In situ experiments to determine limiting nutrients in some Iowa streams

by

Steven Jerold Bushong

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ABSTRACT

Four agricultural streams in central Iowa were investigated to determine if nitrogen or phosphorus were limiting the growth of attached algae. Experiments were conducted in situ using nutrient diffusing artificial substrates. Substrates consisted of sealed clay flowerpots which contained potentially limiting nutrients. The nutrients diffused across the porous clay walls and became available for the periphyton colonizing the outer wall. Treatments included: 1.Ø M KH_2PO_4, 2.5 M $NaNO_3$, Ø.5 M NH_4Cl, 1.Ø M KH_2PO_4 + Ø.5 M NH_4Cl, and a control (no nutrients). A 1.Ø M NH_4Cl treatment was used in the first experiment in place of the ammonium + phosphorus treatment. Six experiments, 7-14 days in length, were conducted between July and November, 1984. Each experiment consisted of four streams, three sites each, with one pot of each treatment per site (n=6Ø). Chemical and physical stream parameters were monitored during experiments.

Algal biomass growing on pots was determined as chlorophyll a. Phosphorus addition alone never enhanced algal growth. The low level ammonium addition significantly ($P<Ø.Ø5$) enhanced growth in the first four experiments. High level ammonium addition significantly inhibited growth. Nitrate addition enhanced growth in only one experiment.

Positive algal response to ammonium and not nitrate addition was attributed to ammonium being more energetically favorable for algal utilization. Energetic implications are discussed. The apparent tradeoff between ammonium stimulation and toxicity is discussed.

Results show that nutrients were typically not limiting in Iowa streams. However, nitrogen was found limiting in one experiment characterized by low flow and warm water temperature. Large algal mats prevalent under these conditions may be responsible for reducing nutrients to a limiting level. The importance of storm events in resetting the system is discussed. Water temperature is an important factor in controlling algal biomass accumulation ($R=0.78$; $P=0.0001$).

INTRODUCTION

Agricultural activities play a predominant role in shaping the structure and function of Iowa's aquatic ecosystems. Virtually 85% of Iowa's land area is devoted to agriculture; 61% rowcrop farming (i.e., corn and soybeans) and 24% pasture, hay and small grains (Iowa Dept. Water Air and Waste Management, 1984). Runoff from agricultural activities such as row cropping with attendent soil disturbance and fertilizer use as well as wastes from livestock production is a chronic nonpoint source of nutrient loading to most of Iowa's 29,000 kms of streams. The role of agriculture in nutrient loading has been well documented in many areas with correlations between land use and nutrient levels in streams (Neilsen et al., 1982; Omernik, 1977; Hill, 1978; Klepper, 1978). Recent studies in Iowa show that surface runoff and related sediment loss from corn and soybean fields results in the annual loss of 427,000 tons of nitrogen and 10,000 tons of phosphorus (Iowa Dept. Water Air and Waste Management, 1984). Heavy fertilizer applications associated with agriculture can increase the leaching of soluble nitrates into the groundwater, thus becoming another important pathway for nutrient loading. Burwell et al. (1976), studying an Iowa stream with drainage tile input, found subsurface discharge accounted for 84 to 95% of the total average annual soluble

nitrogen discharged in stream flow. Farmland streams, therefore, are very rich in the essential nutrients needed for plant growth, particularly nitrogen and phosphorus.

The productivity of any aquatic system is determined to some degree by the availability of nutrients. Based on this relationship, many researchers have used phosphorus or nitrogen concentrations to predict phytoplankton biomass or productivity (Bachmann and Jones, 1974; Dillon and Rigler, 1974; Jones and Bachmann, 1976; Schindler, 1978; Schinder et al., 1978; Canfield and Bachmann, 1981; Prepas and Trew, 1983). In Iowa waters, the high level of nutrient loading can stimulate excessive algal growth and accelerate the eutrophication process. Cultural eutrophication can lead to a basic deterioration of water quality. Large algal blooms decrease the aesthetic and recreational value of aquatic systems and can hamper industrial usage of the water. Respiration by the algae may also deplete oxygen levels causing fish kills or avoidance of the area. In addition, excessive nutrient loading can cause an increase in bluegreen algae. Some strains of bluegreens are toxic to mammals which could be a problem for cattle using the stream as a water source (Collins, 1978).

Managerial policies to control algal blooms are often based on regulating nutrient sources since nutrients are one of the few essential factors for algal growth that is

amendable by humans. Much research has, therefore, been focused on nutrients as limiting elements of primary production. This is often thought of in terms of Liebig's law of the minimum; the single requirement in shortest supply relative to its need will have the greatest, if not exclusive effect of limiting further growth. If this limiting factor is added, phosphorus for example, then the population should increase to some higher asymptotic value where a different factor limits further growth. A variety of nutrients such as carbon, silica, vitamins, and trace elements have been implicated as potentially limiting in some ecosystems but nitrogen and phosphorus are generally considered the most important to freshwater ecosystems (Vollenweider, 1971; Vallentyne, 1974; Smith, 1982).

Until more recently, most nutrient limitation studies examined lakes, oceans, or unialgal laboratory cultures. Because of this, our understanding of nutrient limitation in streams has been comparatively limited. Nutrient studies in streams are complicated by the dynamic nature of streams. Nutrient concentrations can vary temporally (Manny and Wetzel, 1973), and spatially (Marcus, 1980; Fisher et al., 1982; Hill, 1982; Sebetich et al., 1984). Storm events can result in scouring of attached algae and decreasing light penetration because of elevated turbidity. A number of techniques have been used to examine nutrient limitation in streams. Some

researchers have inferred limitation by looking at nutrient levels or ratios in streams (Thut and Haydu, 1971; Fredriksen, 1971; Goldman, 1972; Crawford, 1979; Grimm et al., 1981). A somewhat more direct method is to extract and analyze algal cell content to determine ratios of critical nutrients (Goldman, 1972; Wong and Clark, 1976). Other researchers have attempted to determine limiting nutrients by correlating some measurement of productivity with nutrient concentration (Kilkus et al., 1975; Moore, 1977; Crawford, 1979; Marcus 1980; Schanz and Juon, 1983; Perrin et al., 1984). Laboratory nutrient bioassays using stream water samples are a common experimental approach for determining limiting nutrients (LaPerriere, 1971; Goldman, 1972; Crawford, 1979; Burkholder-Crecco and Bachmann, 1979). A drawback of the laboratory bioassay is that it is a static test for a lotic environment. These methods all have the advantage of being relatively easy and inexpensive to conduct, yet they may oversimplify the stream environment by not taking into consideration the dynamic nature of streams or the recent chemical and physial history of the streams. They, therefore, tell us only what nutrient might potentially have been limiting at the time the water or algal sample was taken. Recently, methods have been used that more realistically represent the environment; they may, however, be more expensive and difficult to replicate. Probably the most

convincing demonstration of nutrient limitation is studies that enrich whole stream segments (Elwood et al., 1981; Newbold et al., 1983). However, widespread or routine application of this approach may often not be practical. Artificial stream channels have been used successfully to test nutrient limitation (Stockner and Shortreed, 1978; Triska et al., 1983). Though this approach is somewhat artificial, it does have the advantage of simulating a stream while maintaining control over some of the variables. Peterson et al. (1983) modified this technique by suspending artificial channels in a stream. Another in situ method devisd by Pringle and Bowers (1984) consisted of using an enriched substratum for periphytic colonization.

Most general principles in stream ecology, including those involving nutrient dynamics, are based on the study of undisturbed forested ecosystems. Comparatively little information has been generated on streams impacted by agricultural nonpoint pollution even though many major rivers in this country are affected. Agricultural streams in Iowa are characterized by high nutrient levels similar to other agricultural regions. In a survey of 14 relatively large rivers in central Iowa, Kilkus et al. (1975) found averages of Ø.16 mg/l ortho-P, Ø.54 mg/l ammonia-N, and 1.75 mg/l nitrate-N, although concentrations can vary drastically. Values as high as 45 mg/l nitrate-N and 3 mg/l ortho-P

(Baumann and Kelman, 1970) and as low as 0 mg/l for nitrate-N and ortho-P (LaPerriere, 1971) have been reported in Iowa rivers. With such high levels of nutrients it seems unlikely that nutrients limit production. Previous laboratory bioassays examining suspended algae in Iowa streams support this hypothesis (LaPerriere, 1971; Burkholder-Crecco and Bachmann, 1979). These studies, however, examined only suspended algae; no work has been done on the periphyton of Iowa farmland streams. Kortge (1984) demonstrated that most biological activity in a small Iowa stream was associated with the attached algae and not the suspended algae. The major purpose of this study will, therefore, be to test for nutrient limitation of the periphyton in Iowa streams.

This study modifies a relatively new technique first used to study nutrient limitation of periphyton in lakes (Fairchild and Lowe, 1984; Fairchild et al., 1985) and applies it to streams. The technique employs substrates (flower pots) for algal colonization which leach a potentially limiting nutrient. Flower pots were first used as a vehicle to dispense nutrients and enrich marine environments (Chapmann and Craigie, 1977; Harlin and Thorne-Miller, 1981). The nutrients are sealed within a clay flower pot. Because the clay walls are porous, the nutrients diffuse across the concentration gradient and become available for the periphyton community growing on the outside. Nutrient limitation can

then be detected by comparing algal biomass on flower pots treated with a nutrient to controls with no nutrients. If there is no significant increase of production on the treatment substrates relative to controls then there is no nutrient limitation. This approach has recently been applied to streams (Bachmann and Bushong, 1985; Tate, 1985).

The principal objective of this study is to examine the impacts of ammonium, nitrate, and phosphorus additions on the attached algal communities of eutrophic farmland streams in central Iowa, and to determine if these streams are nutrient limited.

METHODS AND MATERIALS

Study site locations

Experiments were conducted on four streams near Ames, Iowa. The streams appear representative of other agricultural streams in central Iowa with respect to gradient and watershed land use. General site locations are depicted in Figure 1. Big Creek is a small agricultural stream in Boone County and part of the Des Moines River drainage basin. Sites were located near the headwaters (Sec. 13, T83N, R26W) just south of U.S. highway 30. The creek is typically 2-3 m wide and shallow with sand, gravel or silt substrate. The watershed is dominated by row crops (approx. 84%) and some livestock production. The drainage area upstream from the sites is 18.3 km^2. Keigley Creek is a meandering agricultural stream slightly larger than Big Creek. Sites were located north of the E23 bridge (Sec. 7, T84N, R23W) about 1 km upstream from its convergence with the Skunk River. The creek is generally 3-5 m wide at base flow with mostly sand and gravel bottom. Rowcrops constitute 88% of Keigley Creek's 121.7 km^2 of drainage area upstream from the sites. Squaw Creek is a tributary of the Skunk River. Study sites were located between the 13th St. and Stange Rd. bridges (Sec. 3, T83N, R24W) with an upstream drainage area of 530 km^2. Squaw

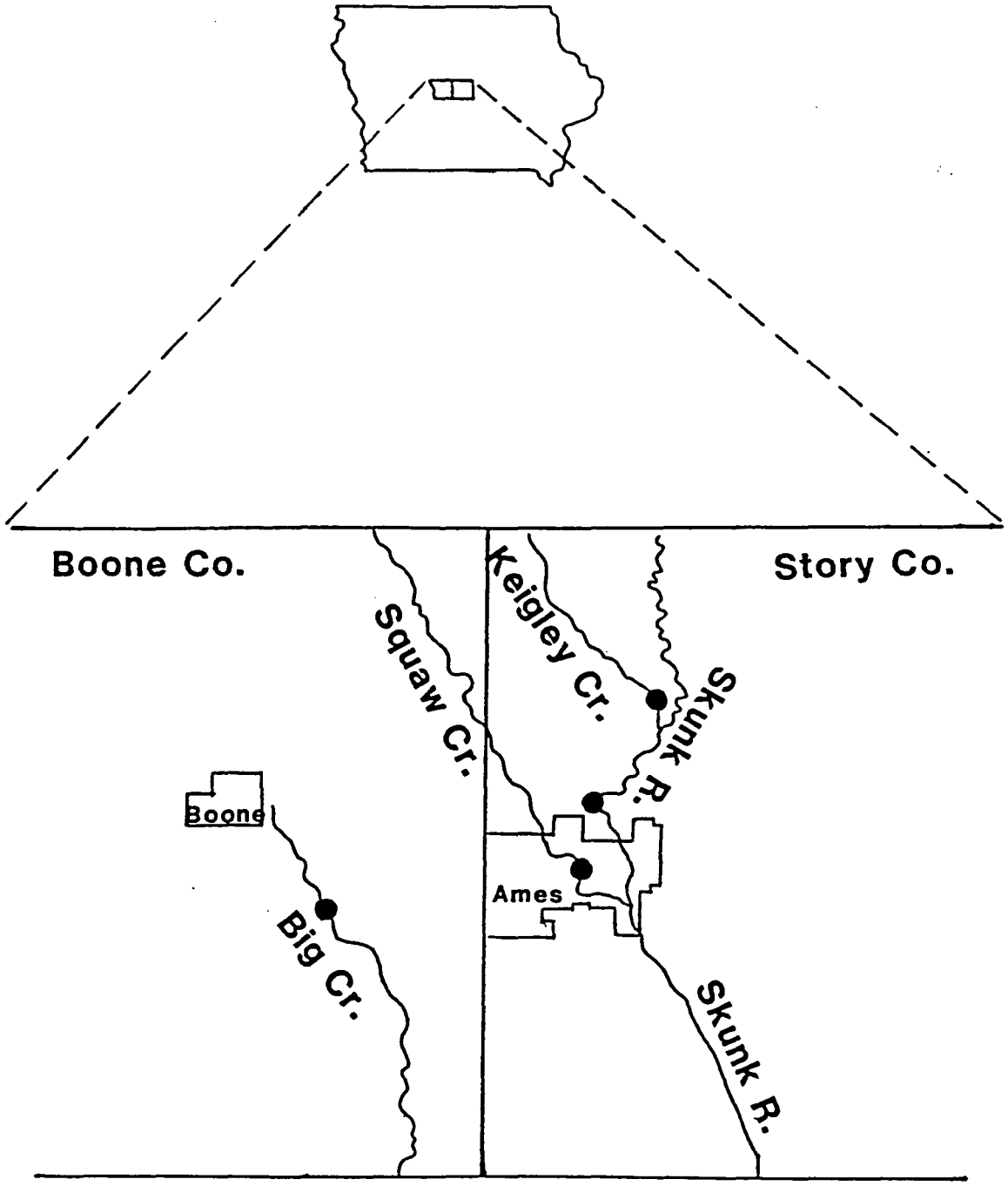

FIGURE 1. Study site locations on four Central Iowa streams

Creek is 8-12 m wide and characterized by shifting sand substrate and gravel. South Skunk River is the largest of the four streams being aproximately 12-15 m wide. It is characterized by a mud, sand or gravel floor punctuated by rocky riffles. Sampling sites were located just south of the Skunk Hollow access point (Sec. 23, T84N, R24W) about 1 km below a Geological Survey Gaging Station. The drainage area upstream is approximately 819 km^2. Like the other streams, the South Skunk River's watershed is dominated by agricultural activities but riparian forest still exists along much of the stream. The Story City Sewage Treatment Plant discharges into the South Skunk River about 10 km upstream from the sampling sites.

