similar trends in algal biomass response were measured in both the clay saucer and artificial channel experiments, in spite of the different methods of nutrient enrichment. In both experiments, chlorophyll a and AFDM were highest in the N + P treatment on the final day (Fig. 5). Rate of accrual of chlorophyll a was fastest for the N + P treatment in the clay saucer enrichment. Mean chlorophyll a for N + P (all measurements as mean ± SE) went from 1.4 ± 0.22 $\mu g/cm^2$ ($n = 3$) on day 14 to 6.5 ± 0.71 $\mu g/cm^2$ ($n = 6$) on day 21; whereas, mean chlorophyll a for C, +N,

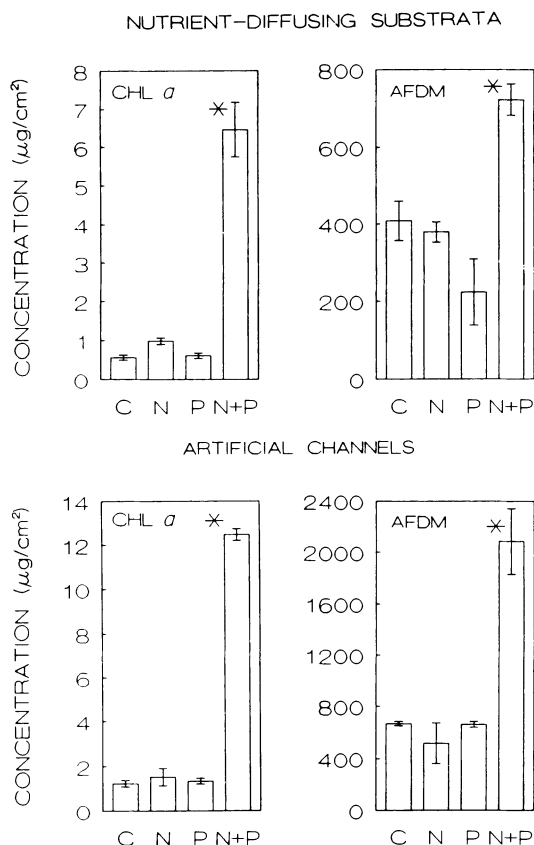NUTRIENT–DIFFUSING SUBSTRATA

ARTIFICIAL CHANNELS

FIG. 5. Mean chlorophyll *a* (CHL *a*) and ash-free dry mass (AFDM) on the final day of collection in the nutrient-diffusing substrata (21-d) and artificial channel (12-d) experiments. Error bars = ±SE; * = significant difference (ANOVA, *P* < .05). C = control, N = nitrate added, P = phosphate added, N + P = nitrate and phosphorus added.

and +P treatments combined went from 0.3 ± 0.04 µg/cm² (*n* = 9) on day 14 to 0.7 ± 0.25 µg/cm² (*n* = 18) on day 21.

Densities of most algal taxa increased on the N + P treatment, following the pattern observed for biomass (Fig. 5). The N + P treatment appeared green on the

final collection compared to other treatments due to the presence of the filamentous green algae (*Chaetophora* and *Stigeoclonium*) in the clay saucer experiment and *Spirogyra* in the artificial channels. Although they were lower in numbers compared to diatoms, they probably made up a large part of the algal biomass. Diatoms composed the greatest proportion of the algal community (>60%) and dominated the N + P treatments (92.6%).

A comparison of relative abundance for diatom taxa indicated a different response to nutrient enrichment in the two experiments (Fig. 6). On the N + P treatment, relative abundance of *Cymbella* and *Cocconeis* increased and *Navicula* and *Synedra* decreased in the clay saucer experiment and *Synedra* increased in the artificial channels experiment compared to other treatments. *Pinnularia* increased only in the +P enrichment in both experiments.

DISCUSSION

Aquatic–terrestrial linkages

Terrestrial vegetation influences the seasonal variation of nitrate concentrations entering prairie streams, seeps, and tributaries. The growing season for most terrestrial vegetation of the Konza Prairie is usually April through September, with some growth continuing until November (Seastedt 1985). Nitrate concentrations in soil water decrease from March to July (Knapp and Seastedt 1986), similar to the pattern of nitrate concentrations observed for streams, seeps, and tributaries (Fig. 4, Table 2). Seasonal variations in nitrate concentrations have been found in many stream ecosystems, with lowest concentrations occurring during summer months corresponding to the growing season of terrestrial vegetation (Likens et al. 1977, Wetzel and Manny 1977, Dahm 1980, Hoare 1982, Calles 1983).