Substrate preparation

The preparation of flower pot substrates for use in the streams was similar to the process described by Fairchild and Lowe (1984) and Fairchild et al. (1985). Unglazed "3 inch" clay flower pots (actual size: outside diameter=8.0 cm.; height=8.8 cm.) were soaked in distilled water for several days to condition the pots and leach out any potential contaminants associated with their manufacture. A size 00 cork stopper was then inserted into the small aperture on the

bottom and marked with a color coded tag to identify the treatment the pot would receive. The stopper was then sealed from the outside with 100% silicone sealant. The silicone was spread out evenly from the cork to completely cover the circular area on the pot bottom. This ensured that all pots had an equal surface area sealed by the silicone and also reduced the surface area for nutrient leaching. This may prolong a higher leaching rate from the unsealed surface area as indicated in laboratory studies (unpublished data). After the silicone was allowed to cure, each pot was placed inside another pot, large opening up, which functioned as a holding container. A hot 4% agar solution (270-275 mls of Bacto Agar) either spiked with a potentially limiting nutrient (treatment) or without nutrients (control) was poured into each pot. After the agar solidified, a standard 100x15 mm plastic petri dish was fitted over the large opening and sealed with silicone. The remaining 125 cm^2 of unsealed surface area between the enlarged lip and the sealed bottom of the pot was the area sampled for periphyton in the experiments.

Treatments and diffusion rates

Each experiment consisted of five different substrate types, one control and four nutrient treatments (Table 1).

Table 1. Treatments and Corresponding Nutrient Concentrations

Treatment	Ingredients
Control	4% agar solution
Nitrate (N)	2.5 M $NaNO_3$ + agar
Ammonium (Am)	Ø.5 M NH_4Cl + agar
Phosphorus (P)	1.Ø M KH_2PO_4 + agar
Ammonium + Phosphorus (AmP) (Experiments 2-6)	Ø.5 M NH_4Cl + 1.Ø M KH_2PO_4 + agar
Ammonium (Amx) (Experiment 1 only)	1.Ø M NH_4Cl + agar

The first experiment included a comparison of two ammonium treatments of different concentrations ("Amx" and "Am"). All following experiments used the lower ammonium concentration, treatment "Am", and an ammonium plus phosphorus treatment combination ("AmP"). The nutrient concentrations were established in a series of laboratory experiments where agar densities, nutrient concentrations, and pot manufacturing techniques were varied. Because Iowa streams are generally rich in nutrients, treatments were chosen that exhibited relatively prolonged high leaching rates.

Laboratory experiments on leaching rates were conducted by placing a prepared flower pot into a small acid-washed aquarium (25 cm x 16cm x 18 cm) with 3.5 liters of distilled

water. A mild current was generated in the aquarium by bubbling air and the top of the aquarium was loosely sealed with foil. Every 24 hours the pot was removed and placed in an identical aquarium. Water samples for the specific treatment ion were taken at this time on days 1, 2, 3, 5, 7, 9, 11, and 14. In addition, nitrate concentrations were periodically measured for ammonium treatments and vice versa. All three ions (ammonium, nitrate, and phosphorus) were sampled in controls. Samples were placed in acid-washed plastic bottles and immediately frozen. Ammonia-N and Nitrate-N were analyzed with the Orion Ammonia Probe Model 95-12 and Orion Nitrate Probe Model 930700, respectively. Total phosphorus was analyzed using the method described by Murphy and Riley (1962) after a persulfate oxidation (Menzel and Corwin, 1965). A DU-2 spectrophotometer was used to measure absorbence.

In situ experimental design

Three sites were chosen for each of four streams. The sites within a stream were chosen to be as similar as possible with respect to current velocity, water depth, stream orientation and riparian shading (all sites had little to no shading). Sites were up to 100 m apart in the small streams

and as little as 40 m apart in the larger streams. Each stream site consisted of two 1.5 m t-shape fence posts pounded into the stream bed to hold a 1.5 m, 2x14 cm wood board in place perpendicular to the current. Each post fit through a t-shaped hole near the ends of the board so that the board could be slid up or down on the posts. Five pots, one of each treatment, were secured to each board with a rope threaded through springs attached to the board with eyescrews (Fig. 2). The pots were placed with the petri dish face down on the board. The rope was laid on top of the sealed pot surface in front of the cork stopper with tension pressure applied by the springs. A small, 7-cm wooden block (2.5x2.5 cm) was placed on the downstream side of each pot to keep the pot from sliding from underneath the rope. The pots were placed randomly on each board with order decided by the roll of dice; thus, each stream had a randomized block design. Pots were spaced 15 cm apart (measured from the outside edge of the pots) on the board so that current disturbances by one pot did not affect adjacent pots. Later in the season two additional posts were placed at each site, one post 1-2 meters in front of the board and the other 1-2 meters behind. A rope tied around the four posts effectively kept out disturbances such as cattle, horses, and canoes. The posts maintained a permanent site in the stream while the height of the board

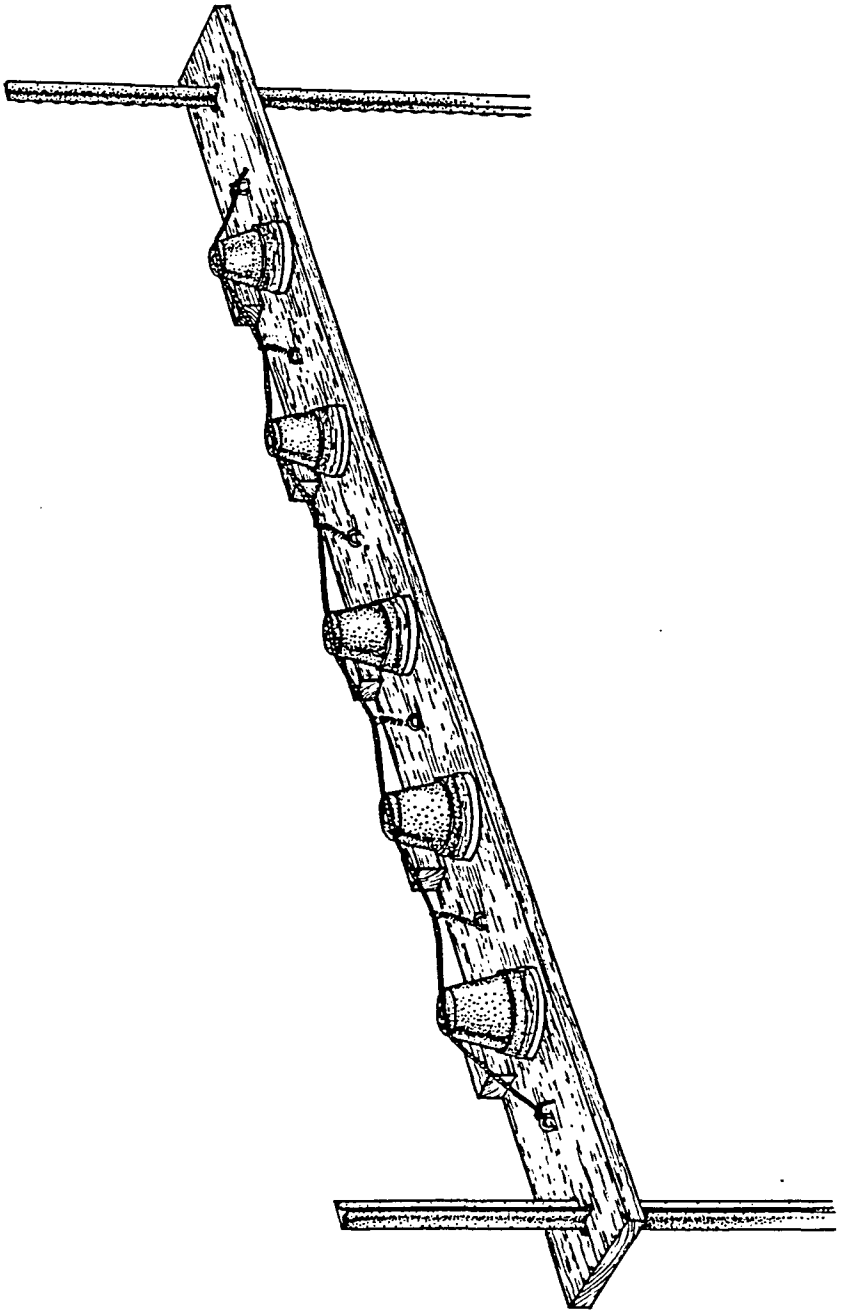

FIGURE 2. Diagram of board design with flower pots in place. Each board constituted a site with three sites per stream

was adjusted up or down the posts to accommodate change in stream stage. Pots were easily removed or new ones added by lifting the rope and sliding the pots in or out.

In situ field experiments

Experiments were initiated in May, 1984 with the last experiment completed in late November, 1984. Experiments were 7-14 days with experiment length dependent upon growth rates of algae. Typically shorter experiments were conducted in warmer months and longer experiments in colder months. Thick algal mats on the substrates were avoided since they would more likely experience sloughing which could obscure results. There was also a concern that the further the periphyton grew away from the substrate, the less impact the nutrient leaching would have. Substrates were, however, left out long enough to assure enough growth for adequate sampling.

Experiments were conducted on the four streams simultaneously (n=60 observations). At the end of each experiment, the pots were removed from the board and inverted into 400-ml neoprene beakers containing 255 mls of stream water as described by Fairchild et al. (1985). Each pot was then placed into a large plastic funnel and the 125 cm^2 of surface area above the enlarged lip and below the sealed

circular top was scraped with a firm bristle toothbrush and knife blade to remove the attached algae. The pot was rinsed with stream water and the scrapings, rinse water and water from the 400-ml beaker were collected in a 500-ml neoprene bottle. Bottles were immediately placed in the dark on ice for transport. All pots were shaded during sampling to avoid exposure to direct sunlight.

In the laboratory, algal samples were poured into 1000-ml graduated cylinders. Sample were thoroughly mixed using a "periphyton plunger" (a small plastic funnel attached to a glass rod) which fits loosely in the cylinder. The plunger is moved rapidly up and down till the sample is evenly suspended in the water column. Two subsamples of known amounts were poured off from each sample; one preserved with Lugol's iodine solution (1 ml/100 mls), the second filtered through a 4.25 cm Whatman GF/C glass fiber filter and frozen in a container with desiccant for later chlorophyll a analysis.

Pigment extraction was carried out with dimethyl sulfoxide and 90% acetone (8 mls of 50:50 mixture), (Shoaf and Lium, 1976). Samples were soaked for 20 hours, then shaken and centrifuged (Jones, School of Forestry, Fisheries and Wildlife, U. of Missouri, Pers. Communication). Optical densities were determined on a Beckman DU-2 spectrophotometer using the trichromatic method and equations of Strickland and

Parsons (1968) with correction for phaeopigments (Wetzel and Likens, 1979). Chlorophyll a values were expressed as mg/m^2 of substrate surface.

Measurements and analyses of stream water

Various chemical and physical parameters were monitored in each stream during the experiments. Measurements and water samples were taken before noon on the first day, approximately the middle day, and the last day of each experiment. Current velocity was measured at the middle of each board by averaging the time it took for a pulse of fluorescent dye placed below the water surface to travel 1 m. Water depth and pot depth were also recorded for each site. Discharge was determined in the two smaller streams (Big Creek and Keigley Creek) by measuring current velocity with dye in small stream sections of known width and depth along a transect. The summation of each segment's discharge equals the total stream's discharge. For the Skunk River and Squaw Creek, discharge data were obtained from Geological Survey Gaging Stations near the sampling sites. Water and air temperature were measured at each stream with a mercury laboratory thermometer and pH was measured on location with an Orion pH Probe Model 407A. Turbidity (JTU) was measured with a Hach Laboratory

Turbidimeter Model 2100 and specific conductance (micromhos/cm) with a Hach Conductivity Meter Model 2511. Duplicate water samples for nitrate and ammonia analyses were taken in acid-washed polyethelene bottles just above the most upsteam site at each stream. Samples were placed immediately on ice with nitrate samples being first acidified with concentrated H_2SO_4 (1 ml/l). Duplicate 50-ml samples were taken for total phosphorus in acid-washed 125-ml Erlenmeyer flasks. These were placed in the cooler for transport. Periodically, water samples were taken just above the most downstream site to compare with samples taken from above the upstream site. Ammonia and nitrate samples were immediately filtered upon returning to the lab with 4.25 cm Whatman GF/C glass fiber filters. Ammonia analyses were conducted immediately after filtering using the colorimetric phenate method (APHA, 1976) and the Beckman DU-2 spectrophotometer to measure absorbance. Nitrate-nitrite analyses were conducted using cadmium reduction columns as described by Wetzel and Likens (1979) after samples were first neutralized with NaOH. Total phosphorus samples were stored at 8-12 C and later analyzed using the method described for the laboratory leaching rate study. In addition to sampling, each site was checked every other day to adjust boards to stream stage. Boards were maintained at equal depths between sites with the flower pots typically 12-15 cm below the water

surface though this varied with flow. Any debris, like twigs or leaves, entangled on the boards or rope was removed at this time.

RESULTS

Laboratory experiments on diffusion rates

Laboratory experiments lasted 14 days. During this time water temperature ranged from 20 C to 22 C. Data are presented in mgs of nutrient leached per pot per day. Each value is an average from two experiments.

Both the phosphorus "P" and ammonium + phosphorus "AmP" treatments demonstrated similar trends in phosphorus leaching rates (Fig. 3). After an initial pulse on day 1 there was a sharp drop in the phosphorus diffusion rate. This was followed by an increase in phosphorus leaching throughout the experiment until after day 11 when the leaching rate started to decline. Though both treatments contained equal concentrations of phosphorus, the amount of phosphorus leached out of the "AmP" treatment was generally less than the "P" treatment. At the end of day 14, 77% and 83% of the original phosphorus concentration for "P" and "AmP" respectively, remained in the pots.

The nitrogen leaching rate from the ammonium treatment "Am" declined only slightly in 14 days (Fig. 4). Treatment "AmP" which contained the same concentration of ammonium had a slower leaching rate initially but the difference was negligible after five days. Treatment "Amx", with double

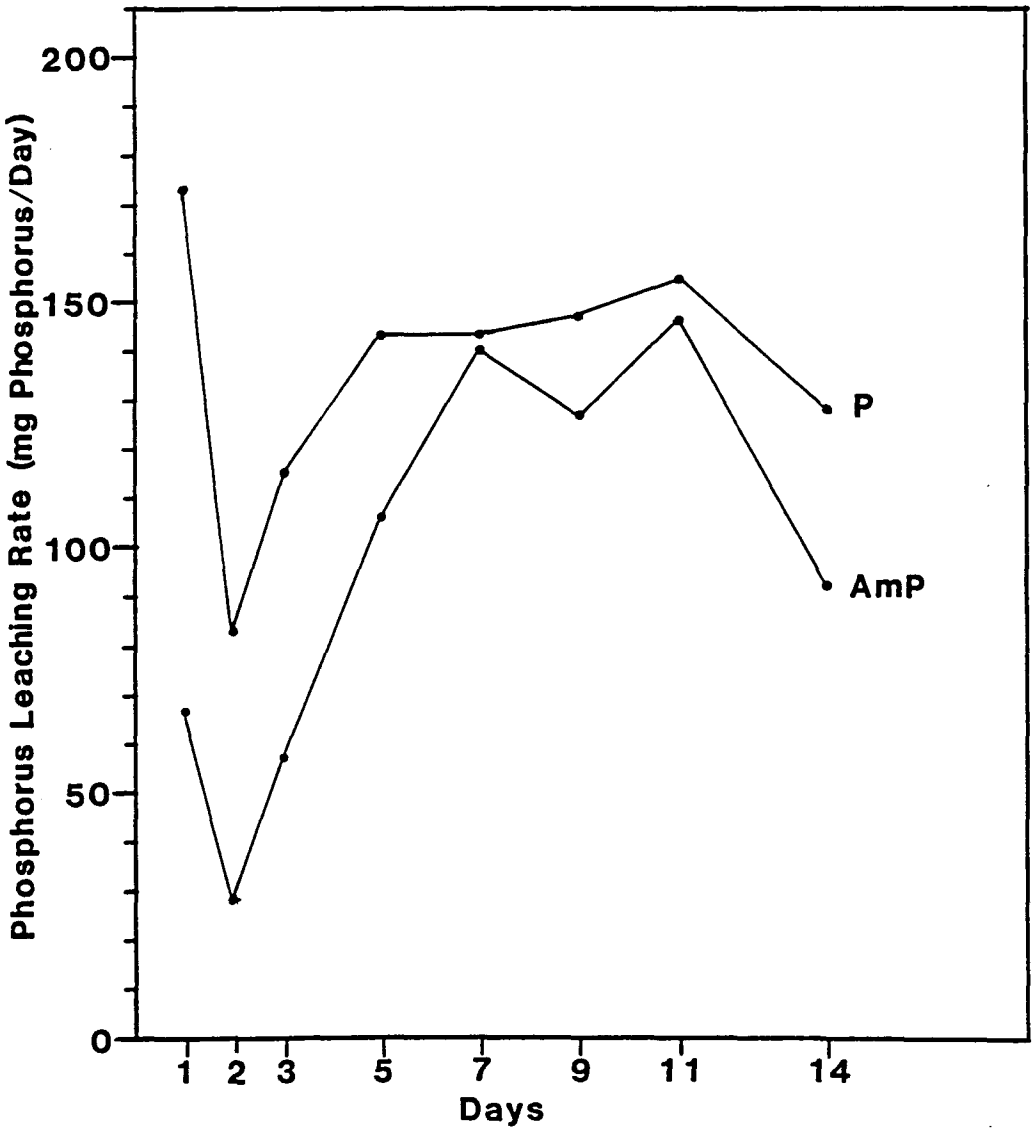

FIGURE 3. Phosphorus leaching rates (mg P/day/pot). Each value is an average of two experiments. ("P"= Phosphorus treatment, "AmP=Ammonium + Phosphorus treatment)

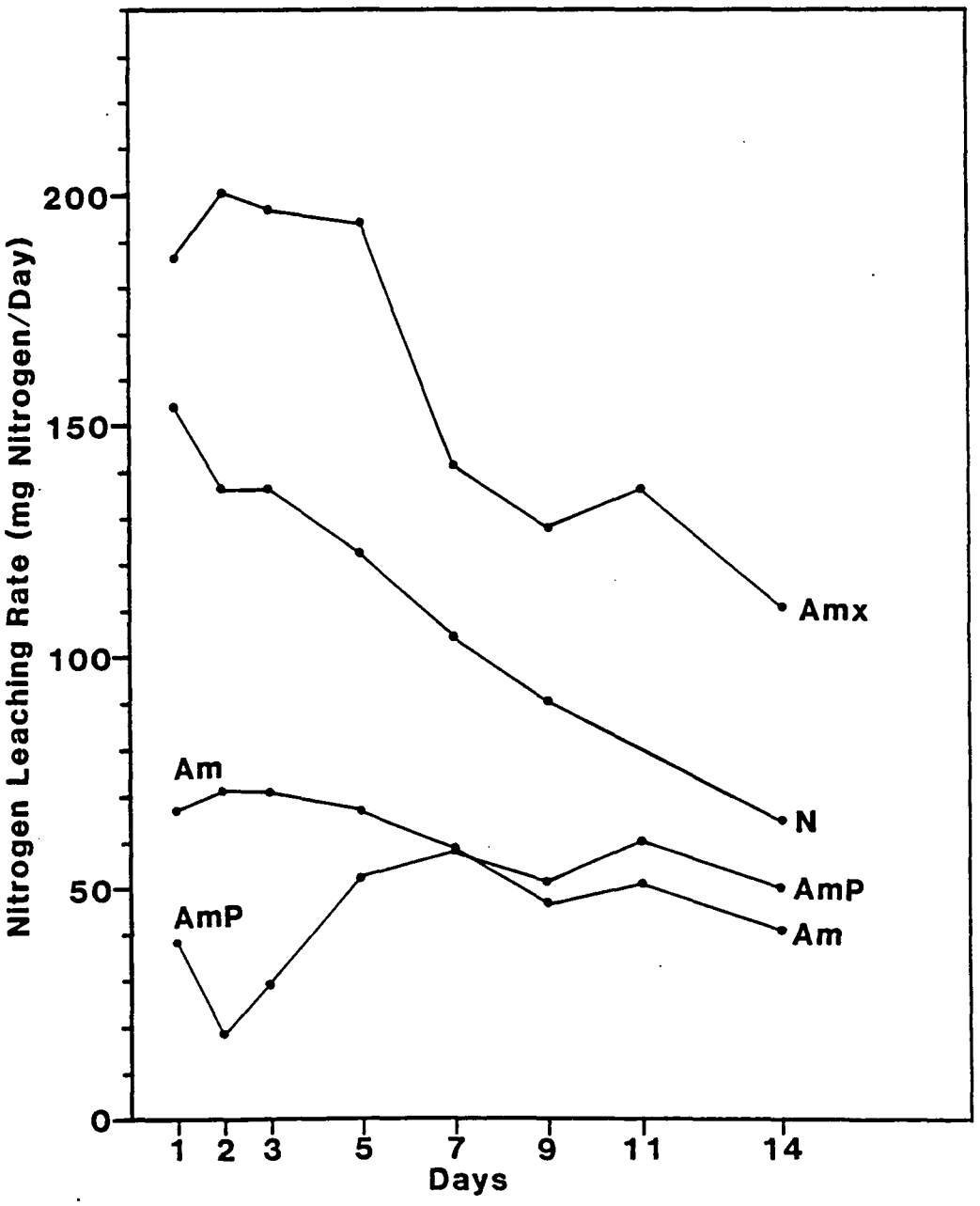

FIGURE 4. Nitrogen leaching rates (mg N/day/pot). Each value is an average of two experiments. ("Am"= Ammonium treatment (low level conc.), "Amx"= Ammonium treatment (high level conc.), "N"=Nitrate treatment)

the ammonium, had a leaching rate over twice that of treatments "Am" and "AmP" but the rate of decline was much greater. The percent of the original nitrogen concentration remaining in the pots after 14 days was 58%, 64% and 43% for "Am", "AmP", and "Amx" respectively. The nitrate containing treatment "N" demonstrated a steady linear decrease in its leaching rate yet still contained 84% of the original nitrogen concentration after 14 days.

The water tested from the ammonium treatments contained no nitrates-nitrites and no ammonium was present in the "N" treatment water. No nitrogen and only trace amounts of phosphorus were measured leaching from control substrates.

In situ stream experiments

Heavy rains in an extraordinarily wet spring and early summer severely hampered experiments conducted between May and mid-July, 1984. In many instances, water levels were too high to allow sites to be visited and prolonged flooding with associated scouring destroyed experiments. Some data were obtained from an experiment between July 16 and July 30 but since many substrates were lost the results were used only for preliminary analyses. The first experiment conducted without severe flooding was initiated July 31 and will henceforth be

considered experiment #1. Five successive experiments followed with experiment #6 ending on Nov. 27 (Table 2).

TABLE 2. Starting and ending dates of the six field experiments

Experiment #1	July 31-Aug. 10
Experiment #2	Sept. 6-13
Experiment #3	Sept. 20-27
Experiment #4	Oct. 4-16
Experiment #5	Oct. 23-Nov. 6
Experiment #6	Nov. 13-27

Between experiment #1 ending August 10th, and experiment #2 beginning September 6th, water levels dropped dramatically with Keigley Creek becoming dry for several days between the experiments. After experiment #2, flows remained low but increased slightly until the last two experiments where flows increased more dramatically. Trends in discharge for each stream are depicted in Figure 5. Though the streams have very different levels of discharge, they all generally fluctuate in a similar manner.

Heavy thunderstorms caused some problems if stream parameters were measured shortly thereafter. Since parameters were measured only three times during an experiment, the excessively high turbidity, discharge and nutrient measurements present immediately following a storm would not be characteristic of the experimental time period,

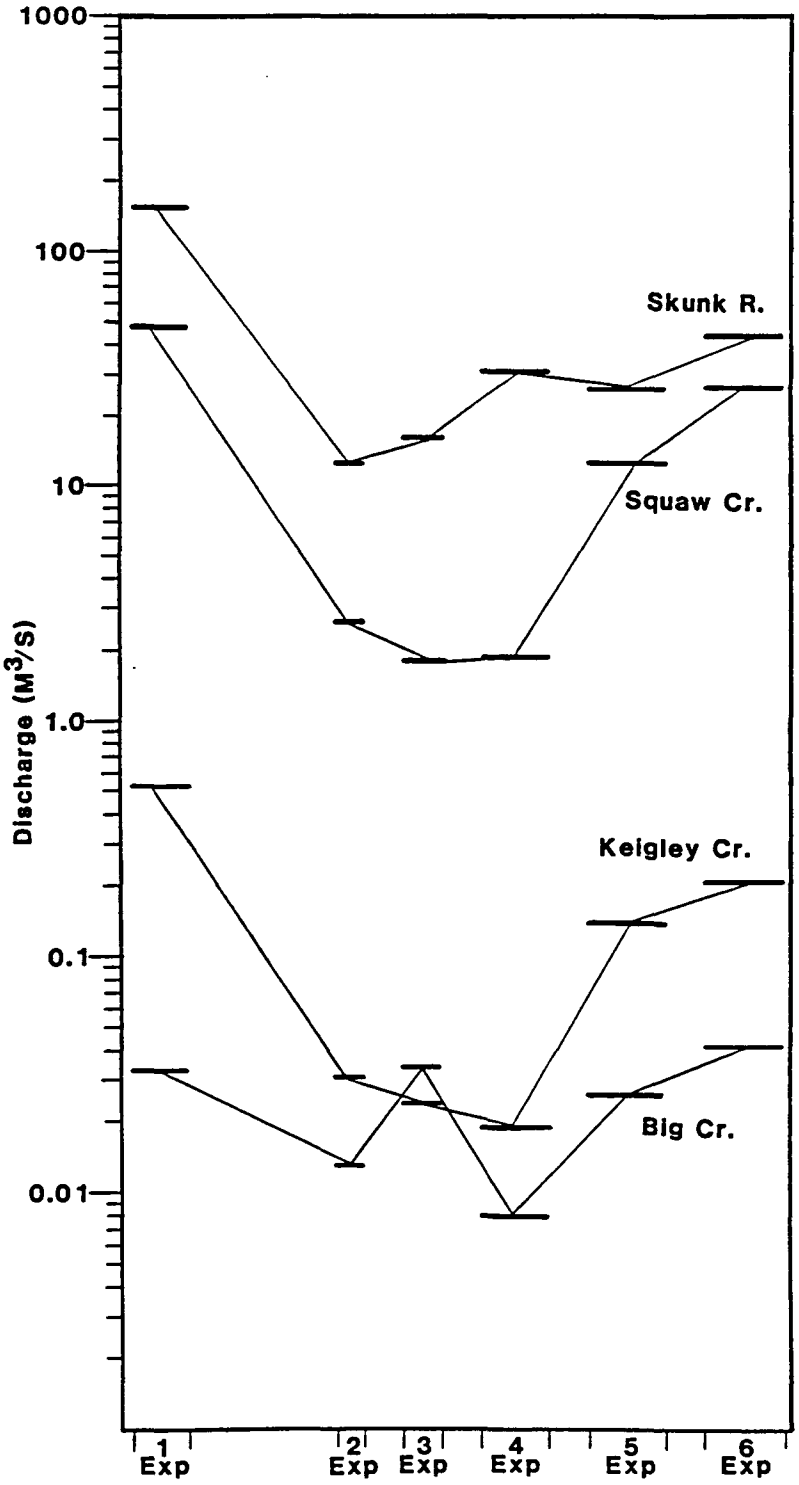

FIGURE 5. Mean discharge (M^3/S) values compared between streams. Each value is an average over three sampling dates during an experiment

especially when these elevated levels are short-lived. Only in two instances was the effect of including such values into the mean considered a gross misrepresentation and therefore deleted. One case was in Squaw Creek, experiment #3, when an extraordinarily large discharge was measured at the half-way point of the experiment. Data from the Geological gaging station on the river showed that water levels returned to near base flow in less than 24 hours. Since flow is measured only three times in an experiment, the large value was deleted from the mean discharge for that period. The second case was the last day of experiment #4 when heavy rains that day caused discharge, turbidity, and in some cases nutrient levels to not be representative of conditions that had persisted up until that day for all streams. Mean values for measured stream variables are listed by experiment in Table 3, with a * to denote means values with some value omitted. For more detail, each individual measurement including those omitted from the means are displayed in Appendix 1. It should be noted that the storm on Oct. 16, the last day of experiment #4, became more severe as the day progressed and had a larger effect on Big Creek and Squaw Creek where some scouring of the artificial substrates is likely. Discharge in Big Creek for example rose 500 to 1,000 fold from a base flow of 0.005-0.01 m^3/s to 0.56 m^3/s in less than one-half a day. Since this increase occurred the day the substrates were pulled,