Upstream–downstream linkages

Once nitrate entered the stream through groundwater, seeps, or tributaries, aquatic biota removed ni-
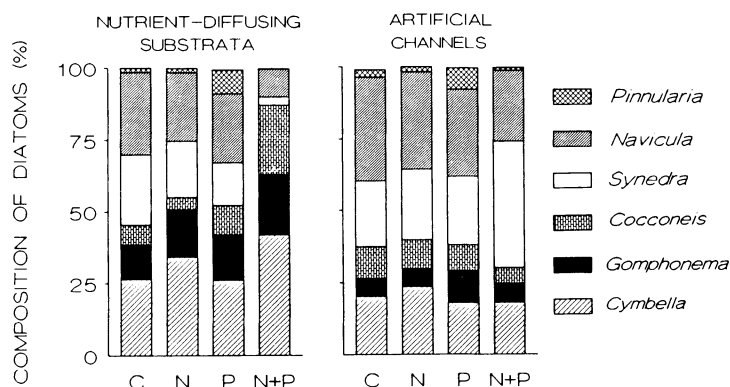

FIG. 6. Relative abundance (% of total diatoms) of diatoms for nutrient-diffusing substrata and artificial channel experiment. Symbols as in Fig. 5.

trate from stream water (Figs. 1, 2, and 3) and/or transformed the nitrate to organic N (Fig. 2). Similarly, nitrate concentrations decreased downstream from a source in hot desert streams of the Southwest, and the decrease was attributed to autotrophic activity (Grimm et al. 1981). Evidence for algal influence on nitrate concentrations comes from diel variation in nitrate concentrations in both intermittent and perennial streams and diel variation in nitrate uptake rates in the intermittent stream (Table 3). Similar patterns of diel variation in nitrate concentrations have been reported in other studies (Gregory 1980, Triska et al. 1983, Grimm 1987). Experimental addition of nitrate in the perennial stream resulted in faster nitrate uptake rates during the day than night, again suggesting that algae (and possibly riparian vegetation) were important in removing nitrate from stream water. The rate of nitrate removal from stream water, however, varied spatially and temporally and was influenced by nitrate concentrations in the perennial stream and by nitrate concentration and algal type in the intermittent stream (Table 3).

In other stream ecosystems, denitrification may be a major loss of nitrate within a stream reach (Kaushik and Robinson 1976, Hill 1979, 1983, Swank and Caskey 1982). These sites had higher nitrate concentrations than Kings Creek and rates of denitrification are dependent on nitrate concentrations (Knowles 1982, Ventullo and Rowe 1982). Hooker (1987) found potential nitrate uptake by sediments from Kings Creek amended with high nitrate concentrations (N, 100 and 1000 μg/L) to be biologically mediated and to occur under aerobic and anaerobic conditions in laboratory studies. Thus, algal and microbial uptake and denitrification are potential biological processes altering the forms and concentrations of nitrogen available to downstream biotic communities in Kings Creek.

Nutrient limitations in prairie streams

Both nitrogen and phosphorus (P) limited algal growth as indicated by two algal standing crop measurements, chlorophyll a and ash-free dry mass (AFDM) in both experiments (Fig. 5), and by rate of accrual of chlorophyll a in the clay saucer experiment. In contrast, other studies have found either N or P to limit algal growth in stream ecosystems. P was the primary limiting nutrient to algal production in Vancouver rainforest (Stockner and Shortreed 1978), Tennessee woodland (Elwood et al. 1981), Alaskan tundra (Peterson et al. 1983), and Michigan woodland (Pringle and Bowers 1984) streams. In Sycamore Creek, a lowland desert stream in Arizona, N limited primary production, nitrogen uptake by algae, and the rate of chlorophyll a accrual, but not periphyton standing crops (Grimm and Fisher 1986). N was also limiting to algal growth in forested streams of the Pacific Northwest and California if light was available (Gregory 1980, Triska et al. 1983, Hill and Knight 1988).

Atomic ratios of nitrogen to phosphorus (N:P) have been used to indicate potential nitrogen or phosphorus limitations to algal growth in aquatic ecosystems (Redfield 1958, Rhee 1978, Schanz and Juon 1983). An N:P ratio of <16–30 (Redfield 1958, Rhee 1978) indicates N limitation, and above this number, P limitation. The N:P ratio in stream water was <10 during both experiments, predicting N to be potentially limiting to algal growth. Both N and P actually limited algal growth in Kings Creek, suggesting an additive effect of N and P enrichment. That is, when N and P concentrations are low, supplying the primary limiting nutrient (e.g., N) rapidly depletes the secondary limiting nutrient (e.g., P) (Grimm and Fisher 1986).

Further, the optimum N:P varies among species (Rhee and Gotham 1980) and the periphyton community is a mixture of species with different optimal N:P requirements (Grimm and Fisher 1986). N and P concentrations and N:P ratios were variable in the clay saucer experiment and constant during the artificial channel experiment. Although the algal biomass was N and P limited (Fig. 5), the algal taxa (Fig. 6) responded to specific N and P concentrations or N:P ratios (e.g., *Stigeoclonium*, *Chaetophora*, *Cymbella*, and *Cocconeis* in clay saucer, *Spirogyra* and *Synedra* in artificial channels, and *Pinnularia* in both). Other studies have shown periphyton biomass increases when the limiting nutrient is supplied, and variable species responses to different levels of N and P concentrations and/or N:P ratios (Stockner and Shortreed 1978, Pringle and Bowers 1984, Fairchild et al. 1985).