Table 3. Mean values for stream parameters averaged over three sampling periods per experiment. * signifies a value omitted from the mean. (Str=Stream, Exp= Experiment, T-H2O=Water temperature, Disch= Discharge, Total-P=Total Phosphorus, NO_3-N=nitrate + nitrite, Turb=Turbidity, Cond=Conductivity)

Str	Exp	T-H2O	Disch	Total-P	NO_3-N	NH_3-N	Turb	Cond	pH
		C	M^3/S	mg/L	mg/L	mg/L	JTU	umhos/cm	
Kg	1	23.0	0.540	0.079	7.820	0.238	7.8	592	8.3
Sk	1	23.0	105.700	0.163	7.310	0.210	7.8	592	8.0
Sq	1	27.3	47.300	0.094	6.709	0.129	6.4	548	8.2
Bg	1	22.2	0.033	0.107	7.460	0.117	7.0	669	7.6
Kg	2	17.0	0.031	0.065	0.551	0.043	8.8	458	8.0
Sk	2	16.3	12.700	0.194	1.320	0.450	16.5	650	7.9
Sq	2	18.3	2.670	0.110	0.240	0.059	10.4	518	8.1
Bg	2	15.9	0.013	0.199	0.545	0.148	13.3	505	7.6
Kg	3	12.7	0.024	0.086	0.156	0.043	12.3	492	8.0
Sk	3	14.8	16.200	0.128	0.440	0.180	10.5	437	7.8
Sq	3	13.0	*1.800	0.151	0.286	0.169	22.3	437	7.8
Bg	3	13.3	0.034	0.250	1.150	0.041	18.7	413	7.5
Kg	4	11.8	*0.019	*0.053	*0.121	0.046	*8.5	463	7.8
Sk	4	13.2	31.000	*0.166	0.400	0.160	*8.5	610	8.1
Sq	4	12.2	*1.900	*0.065	*0.150	*0.230	*7.9	443	8.0
Bg	4	12.2	*0.008	*0.118	*0.646	*0.026	*8.1	615	7.8
Kg	5	5.3	0.140	0.110	4.725	0.093	6.2	615	8.5
Sk	5	6.3	26.700	0.325	3.740	0.079	6.1	652	8.4
Sq	5	5.0	12.800	0.140	2.230	0.101	4.2	590	8.4
Bg	5	9.0	0.026	0.149	5.520	0.028	7.5	802	8.2
Kg	6	2.7	0.211	0.070	9.100	0.131	3.8	708	8.2
Sk	6	3.3	44.300	0.260	7.180	0.150	4.8	773	8.3
Sq	6	4.5	26.700	0.153	5.210	0.125	4.8	712	8.3
Bg	6	7.0	0.042	0.117	7.700	0.016	3.6	983	8.0

the large discharge and other associated parameters were not representative of the true conditions existing during the experiment.

Mean nutrient values combined for all streams during each experiment are shown in Figure 6. Generally nitrate-N concentrations follow the pattern of discharge seen in Figure 4. Total phosphorus and ammonia-N in contrast showed no obvious trends. Mean nutrient levels for individual streams during experiments are given in Table 3. All streams displayed a similar pattern in nitrate-N concentrations with Big Creek typically having higher concentrations than the other streams at periods of low discharge. South Skunk River also displayed higher than average levels. Nitrate levels in the streams were highly correlated to conductivity (R=Ø.7Ø; P=Ø.ØØØ1). When different stream sizes are accounted for by conducting four separate correlations, nitrate levels are also highly correlated with discharge (Keigley Creek, R=Ø.79; South Skunk River, R=Ø.76; Squaw Creek, R=Ø.98; Big Creek, R=Ø.73). All streams showed similar fluctuations in total phosphorus levels except for the South Skunk River which also typically had higher concentrations of total phosphorus. There appears to be no similarity in ammonia-N concentration fluctuations between streams. Big Creek was unique in that it generally had lower ammonia levels. Data from all sampling periods during each experiment are shown in Appendix 1.

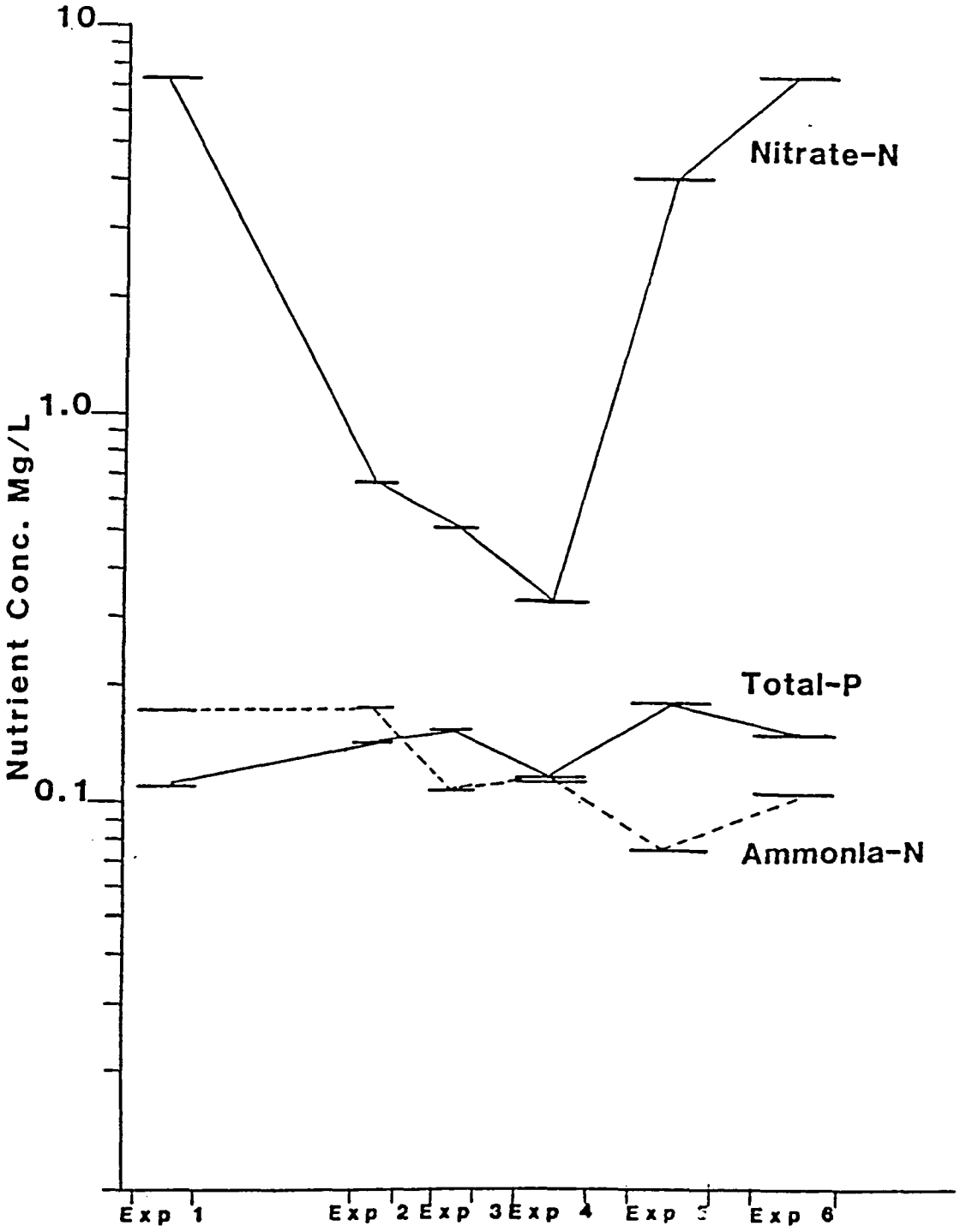

FIGURE 6. Nutrient levels for total phosphorus, nitrate-N, and ammonia-N over time. Each value is an average over the four streams with three sampling dates per experiment (n=12)

Nutrient analyses conducted periodically on water samples taken in front of the most downstream site were similar to those measured upstream of the first site.

Water temperature decreased throughout the experiments, plateauing between experiments #3 and #4 before dropping off sharply at experiments #5 and #6. The change in water temperature is depicted in Figure 7 using values averaged over all four streams. The last two experiments were characterized by winter-like conditions and periodic ice formation on all streams except Big Creek.

Of the six field experiments, three had less than the full 60 observations. Three substrates were lost from site 3 at Keigley Creek during experiment #1 due to cattle and three substrates were lost from site 3 in the South Skunk River during experiments #3 and #4, presumably due to canoes. After a post was placed in front and behind each site with a rope tied around the four posts as described earlier in methods, no further substrates were lost.

Analysis of variance was conducted after Chlorophyll *a* data were sorted by experiment. Treatments differed significantly in terms of mean chlorophyll *a* concentrations in experiment #1 ($P=0.0004$; d.f.:4,29), #2 ($P=0.01$; d.f.:4,32), #3 ($P=0.0001$; d.f.:4,29), and #4 ($P=0.0001$; d.f.:4,29). Experiments #5 ($P=0.34$; d.f.:4,32) and #6 ($P=0.86$; d.f.:4,32) in contrast demonstrated no significant

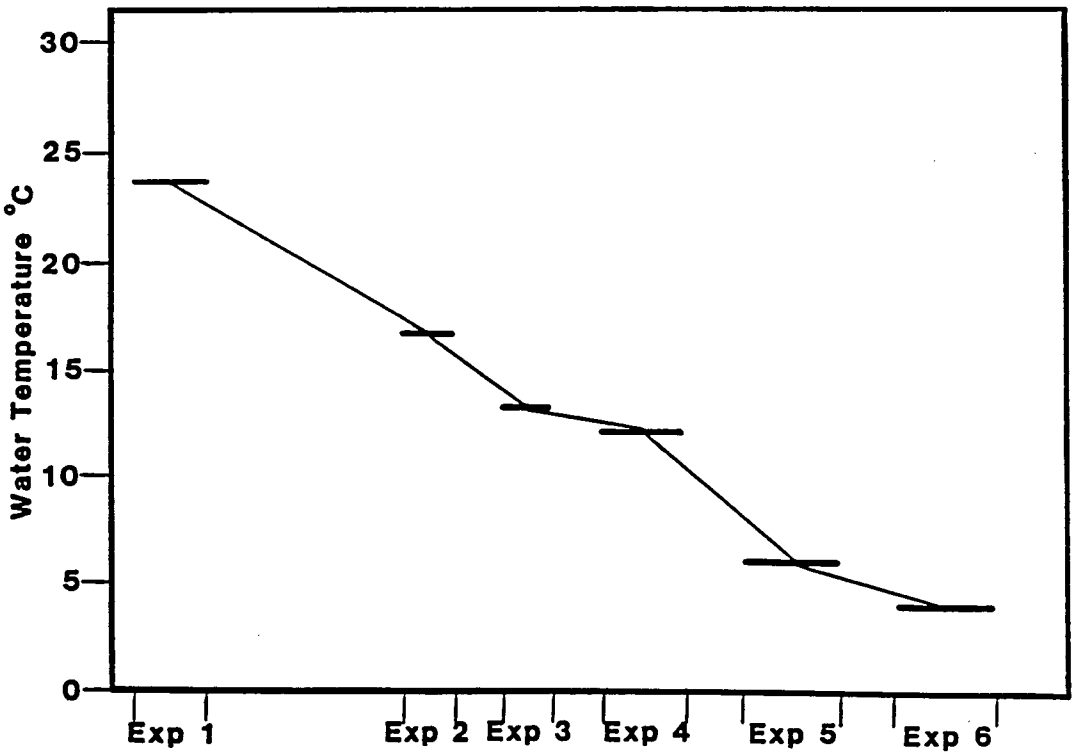

FIGURE 7. Water temperature over time. Each value is an average over the four streams with three sampling dates per experiment (n=12)

differences among treatment chlorophyll a values. Figure 8 graphically depicts the mean chlorophyll concentrations (n=12) for each treatment during the six experiments. The letter above each bar denotes significance as determined by the least significant difference test (LSD) with alpha=0.05. Control (C) and Phosphorus (P) treatments were never significantly different. The ammonium treatment (Am) had significantly higher chlorophyll a values than the control in experiments #1-4 while nitrate (N) demonstrated significantly higher values in experiment #4 only. The "Amx" treatment, applied only in experiment #1 in place of "AmP", had significantly lower chlorophyll values than the control. "AmP" had significantly higher chlorophyll values than the control in experiments #3 and #4 and demonstrated a significantly greater value than the ammonium treatment in experiment #3. Experiments #5 and #6 demonstrated no treatment effects.

The analysis of variance conducted on the chlorophyll a data demonstrated significant differences between stream for each experiment (P=0.0001 for experiments #1-5 and P=0.002 for experiment #6). When all data are pooled (minus the "Amx" and "AmP" treatments since they are not present in all experiments), the stream*treatment interaction (P=0.4; d.f.:9,152) and stream*treatment*experiment interaction (P=0.15; d.f.:45,152) are not significant. This indicates

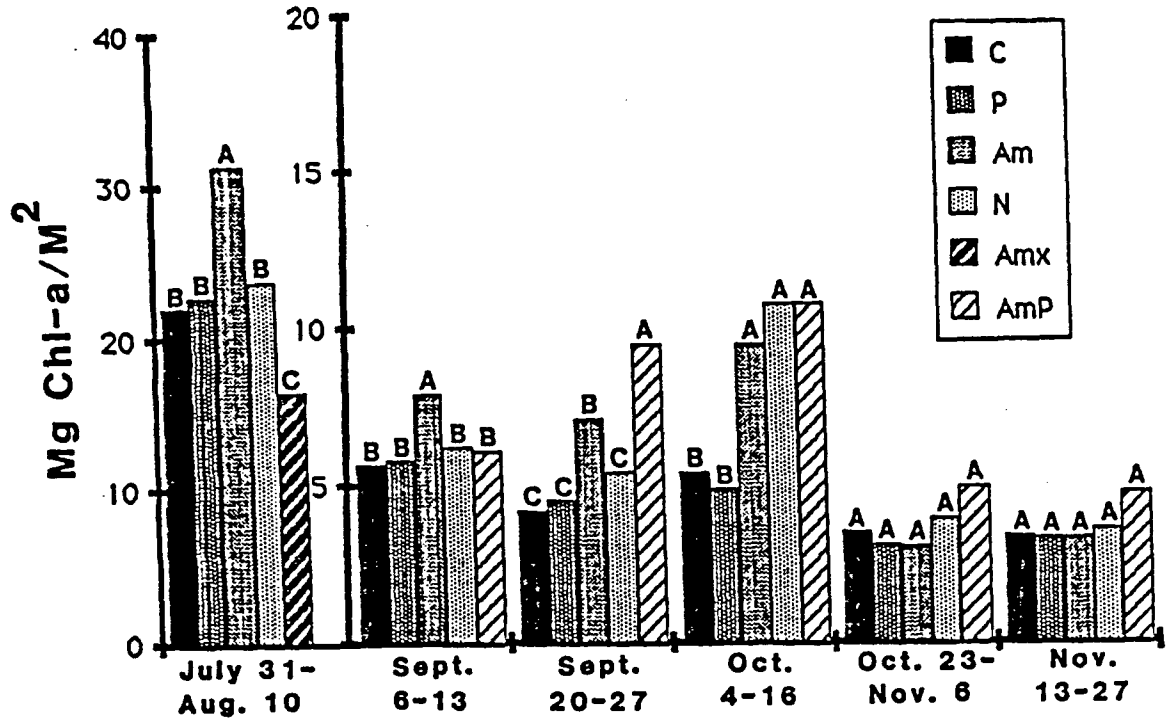

FIGURE 8. Treatment chlorophyll a values for each experiment. Values are averaged over streams (n=12). Letters above each bar denote significant differences between treatments within each experiment as determined by Least Significant Difference. (Treatments with no letters in common are significantly different). ("C"=Control pots, "P"=Phosphorus pots, "Am"=Ammonium pots (low level conc.), "Amx"=Ammonium pots (high level conc.), AmP"=Ammonium + Phosphorus)

that even though streams may have significantly different mean chlorophyll a values, the treatment effects are generally similar. Figure 9 graphically depicts the mean chlorophyll a values for treatments "C", "P", "Am" and "N" over all six experiments for each stream. South Skunk River, Squaw Creek and Keigley Creek appear to have similar treatment differences while Big Creek showed no overall treatment differences and generally higher chlorophyll values. Letters above each bar denote significance as determined by LSD ($P<0.05$). As would be expected from the findings in Figure 8, ammonium stimulated significantly higher algal growth in the three streams that demonstrated treatment differences.

Differences were examined between streams for each experiment without the effect of nutrient addition by comparing mean chlorophyll values for the control treatments. The effect of different experiment lengths was accounted for by dividing each stream's control chlorophyll a mean by the length of the experiment in days to approximate a control growth rate. The values depicted in Figure 10 show Big Creek to generally have a higher growth rate than the other streams. Overall, mean control chlorophyll levels for Big Creek were over 2 times those of Keigley Creek and between 1.5 and 2 times those of Squaw Creek and South Skunk River. Big Creek has the largest control growth rate in experiments #1-5 but only in experiments #3 and #5 is it a large difference.

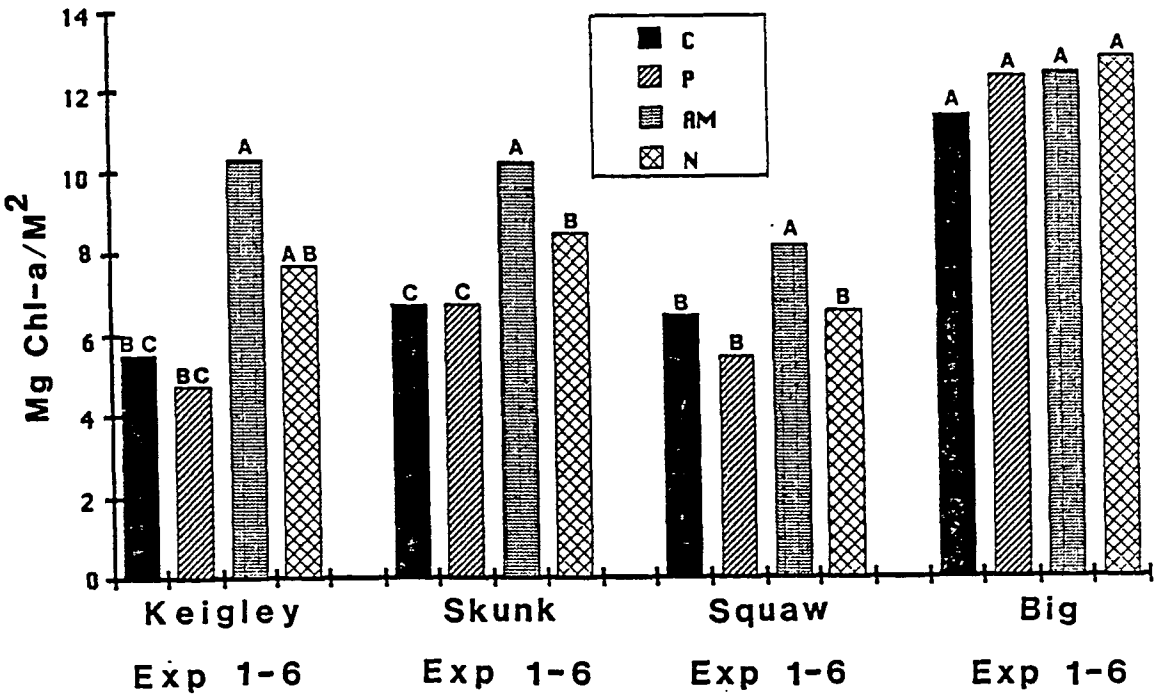

FIGURE 9. Treatment chlorophyll a values for each stream averaged over experiments #1-6. Letters above each bar denote significant differences between treatments within a stream as determined by Least Significant Difference. (Treatments with no letters in common are significantly different). ("C"=Control pots, "P"=Phosphorus pots, "Am"= Ammonium pots (low level conc.), "N"=nitrate pots)

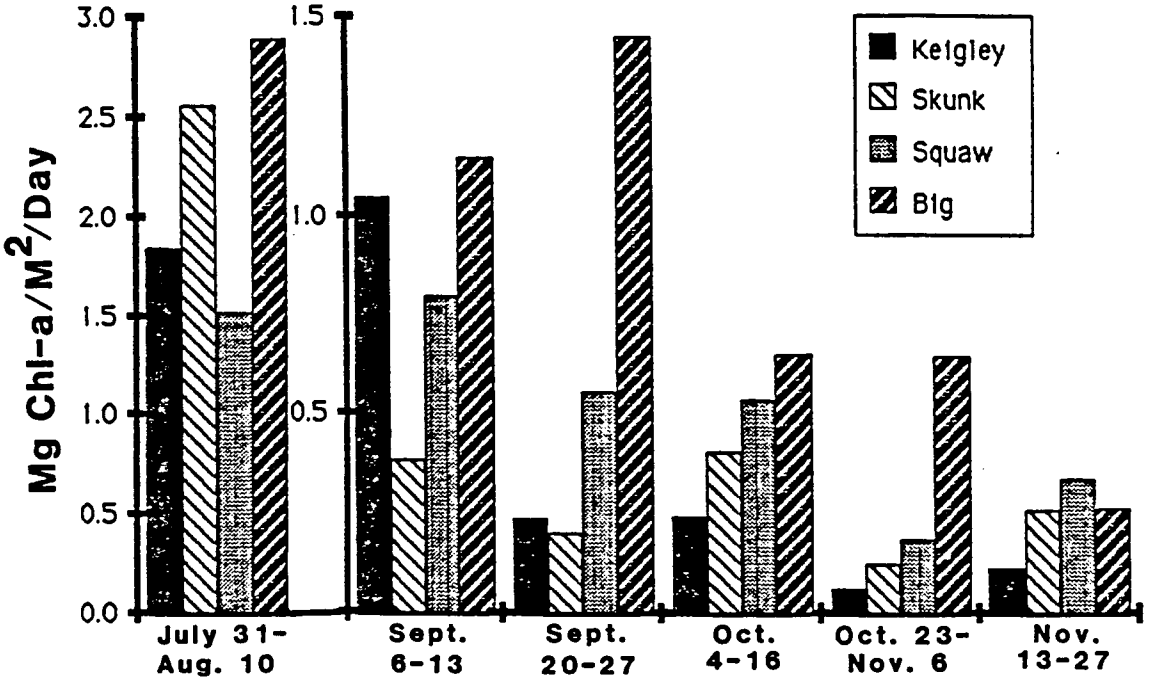

FIGURE 1Ø. Comparison of control growth rate chlorophyll a values (mg chl a/m^2/day) between streams for each experiment. Control growth rate was determined by averaging the three control substrate chlorophyll a values for each stream and dividing by the length of the experiment in days

The control growth rate for experiment #4 was most likely severely reduced for Big Creek and possibly reduced somewhat for Squaw Creek due to the heavy rains on the last day of the experiment.

The twenty-four control growth rate values were correlated with measured stream parameters. Of importance is the strong relationship between stream water temperature and stream growth rate with a correlation of R=Ø.78 (P=Ø.ØØØ1) Figure 11. No other variables were significantly correlated with control growth rate though nitrate concentrations were positively correlated R=Ø.33 (P=Ø.12), and pH negatively correlated R=-Ø.39 (P=Ø.Ø6).

Each experiment was divided into its stream components creating twenty-four stream-experiments with fifteen observations each (three observations per treatment). Treatment means for the stream-experiments are listed in Table 4 with accompanying LSD test results. Eight of the twenty-four experiments had one or more treatments with significantly higher chlorophyll a values than the control (P<Ø.Ø5). Five additional experiments showed some other significant treatment differences such as experiment #1, Keigley Creek, where "Am" was significantly greater than "Amx" but not "N", "C" or "P". Eleven stream-experiments showed no treatment effect with six occurring in the last two experiments. In the first four experiments, 15 out of the 16

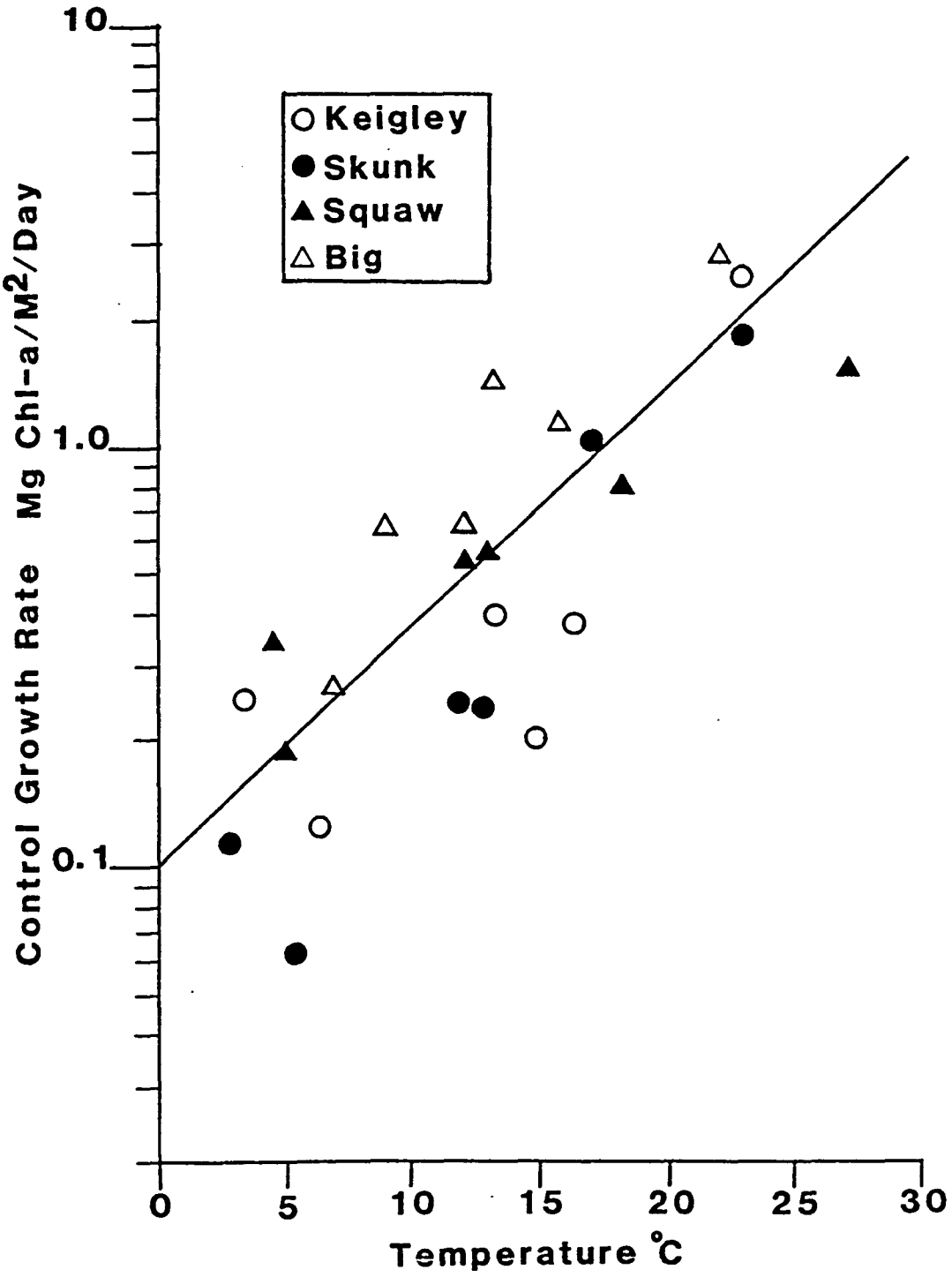

FIGURE 11. Correlation between mean stream water temperature for each experiment and the corresponding stream's mean control growth rate (n=24; R=Ø.78)

Table 4. Summary of mean chlorophyll *a* values (mg/m^2) for treatments in each stream for an experiment. Significant treatment differences as determined by LSD ($P<.05$) for each stream within an experiment and are denoted by letters. (Exp=Experiment, Str=Stream, Trt=Treatment, N=number of observations, LSD=Least Significant Difference; treatments with no letters in common are significantly different)