Algal response to N + P enrichment was faster and chlorophyll a and AFDM biomass greater in the artificial channel than the clay saucer experiments (Fig. 5) and algal taxa varied between experiments (Fig. 6). Differences in algal biomass and organism response between experiments were likely due to the type of experiment (substratum vs. stream water enrichment; Pringle 1987), water temperature, time at which the experiment was conducted, and differing nutrient regimes.

Most streams on Konza Prairie have low N (Table 2, Fig. 4, and McArthur et al. 1985) and P (<3 μg/L) during summer. Mean baseflow nitrate concentrations in intermittent streams draining annually (N: 1.6 μg/L) and biannually burned (3.2 μg/L) watersheds of the Swede Creek Basin of the Konza Prairie (McArthur et al. 1985) are similar to concentrations in the perennial reach of the Kings Creek basin (Table 2). Thus, N and P limitations to algal growth are likely a common occurrence in tallgrass prairie streams of the Flint Hills. There is the potential for different nutrients to limit periphyton growth seasonally (e.g., N:P > 30 during dormant season; N:P < 16 during growing season in the perennial stream) and spatially (Fig. 1). Nutrient inputs of seeps or tributaries can also contribute to localized spatial variation in N dynamics (Fig. 3).

Grimm and Fisher (1986) proposed that nutrient

availability does not limit the standing crop of algal biomass, but does limit the maximum accrual rate of algal biomass, rates of primary production, and the time required to reach maximum standing crop. When streams are "reset" by scouring floods, then nutrient availability can strongly influence rates and patterns of post-flood ecosystem recovery, but not steady-state standing crop. Sonoran Desert streams seem to fit this model, with N being the critical nutrient for algal growth (Grimm and Fisher 1986). In Kings Creek, rate of accrual of algal biomass appears to be limited by both N and P availability during summer months, which supports their model. Periphyton growth (chlorophyll a) on C, +N, and +P treatments, however, did not appear to be converging with N + P treatment. Because my study was terminated after 3 wk, maximum standing crops may not have been reached. Regardless, nutrient availability can be an important controlling factor in biotic recovery after storm flows in prairie streams, but the specific limiting nutrient or nutrients may vary spatially and temporally.

Hydrologic influence on nutrients and biotic community

Flow is a major factor influencing nutrient dynamics and structuring the biotic community in prairie streams. Prairie streams experience hydrologic extremes from drought to flood. During dry periods, stream biota are inactive and an increase of nitrate concentrations in stream sediments can occur. Dry sediments collected from both prairie and gallery forest reaches of Kings Creek released nitrate when submersed in artificial channels; however, within 12 h nitrate concentrations decreased due to nitrate uptake by biota associated with the sediments (Hooker 1987). Thus, the high nitrate concentrations found immediately after resumption of flow in intermittent channels (e.g., Fig. 4) can potentially stimulate biotic growth.

Variation in the magnitude and frequency of storm flows influences maximum nitrate concentrations during a storm event. Storm flows can have two effects on prairie stream biota. High-magnitude storms scour and reduce biota in streams and thus reduce subsequent biotic uptake of nutrients. If a low-magnitude storm flow occurs and biota are not removed, then a storm flow can provide a pulse of nitrate and phosphate (McArthur et al. 1985) which can stimulate biotic productivity, especially during summer. In Brier Creek, a prairie-margin stream in Oklahoma, moderate increases in discharge following low-magnitude storm flows stimulate algal growth, presumably due to increased nutrient availability (Power and Stewart 1987).

Comparison with other stream ecosystems

The spatial and temporal variability in nitrogen concentrations in Kings Creek is greater than the variability found in temperate forested and desert stream ecosystems. The longitudinal pattern of riparian vegetation for first to fifth order in prairie streams is opposite to that for temperate forested streams, and allows for extensive algal growth in open channels (similar to hot desert streams). Yet, in contrast to desert streams, the inorganic nitrogen concentrations in Kings Creek are "tightly coupled" with terrestrial vegetation activity, similar to many temperate forested streams (e.g., Likens et al. 1977, Wetzel and Manny 1977, Dahm 1980). Prairie streams are similar to Southwestern desert streams; both exhibit spatially and temporally intermittent flow, unpredictable flooding, dominance of periphyton community in open channels, downstream decrease in nitrate from sources, and nutrient limitation to algal growth (Table 3, Figs. 1, 2, and 5, and Grimm et al. 1981, Fisher et al. 1982, Gurtz et al. 1982, Grimm and Fisher 1986, Mathews 1988). Prairie streams differ from desert streams because of greater seasonal variation in temperature and nitrate concentrations.

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