Exp	Str	Trt	Chl *a*	N	LSD	Exp	Str	Trt	Chl *a*	N	LSD
1	Kg	C	18.43	3	BC	4	Kg	C	2.94	3	C
1	Kg	P	12.51	2	BC	4	Kg	P	4.51	3	C
1	Kg	Am	38.07	2	AB	4	Kg	Am	15.74	3	B
1	Kg	N	17.57	2	BC	4	Kg	N	18.08	3	B
1	Kg	Amx	1.27	3	C	4	Kg	AmP	23.70	3	A
1	Sk	C	25.45	3	B	4	Sk	C	4.90	2	AB
1	Sk	P	28.65	3	B	4	Sk	P	3.80	3	B
1	Sk	Am	40.45	3	A	4	Sk	Am	7.46	3	A
1	Sk	N	32.38	3	AB	4	Sk	N	5.54	2	AB
1	Sk	Amx	26.06	3	B	4	Sk	AmP	5.14	2	AB
1	Sq	C	15.49	3	AB	4	Sq	C	6.48	3	A
1	Sq	P	11.12	3	BC	4	Sq	P	5.53	3	A
1	Sq	Am	17.70	3	A	4	Sq	Am	6.31	3	A
1	Sq	N	15.07	3	ABC	4	Sq	N	6.12	3	A
1	Sq	Amx	9.66	3	C	4	Sq	AmP	6.05	3	A
1	Bg	C	28.91	3	A	4	Bg	C	7.87	3	BC
1	Bg	P	35.40	3	A	4	Bg	P	6.41	3	C
1	Bg	Am	31.50	3	A	4	Bg	Am	9.46	3	B
1	Bg	N	27.61	3	A	4	Bg	N	12.71	3	A
1	Bg	Amx	28.63	3	A	4	Bg	Am	7.35	3	BC
2	Kg	C	7.33	3	B	5	Kg	C	0.90	3	A
2	Kg	P	9.07	3	B	5	Kg	P	1.24	3	A
2	Kg	Am	10.31	3	AB	5	Kg	Am	1.71	3	A
2	Kg	N	7.27	3	B	5	Kg	N	2.02	3	A
2	Kg	AmP	12.76	3	A	5	Kg	AmP	2.07	3	A

Table 4 (Continued)

Exp	Str	Trt	Chl a	N	LSD	Exp	Str	Trt	Chl a	N	LSD
2	Sk	C	2.68	3	A	5	Sk	C	1.77	3	B
2	Sk	P	2.83	3	A	5	Sk	P	1.84	3	B
2	Sk	Am	2.73	3	A	5	Sk	Am	1.17	3	B
2	Sk	N	2.46	3	A	5	Sk	N	3.Ø8	3	A
2	Sk	AmP	3.13	3	A	5	Sk	AmP	Ø.72	3	B
2	Sq	C	5.32	3	B	5	Sq	C	2.66	3	A
2	Sq	P	3.45	3	B	5	Sq	P	2.87	3	A
2	Sq	Am	1Ø.61	3	A	5	Sq	Am	2.Ø5	3	A
2	Sq	N	5.52	3	B	5	Sq	N	3.Ø7	3	A
2	Sq	AmP	3.65	3	B	5	Sq	AmP	4.7Ø	3	A
2	Bg	C	8.11	3	AB	5	Bg	C	9.15	3	A
2	Bg	P	8.63	3	AB	5	Bg	P	6.89	3	A
2	Bg	Am	9.1Ø	3	AB	5	Bg	Am	7.6Ø	3	A
2	Bg	N	1Ø.54	3	A	5	Bg	N	8.12	3	A
2	Bg	AmP	5.55	3	B	5	Bg	AmP	12.78	3	A
3	Kg	C	1.7Ø	3	B	6	Kg	C	1.61	3	A
3	Kg	P	1.69	3	B	6	Kg	P	1.95	3	A
3	Kg	Am	3.57	3	B	6	Kg	Am	1.93	3	A
3	Kg	N	2.64	3	B	6	Kg	N	1.76	3	A
3	Kg	AmP	15.93	3	A	6	Kg	AmP	2.ØØ	3	A
3	Sk	C	1.41	3	A	6	Sk	C	3.66	3	A
3	Sk	P	1.Ø1	2	A	6	Sk	P	Ø.17	3	B
3	Sk	Am	6.57	2	A	6	Sk	Am	1.76	3	AB
3	Sk	N	2.34	2	A	6	Sk	N	2.Ø9	3	AB
3	Sk	AmP	4.98	3	A	6	Sk	AmP	3.17	3	A
3	Sq	C	3.95	3	B	6	Sq	C	4.9Ø	3	A
3	Sq	P	5.18	3	AB	6	Sq	P	4.59	3	A
3	Sq	Am	7.43	3	A	6	Sq	Am	4.83	3	A
3	Sq	N	5.68	3	AB	6	Sq	N	3.88	3	A
3	Sq	AmP	7.69	3	A	6	Sq	AmP	1.84	3	A

Table 4 (Continued)

Exp	Str	Trt	Chl *a*	N	LSD	Exp	Str	Trt	Chl *a*	N	LSD
3	Bg	C	10.16	3	A	6	Bg	C	3.80	3	A
3	Bg	P	9.51	3	A	6	Bg	P	6.99	3	A
3	Bg	Am	11.44	3	A	6	Bg	Am	5.07	3	A
3	Bg	N	10.51	3	A	6	Bg	N	7.21	3	A
3	Bg	AmP	10.53	3	A	6	Bg	AmP	12.53	3	A

stream-experiments had larger mean ammonium chlorophyll a values than control mean values. The only exception was Squaw Creek, experiment #4, when scouring was likely. Most notable of the stream-experiments because of the magnitude of the treatment differences, are experiments #3 and #4, Keigley Creek. Figure 12 demonstrates the treatment chlorophyll value for each substrate grouped together by stream site. In experiment #3, the mean chlorophyll value for treatment "AmP" is 9.4 times the control value. In experiment #4, "AmP" is over 8 times the control while "N" and "Am" treatments are 5-6 times greater. Individual substrate chlorophyll a values for all stream-experiments are listed in Appendix 2. Table 5 presents individual parameters measured during experiments #3 and #4 in Keigley Creek for more detailed examination of the prevailing conditions. Similar data for all stream-experiments are available in Appendix 1.

Chlorophyll a levels varied between blocks within a stream. Ten of the twenty-four stream-experiments had significant differences ($P<0.05$) in mean block chlorophyll a levels as determined by 24 seperate F-tests (d.f.; 2,8). More importantly though, the block*treatment(stream) interaction is overall not significant ($P=0.49$). This indicates that although the mean chlorophyll levels may be significantly different between blocks within a stream, the relative treatment differences are typically not. An example

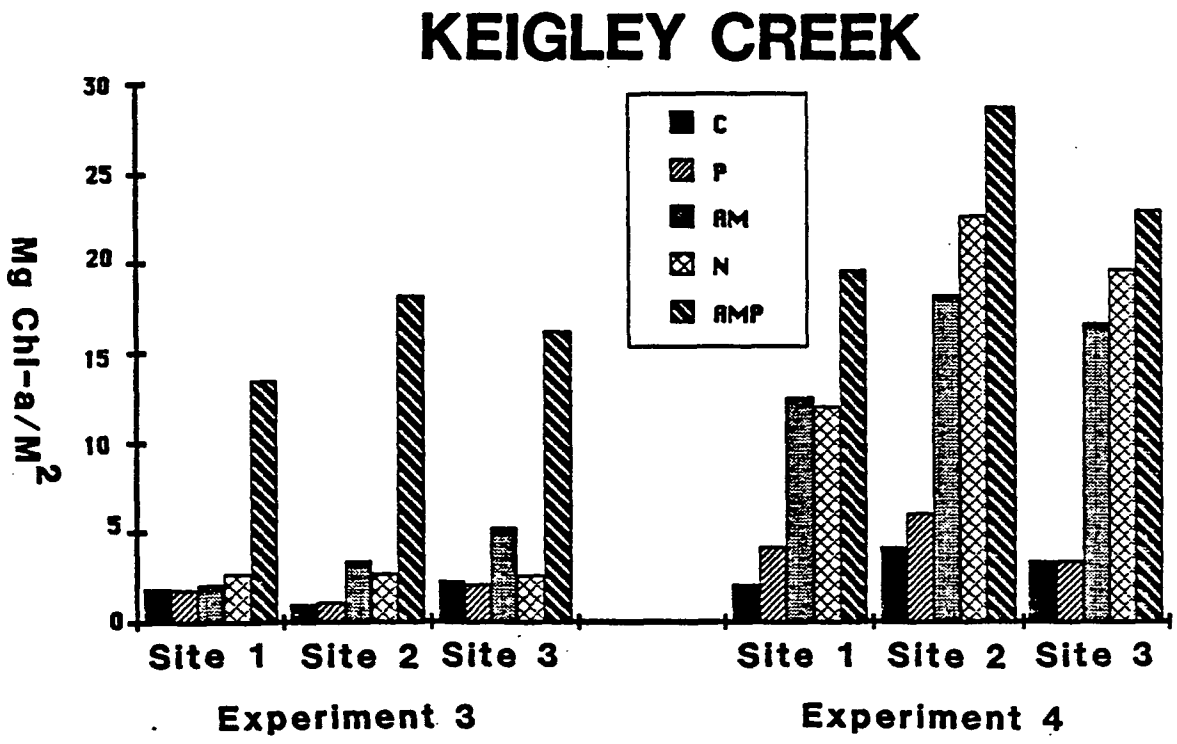

FIGURE 12. Treatment chlorophyll a values for experiments #3 and #4 in Keigley Creek. Treatment levels are grouped by stream site (board) within each experiment

TABLE 5. Stream parameters for Keigley Creek for experiments #3 and #4. (Exp=Experiment, Disch=Discharge, Total-P=Total Phosphorus, NO_3-N=Nitrate-N + Nitrite-N)

Date	Exp	Disch	Total-P	NO_3-N	NH_3-N
		m^3/S	mg/l	mg/l	mg/l
9/20	3	0.012	0.059	0.324	0.000
9/25	3	0.043	0.119	0.066	0.091
9/27	3	0.016	0.080	0.078	0.037
10/4	4	0.015	0.054	0.080	0.036
10/9	4	0.022	0.052	0.161	0.052
10/16	4	0.148	0.124	0.738	0.050

can be seen in Figure 12. Blocks are significantly different in stream-experiment #4, Keigley Creek, (P=0.01; d.f.: 2,8) yet treatment differences are similar in each block. Mean block chlorophyll a values for each stream-experiment are listed in Table 6 along with mean current velocity for each site. The correlation between block chlorophyll mean and current velocity means (n=72) is slightly positive R=0.24 and significant (P=0.04). When variation between streams and experiments are accounted for, the correlation is slightly negative R=-0.24 but not significantly different than zero.

TABLE 6. Summary of current velocity and chlorophyll means for each site within a stream. Current velocities are averaged over three sampling periods. (Exp= Experiment, Str=Stream, C.V.= Current Velocity)

Exp	Str	Site	C.V. (cm/s)	Chl a (mg/m^2)	Exp	Str	Site	C.V. (cm/s)	Chl a (mg/m^2)
1	Bg	1	9.5	26.3	4	Bg	1	21.7	9.6
1	Bg	2	14.Ø	26.4	4	Bg	2	19.Ø	7.7
1	Bg	3	8.5	38.6	4	Bg	3	12.7	9.Ø
1	Sk	1	34.5	4Ø.8	4	Sk	1	13.Ø	6.Ø
1	Sk	2	4Ø.5	28.3	4	Sk	2	15.Ø	4.6
1	Sk	3	46.5	22.7	4	Sk	3	14.3	6.Ø
1	Sq	1	44.Ø	9.2	4	Sq	1	14.7	6.8
1	Sq	2	35.Ø	16.8	4	Sq	2	12.7	6.8
1	Sq	3	34.5	15.3	4	Sq	3	1Ø.Ø	4.7
1	Kg	1	29.Ø	15.Ø	4	Kg	1	13.3	1Ø.Ø
1	Kg	2	67.5	17.5	4	Kg	2	8.7	15.9
1	Kg	3	45.Ø	16.5	4	Kg	3	5.7	13.Ø
2	Bg	1	6.Ø	9.4	5	Bg	1	4.Ø	14.1
2	Bg	2	5.Ø	9.5	5	Bg	2	12.3	5.3
2	Bg	3	6.3	6.2	5	Bg	3	6.3	7.4
2	Sk	1	12.3	3.3	5	Sk	1	25.7	2.1
2	Sk	2	18.3	2.8	5	Sk	2	26.3	1.7
2	Sk	3	23.3	2.2	5	Sk	3	27.3	1.3
2	Sq	1	5.7	5.Ø	5	Sq	1	12.Ø	2.8
2	Sq	2	5.Ø	6.3	5	Sq	2	8.7	2.4
2	Sq	3	3.7	5.8	5	Sq	3	7.Ø	4.3
2	Kg	1	7.7	8.5	5	Kg	1	21.7	1.4
2	Kg	2	4.Ø	7.9	5	Kg	2	14.Ø	1.6
2	Kg	3	3.3	11.6	5	Kg	3	12.7	1.8

Table 6 (Continued)

Exp	Str	Site	C.V. (cm/s)	Chl *a* (mg/m^2)	Exp	Str	Site	C.V. (cm/s)	Chl *a* (mg/m^2)
3	Bg	1	6.7	11.Ø	6	Bg	1	5.7	6.7
3	Bg	2	11.Ø	11.8	6	Bg	2	16.7	7.7
3	Bg	3	9.Ø	8.5	6	Bg	3	9.3	6.9
3	Sk	1	9.3	1.9	6	Sk	1	35.Ø	1.9
3	Sk	2	14.Ø	3.5	6	Sk	2	34.7	2.8
3	Sk	3	12.3	6.Ø	6	Sk	3	3Ø.7	2.2
3	Sq	1	5.Ø	7.2	6	Sq	1	15.Ø	6.7
3	Sq	2	4.3	6.1	6	Sq	2	13.7	4.3
3	Sq	3	3.7	4.7	6	Sq	3	13.Ø	1.Ø
3	Kg	1	3.Ø	4.4	6	Kg	1	33.3	1.6
3	Kg	2	3.Ø	5.3	6	Kg	2	19.3	3.3
3	Kg	3	1.Ø	5.7	6	Kg	3	25.Ø	Ø.7

DISCUSSION

Nitrogen was found to be limiting in one experiment as indicated by co-occurring stimulation by both nitrogen treatments (ammonium and nitrate). Phosphorus, in contrast, had no effect by itself. This is different from the findings of lake surveys in Iowa that have implicated phosphorus limitation from strong correlations found between phosphorus levels and phytoplankton biomass (Bachmann and Jones, 1974; Jones and Bachmann, 1976).

The findings of this study, therefore, demonstrate that nitrogen and phosphorus are usually not limiting the growth of periphyton in central Iowa streams. This is consistent with previous studies on Iowa streams that examined suspended algae using different approaches (LaPerriere, 1971; Kilkus et al., 1975; Burkholder-Crecco and Bachmann, 1979). This also supports the observations of Marker (1976) and Moore (1977) on eutrophic farmland streams in England.

The ammonium treatments, in contrast to nitrate treatments, typically had a positive effect on algal growth. The effects were generally not large, but growth was significantly greater than controls in the first four experiments. In experiments #1-3, ammonium stimulated algal growth yet nitrate addition had no effect. Stimulation by ammonium but not nitrate is not an indication of nitrogen

limitation because both treatments contain nitrogen, instead, it implies that there is a benefit associated with ammonium that nitrate does not have.

Algal preference for ammonium as a nitrogen source has been documented in unialgal laboratory cultures and in field studies with both freshwater and saltwater ecosystems (Syrett, 1962; Dugdale and Dugdale, 1965; Eppley et al., 1969; Prochazkova et al., 1970; McCarthy et al., 1977; Liao and Lean, 1978; Ward and Wetzel, 1980a, 1980b; Round, 1981; McCarthy et al., 1982; Wetzel, 1983). The preference for ammonium is theoretically due to its higher energetic potential. Ammonium is the simplest inorganic nitrogen compound that can be directly incorporated into organic substances in the algal cell. Ammonium-N is, therefore, available for utilization after uptake. Nitrate-N on the other hand must first be reduced to ammonium through a series of energy costly reductive steps before it can be utilized (Syrett, 1962; Morris, 1974). For a relative comparison of cell energy expenditures, it takes 33% more energy to reduce nitrate to ammonium than it takes to fix one molecule of N_2 (Lehninger, 1975). If an algal community is limited by energy, then the energy conserved by the preferential utilization of ammonium will cause increased algal growth (Syrett, 1962). Growth enhancement by ammonium-N over nitrate-N has been documented in laboratory studies (Paasche,

1971; Ward and Wetzel, 1980a) but to my knowledge had not been demonstrated previously in the field. Other researchers have found similar patterns of enhanced efficiency in cell processes in response to ammonium (Samejima and Myers, 1958; Syrett, 1962). The attached algae in Iowa streams appear able to take the energy conserved in utilizing ammonium and channel it into growth, essentially increasing their net productivity by expending less energy on nitrogen utilization. These agricultural streams would, therefore, appear to be often limited by energy, not nutrients.

Though low concentration additions of ammonium can be stimulatory to algae, high ammonia levels may be toxic as indicated by algal response to the two ammonium treatments in experiment #1. The reason for algal inhibition in the presence of high ammonium-N concentrations is not fully understood. Rodhe (1948) found that in highly productive algal cultures growth rates were depressed in the presence of high ammonium concentrations. He attributed this to an increase in pH and the fact that ammonium hydroxide can destroy chlorophyll. Toetz et al. (1977) and Toetz and Cole (1980) also found that ammonium assimilation was inhibited when concentrations were too high. Wetzel (1983) suggested that most reported cases of algae growing better with nitrate-N than with ammonium as a nitrogen source may be partly a result of the toxicity of ammonium at high pH values.

High photosynthetic rates can cause increases in pH, especially within an algal mat. Therefore, the highly productive nature of agricultural streams in Iowa may increase the likelihood of ammonium toxicity at high concentrations. Whatever the mode of toxicity, this experiment demonstrates that at high concentrations, ammonium can be inhibitory to algae yet can stimulate the same algae at lower concentrations. Thus, there seems to be a trade off between the energy conserved with ammonium utilization and the inhibitory conditions prevalent at higher concentrations. Without precise quantification of in situ ammonium release and without knowledge of the pH within the algal mats, further discussion of this phenomenon is only speculation; yet the results do indicate that ammonium can stimulate growth in a system that is not nitrogen limited and supports Wetzel's notion that studies indicating ammonium inhibition may be due to conditons that promoted toxicity (i.e., high pH and/or ammonium concentrations).

The enrichment experiments demonstrated that agricultural streams in Iowa are generally nutrient sufficient in respect to their algal communities. This was further supported by the lack of correlation found between algal growth rates on control substrates and stream nutrient concentrations. On the average, stream nutrient levels were quite high; 3.36 mg/l NO_3-N, Ø.13 mg/l NH_3-N and Ø.14 mg/l total-P.

However, nutrient concentrations were reduced at low discharge to values as low as Ø.Ø66 mg/l NO_3-N, Ø.Ø26 mg/l total-P and below the detectable level (Ø.ØØ5 mg/l) for NH_3-N. During periods of these low nutrient levels, nutrient additions did exert an influence on the growth rate of the periphyton. Experiment #4 was characterized by the lowest mean nitrogen levels in the streams and was preceeded by relatively low and decreasing nitrogen levels. During this time, nitrogen became limiting.

Though phosphorus was never limiting by itself, at low flows during experiment #3 it did enhance growth in conjunction with ammonium. This may indicate that at the higher growth rates associated with ammonium there was an increase in phosphorus demand that exceeded the available phosphorus. An interesting result of these experiments is that nitrogen and not phosphorus became exclusively limiting even though nitrate-N levels were over two orders of magnitude higher than phosphorus levels during the first experiment. It is difficult to make comparisons between measured nitrogen and phosphorus levels in this study since phosphorus was determined as total-P and nitrogen as either nitrate-nitrite or ammonia.

Experiments with low nutrient levels were characterized by extended low flow, warm water temperatures, and infrequent storm events. Under these conditions algal mats may cover

most of the stream bed. Nutrient removal by these large algal mats could be an important factor in reducing nutrient levels at low flow. Activities associated with these algal beds have been shown to have a dramatic effect on the water chemistry of the streams. Kortge (1984), in a study on Big Creek, Iowa, found dissolved oxygen levels to reach 120 to 140% of saturation level by day and 40-60% by night. Bachmann and Bushong (1985) using data from Kortge's study showed that algae in Big Creek could theoretically remove up to 2.75 mg/l of nitrogen from the water column per day. This effect would be magnified at low flow when the volume of water passing over the algae is severely reduced. It would appear that algae play an important role in nutrient transformations in eutrophic agricultural streams. This would indicate that diurnal fluctuations in nutrients, particularly nitrogen, similar to those found by Manny and Wetzel (1973), Triska et al. (1983), Sebetich et al. (1984), and others, might be very pronounced. This was not accounted for in water sampling since samples were generally taken before noon.

Water temperature is an important factor in controlling algal growth rates in Iowa streams. Water temperature explained 61% of the variation in control growth rates. Kilkus et al. (1975) studying Iowa streams also found water temperature could affect levels of suspended algae. Temperature is known to control basic metabolism rates and can

affect periphyton community structure (Hynes, 1970). It is not surprising then that water temperature was also an important factor in controlling algal response to nutrient addition. If the depletion of nutrients in agricultural streams is dependent upon the biochemical activities of algae, then warmer water would increase the likelihood of nutrient limitation by increasing algal activity.

The drop in water temperature between experiment #4 (X=12.4 C) and experiment #5 and #6 (X=6.4 C and 4.4 C respectively) also corresponds to a change in algal response to ammonium addition (i.e., no treatment response). At water temperatures near freezing, the growth rate of the algae is greatly reduced and subsequently the energy requirements are also reduced. Under these conditions, algal growth rates would likely be limited by temperature dependent biochemical reactions. This could explain the lack of ammonium stimulation in the last two experiments.

Other physical variables may be important in controlling algal levels and ultimately the role of algae in nutrient transformations. A factor that appears to be important is the role of storm events in resetting the periphyton community as has been described by Fisher and Minckley (1978), Fisher et al. (1982) and Triska et al. (1983). Scouring associated with heavy rains may limit algal densities (Elwood et al., 1981) and could keep the community from becoming nutrient limited.

Large increases in discharge were observed to remove much of the large algal mats on the stream bottoms which would decrease the total amount of nutrients assimilated by the algae.

Rains also tend to increase nitrate levels in the stream due to agricultural runoff and erosion with subsequent leaching of nitrates from Iowa's rich soils. The strong correlation between discharge and nitrate levels found in every stream is evidence of this relationship. Other researchers have found similar correlations between nitrate-N and discharge in streams (LaPerriere, 1971; Jones, 1972; Kilkus et al., 1975; Kennedy and Malcolm, 1977; Fisher and Minckley, 1978). Periphyton communities may be able to take advantage of the intermittent pulses of nitrogen associated with storm events. Therefore, the time since the last storm resetting may influence nitrogen uptake kinetics. This emphasizes the importance of the immediate stream history in determining the likelihood of nutrient limitation.

It seems unlikely, therefore, that nutrients are limiting in these streams except under the proper conditions which appear to be characterized by extended low flows, warm water temperatures and no major storm events. Large algal mats which typify these conditions may be tying up most of the available nutrients in cell material. Storm events would reset the system by scouring the large algal mats and

increasing the nutrient levels.

Other physical factors have been determined as important in controlling algal growth in past studies. Increases in current velocity for example, can enhance nutrient uptake and increase respiration (Whitford and Schumacher, 1961; Schumacher and Whitford, 1965; Lock and John, 1979), increase productivity (McIntire, 1966) and affect species composition and succession rates (McIntire, 1966). In this study, block chlorophyll means were positively correlated with increases in current velocity (R=Ø.24; P=Ø.Ø4) yet this is potentially misleading. When differences between streams and experiments were accounted for in a nested correlation analysis, there was no significant correlation between block chlorophyll means and current velocities. A complicating factor in this correlation analysis is that different species have different current velocity demands (McIntire, 1968), and data used in the correlation comes from numerous different algal communities present throughout the testing period (July-November). This could obscure effects by current velocity. It could also be that little current velocity is needed to satisfy the "current demand" of periphyton (Lock and John, 1979).

Shading by riparian vegetation, steep banks, turbidity or ice cover could also be an important physical factor in a field study such as this. Numerous studies have shown the rate-limiting effect of light (Phinney and McIntire, 1965;

McIntire, 1968; Evans and Stockner, 1972; Moore, 1977; Sumner and Fisher, 1979; Gregory, 1980; Triska et al., 1983). Light can also directly affect nutrient assimilation (Toetz, 1971). It is doubtful that variations in light intensities caused the significant differences observed between some blocks within a stream. Sites were chosen to minimize these differences and at most sites there was little shading. Differences between blocks may have been due to variations in colonization rates at different stream reaches or to some other physical factor not measured. More important to this study is that generally the relative treatment differences did not vary between sites within a stream.

A comparison between streams demonstrated that three of the four streams behaved in a similar fashion (i.e., significant enhancement of periphyton biomass by ammonium enrichment). Big Creek in contrast showed no overall treatment response and typically had larger growth rates. It is difficult to determine from this study what factors unique to Big Creek make it different from the other streams. It may be important that Big Creek was the only stream to have its study sites at the headwaters. This limits the role of algae in reducing nutrient levels by assimilation. Longitudinal decreases in nitrogen (Manny and Wetzel, 1973; Marcus, 1980; Fisher et al., 1982; Hill, 1982; Sebetich et al., 1984) can potentially reduce nutrients to a limiting level in downstream

areas (Grimm et al., 1981). This factor along with the importance of nitrate-rich tile drainages in Big Creek may in part explain why Big Creek typically had higher nitrogen levels at low flow than other streams but does not explain why Big Creek was not overall energy limited. Warmer water temperatures in Big Creek during experiment #5 may also have been important in stimulating faster control growth rates for that experiment but appears to not be a factor otherwise.

An important factor that has not been discussed yet is the importance of changes in species composition of the algal community through seasonal succession. This can greatly impact the response to nutrient treatment. Ammonium, for example has been demonstrated to be the preferential nitrogen source for many algal species yet for some species this may not be true (Vollenweider, 1971). It is also conceivable that certain algal species use only ammonium as a nitrogen source and would, therefore, not be stimulated by nitrate addition even if nitrogen limited. It was observed in the field that in some instances a treatment appeared to promote one general algal group over another. This was most obvious during times when the algal community was going through a period of change for example from a flora dominated by green algae in early fall to one dominated by diatoms in late fall. Preliminary algal identification on samples from Keigley Creek experiment #4 showed that the control substrates were dominated by

diatoms while the AmP, Am and N substrates were dominated by small coccoid green algae (unpublished data). It was also observed in the field that the periphyton were usually bound more tightly to the ammonium substrates than to other treatments. This suggests a need for further investigation into how different algal species respond to nutrient additions.

Another important element neglected in this study is the impact of grazing. Elwood et al. (1981) suggested that grazing could be an important factor that might obscure enrichment of aufwuchs biomass by nutrient input. Work by Elwood and Nelson (1972) suggests grazing limited periphyton production rates in their stream by controlling standing crop. Gregory (1980) also demonstrated the importance of heavy grazing pressure but found little effect at low grazing densities. Moore (1977) found little effect by grazing in an observational study on agricultural streams except for a two month period in the spring. No exclusion experiments were conducted but from field observations on the number of grazers on substrates and boards the grazing pressure was minimal. Few grazers were found on Squaw Creek, Big Creek, or Keigley Creek while moderate amounts of baeitids were found on the boards in the Skunk River. The fact that the boards and substrates were typically raised above the natural substrate probably reduced grazing pressure.

Nutrient-diffusing substrates appear to be a viable method for studying nutrient limitation in lotic environments. The technique has the advantage of being an experimental approach that is simple and inexpensive yet can incorporate the complexity of stream dynamics into the final results of periphyton response. The method proved capable of demonstrating large treatment differences in a short time (i.e., Keigley Creek, experiments #3 and #4) and less dramatic differences (i.e., ammonium enrichment in experiments #1-3).

Modifications of the original technique (Fairchild and Lowe, 1984; Fairchild et al., 1985) were necessary because of the rigors of agricultural streams and because of their nutrient-rich waters. Fairchild's previous work was on the littoral zone of a relatively oligotrophic lake. By sealing more surface area of the flower pots with silicone and increasing both the agar density and nutrient concentrations a prolonged higher leaching rate was obtained that was more suitable for Iowa streams. The method of using fence posts pounded into the streambed to hold the board design and pots in place was also a helpful modification. The shifting sand substrate and infrequent scouring floods characteristic of agricultural streams in Iowa would have made other more fragile designs of little value. The board design was useful by facilitating easy removal and addition of new pots while maintaining a permanent site in the stream.

The usefulness of this technique could be further enhanced with a better understanding of the conditions at the clay surface-water interface which the periphyton community is subjected to. Results from both the field experiments and laboratory studies demonstrate that enough nutrients were leaching out of the substrates to have an effect on the periphyton, yet there is a need to better understand how the leaching rates are affected by changing stream conditions. Without a more precise quantifiaction of nutrient diffusing rates the method is a qualitative approach to studying nutrient limitation. If in situ diffusion rates were better quantified, the technique could be used for other facets of stream ecology such as in situ toxicology bioassays on periphyton.

LITERATURE CITED

American Public Health Association. 1975. Standard Methods for the Examination of Water and Wastewater. 14th ed. A.P.H.A., New York. 1193 pp.

Bachmann, R. W., and S. J. Bushong. 1985. Impact of nitrogen additions on algae in Iowa streams. First Annual Symposium on Iowa Water Resources. ISWRRI, Ames. (In press).

Bachmann, R. W., and J. R. Jones. 1974. Phosphorus inputs and algal blooms in lakes. Iowa State J. Res. 49:155-160.

Baumann, E. R., and S. Kelman. 1970. Effects of surface runoff on the feasibility of municipal advanced waste treatment. In T. L. Willrich and G. E. Smith (eds.). Agricultural Practices and Water Quality. Iowa State Univ. Press, Ames.

Burkholder-Crecco, J. M., and R. W. Bachmann. 1979. Potential phytoplankton productivity of three Iowa streams. Proc. Iowa Acad. Sci. 86:22-25.

Burwell, R. E., G. E. Schuman, K. E. Saxton, and H. G. Heineman. 1976. Nitrogen in subsurface discharge from agricultural watersheds. J. Environ. Qual. 5:325-329.

Canfield, D. E. and R. W. Bachmann. 1981. Prediction of total phosphorus concentrations, chlorophyll a and secchi depths in natural and artificial lakes. Can. J. Fish. Aquat. Sci. 38:414-423.

Chapmann, A. R. O. and J. S. Craigie. 1977. Seasonal growth in Laminaria longicruris: relations with dissolved inorganic nutrients and internal reserves of nitrogen. Mar. Biol. 40:197-205.

Collins, M. 1978. Algal Toxins. Microbiol. Rev. 42:725-746.

Crawford, J. K. 1979. Limiting nutrients in streams: a case study of Pine Creek, Pennsylvania. Ph. D. Thesis. Pennsylvania State University, University Park, Pennsylvania. 139 pp.

Dillon, P. J. and F. H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19:767-773.

Dugdale, V. A. and R. D. Dugdale. 1965. Nitrogen metabolism in lake III. Tracer studies of the assimilation of inorganic sources. Limnol. Oceanogr. 10:53-57.

Elwood, J. W. and D. J. Nelson. 1972. Periphyton production and grazing rates in a stream measured with a ^{32}P material balance method. Oikos 22:295-303.

Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The limiting role of phosphorus in a woodland stream ecosystem:effects of P enrichment on leaf decomposistion and primary producers. Ecology 62:146-158.

Eppley, R. W., J. L. Coatsworth, and L. Solorzano. 1969. Studies of nitrate reductase in marine phytoplankton. Limnol. Oceanogr. 14:194-205.

Evans, D. and J. G. Stockner. 1972. Attached algae on artificial and natural substrates in Lake Winnipeg, Manitoba. J. Fish. Res. Bd. Can. 29:31-44.

Fairchild, G. W. and R. L. Lowe. 1984. Artificial substrates which release nutrients:effects on periphyton and invertebrate succession. Hydrobiologia 114:29-37.

Fairchild, G. W., R. L. Lowe and W. B. Richardson. 1985. Algal periphyton growth on nutrient-diffusing substrates: an in situ bioassay. Ecology 66:465-472.

Fisher, S. G. and W. L. Minckley. 1978. Chemical characteristics of a desert stream in flash flood. J. Arid Environ. 1:25-33.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecol. Monographs 52:93-110.

Fredriksen, R. L. 1971. Comperative chemical water quality-natural and disturbed streams following logging and slash burning. Pages 125-137 in J. T. Krygier and J. D. Hall (eds.). A Symposium-Forest Land Uses and the Stream Environment. Oregon State Univ. Press, Corvallis.

Goldman, C. R. 1972. The role of minor nutrients in limiting the productivity of aquatic ecosystems. In G. E. Likens (ed.). Proceedings of the Symposium on Nutrients and Eutrophication: The Limiting-nutrient Controversy. Allens Press Inc., Lawrence, Kansas. 328 pp.

Gregory, S. V. 1980. Effects of light, nutrients and grazing on periphyton communities in streams. Ph.D. Thesis. Oregon State University, Corvallis. 150 pp.

Grimm, N. G., S. G. Fisher, and W. L. Minckley. 1981. Nitrogen and phosphorus dynamics in hot desert streams of southwestern USA. Hydrobiologia 83:303-31.

Harlin, M. M. and B. Thorne-Miller. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. Mar. Biol. 65:221-229.

Hill, A. R. 1978. Factors affecting the export of nitrate-nitrogen from drainage basins in southern Ontario. Water Res. 12:1045-1057.

Hill, A. R. 1982. Phosphorus and major cation mass balance for two rivers during low summer flows. Freshwater Biol. 12:293-304.

Hynes, H. B. N. 1970. The Ecology of Running Waters. University of Toronto Press, Toronto. 555 pp.

Iowa Dept. Water Air and Waste Management. 1984. Water Quality in Iowa. Author, Des Moines, Iowa. 108 pp.

Jones, J. R. 1972. A limnological survey of the upper Skunk River, Iowa. M. S. Thesis. Iowa State University, Ames. 149 pp.

Jones, J. R. and R. W. Bachmann. 1976. Predictions of phosphorus and chlorophyll levels in lakes. J. Water Pollut. Control 48:2176-2181.

Kennedy, V. C. and R. L. Malcolm. 1977. Geochemistry of the Mattole River of northern California. Open-file Report 78-201. U.S. Geological Survey, Menlo Park, California.

Kilkus, S. P., J. D. LaPerriere, and R. W. Bachmann. 1975. Nutrients and algae in some central Iowa streams. J. Water Pollut. Control Fed. 47:1870-1879.

Klepper, R. 1978. Nitrogen fertilizer and nitrate concentrations in tributaries of the Upper Sangamon River in Illinois. J. Environ. Qual. 7:13-22.

Kortge, K. J. 1984. Dissolved oxygen and primary productivity in a small agricultural stream in Iowa. M.S. Thesis. Iowa State University, Ames, Iowa. 76 pp.

LaPerriere, J. D. 1971. A nutrient bioassay of phytoplankton from the Des Moines River, Iowa. M.S. Thesis. Iowa State University, Ames, Iowa. 50 pp.

Lehninger, A. L. 1975. Biochemistry. 2nd ed. Worth, Pub. Inc., New York. 1104 pp.

Liao, C. F. H. and D. R. S. Lean. 1978. Nitrogen transformations within the trophogenic zone of lakes. J. Fish. Res. Board Can. 35:1102-1108.

Lock, M. A. and P. H. John. 1979. The effect of flow patterns on uptake of phosphorus by river periphyton. Limnol. Oceanogr. 24:376-383.

Manny, B. A. and R. G. Wetzel. 1973. Diurnal changes in dissolved organic and inorganic carbon and nitrogen in a hardwater stream. Freshwater Biol. 3:31-43.

Marcus, M. D. 1980. Periphytic community response to chronic nutrient enrichment by a reservoir discharge. Ecology 61:387-399.

Marker, A. F. H. 1976. The benthic algae in some streams in southern England. I. Biomass of the epilithon in some small streams. J. Ecol. 64:343-358.

McCarthy, J. J., W. R. Taylor, and J. L. Taft. 1977. Nitrogenous nutrition of the phytoplankton in the Chesapeake Bay. 1. Nutrition availability and phytoplankton preferences. Limnol. Oceanogr. 22:996-1011.

McCarthy, J. J., D Wynne, and T. Berman. 1982. The uptake of dissolved nitrogenous nutrients by Lake Kinneret (Israel) microplankton. Limnol. Oceanogr. 27:673-680.

McIntire, C. D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiologia 27:559-570.

McIntire, C. D. 1968. Structural characteristics of benthic algal communities in laboratory streams. Ecology 49:520-53.

Menzel, D. W. and N. Corwin. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10:280-282.

Moore, J. W. 1977. Some factors affecting algal densities in a eutrophic farmland stream. Oecologia 29:257-267.

Morris, I. 1974. Nitrogen assimilation and protein synthesis. In W. D. P. Stewart (ed.). Algal Physiology and Biochemistry. Univ. of California Press, Berkeley. 989 pp.

Murphy, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27:31-36.

Neilsen, G. H., J. L. B. Culley, and D. R. Cameron. 1982. Agriculture and water quality in the Canadian Great Lakes Basin: IV. Nitrogen. J. Environ. Qual. 11:493-496.

Newbold, J. D., J. W. Elwood, M. S. Schulze, R. W. Stark, and J. C. Barmeier. 1983. Continuous ammonium enrichment of a woodland stream: Uptake kinetics, leaf decomposition, and nitrification. Freshwater Biol. 13:193-204.

Omernik, J. M. 1977. Nonpoint source-stream nutrient level relationships: A nationwide study. EPA-600/3-77-105. Environmental Protection Agency, Corvallis, Oregon. 151 pp.

Paasche, E. 1971. Effect of ammonia and nitrate on growth, photosynthesis and ribulose diphosphate carboxylase content of Dunaliella tertiolecta. Physiologia Plant. 25:294-299.

Perrin, C. J., K. S. Shortreed, and J. G. Stockner. 1984. An integration of forest and lake fertilization: transport and transformations of fertilizer elements. Can. J. Fish. Aquat. Sci. 41:253-262.

Peterson, B. J., J. E. Hobbie, T. L. Corliss, and K. Kriet. 1983. A continuous-flow periphyton bioassay: tests of nutrient limitation in a tundra stream. Limnol. Oceanogr. 28:583-591.

Phinney, H. K., and C. D. McIntire. 1965. Effects of temperature on metabolism of periphyton communities developed in laboratory streams. Limnol. Oceanogr. 10:341-344.

Prepas, E. E. and D. O. Trew. 1983. Evaluation of the phosphorus-chlorophyll relationship for lakes off the Precambian Shield in western Canada. Can J. Fish. Aquat. Sci. 40:27-35.

Pringle, C. M., and J. A. Bowers. 1984. An in situ substratum fertilization technique: Diatom colonization on nutrient-enriched, sand substrata. Can. J. Fish. Aquat. Sci. 41:1247-1251.

Prochazkova, L., B. Blazka, and M. Kralova. 1970. Chemical changes involving nitrogen metabolism in water and particulate matter during primary production experiments. Limnol. Oceanogr. 15:797-807.

Rodhe, W. 1948. Environmental requirements of fresh-water plankton algae; experimental studies in the ecology of phytoplankton. Symbol. Bot. Upsalien. 10(1), 149 pp.

Round F. E. 1981. The Ecology of Algae. Cambridge Univ. Press, Cambridge. 653 pp.

Samejima, H. and J. Myers. 1958. On the heterotrophic growth of Chlorella pyrenoidosa. J. Gen. Microbiol. 18:107-117.

Schanz, F. and H. Juon. 1983. Two different methods of evaluating nutrient limitations of periphyton bioassays, using water from the River Rhine and eight of its tributaries. Hydrobiologia 102:187-195.

Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnol. Oceanogr. 23:478-486.

Schindler, D. W., E. J. Fee, and T. Ruszczynski. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. J. Fish. Res. Bd. Can. 35:190-196.

Schumacher, G. J. and L. A. Whitford. 1965. Respiration and P^{32} uptake in various species of freshwater algae as affected by current. J. Phycol. 1:78-80.

Sebetich, M. J., V. C. Kennedy, S. M. Zand, R. J. Avanzino, and G. W. Zellweger. 1984. Dynamics of added nitrate and phosphate compared in a northern California woodland stream. Water Res. Bull. 20:93-101.

Shoaf, W. T. and B. W. Lium. 1976. Improved extraction of chlorophyll a and b from algae using dimethyl sulfoxide. Limnol. Oceanogr. 21:926-928.

Smith, V. H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. Limnol. Oceanogr. 27:1101-1112.

Stockner, J. G., and R. R. S. Shortreed. 1978. Enhancement of autotrophic production by a nutrient addition in a coastal rainforest stream on Vancouver Island. J. Fish. Res. Board Can. 35:28-34.

Strickland, J. D. H. and T. R. Parsons. 1968. A Practical Handbook of Seawater Analysis. Bull. Fish. Res. Bd. Canada. 311 pp.

Sumner, W. T. and S. G. Fisher. 1979. Periphyton production in Fort River, Massachusetts. Freshwat. Biol. 9:205-212.

Syrett, P. J. 1962. Nitrogen assimilation. In R. A. Lewin (ed.). Physiology and Biochemistry. Academic Press, New York. 929 pp.

Tate, C. M. 1985. A study of temporal and spatial variation in nitrogen concentrations in a tallgrass prairie stream. Ph. D. Thesis. Kansas State University, Manhattan, Kansas. 99 pp.

Thut, R. N. and E. P. Haydu. 1971. Effects of forest chemicals on aquatic life. In J. T. Krygier and J. D. Hall (eds). A Symposium-Forest Land Uses and the Stream Environment. Oregon State Univ. Press, Corvallis.

Toetz, J. P. 1971. Diurnal uptake of NO_3 and NH_4 by a Ceratophyllum periphyton community. Limnol. Oceanogr. 16:819-822.

Toetz, D. and B. Cole. 1980. Ammonia mineralization and cycling in Shagawa Lake, Minnesota. Arch. Hydrobiol. 88:9-23.

Toetz, D., L. Varga, and B. Huss. 1977. Observations on uptake of nitrate and ammonia by reservoir phytoplankton. Arch. Hydrobiol. 79:182-192.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. In T. Fontaine and S. Bartell (eds.). Dynamics of lotic ecosystems. Ann Arbor Science Pub., Ann Arbor, Michigan.

Vallentyne, J. R. 1974. The algal bowl. Misc. Spec. Publ. Dept. Environ. Fish Mar. Serv., Ottawa. 22:186. 185 pp.

Vollenweider, R. A. 1971. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Organization for Economic Co-operation and Development, Paris. 160 pp.

Ward, A. K. and R. G. Wetzel. 1980a. Interactions of light and nitrogen source among planktonic blue-green algae. Arch. Hydrobiol. 90:1-25.

Ward, A. K. and R. G. Wetzel. 1980b. Photosynthetic responses of blue-green algal population to variable light intensities. Arch. Hydrobiol. 90:129-138.

Wetzel, R. G. 1983. Limnology. 2nd ed. Saunders College Pub., New York. 767 pp.

Wetzel, R. G. and G. E. Likens. 1979. Limnological Analyses. W. B. Saunders Co., Philadelphia. 357 pp.

Whitford, L. A. and G. J. Schumacher. 1961. Effect of current on mineral uptake and respiration by freshwater algae. Limnol. Oceanogr. 6:423-425.

Wong, S. L. and B. Clark. 1976. Field documentation of the critical nutrient concentrations for Cladophora in streams. J. Fish. Res. Board Can. 33: 85-92.

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APPENDIX 1:

STREAM PARAMETERS ON INDIVIDUAL SAMPLING DATES

(* signifies missing value. Str=Stream, Exp=Experiment, Dis=Discharge, TP=Total Phosphorus, NO_3-N=Nitrate + nitrite, NH_3-N=Ammonia + ammonium, Tur=Turbidity, Con=Conductivity, TH2O=Water temperature)

Date	Str	Exp	Dis	TP	NO_3-N	NH_3-N	Tur	Con	pH	TH2O
			m^3/s	mg/l	mg/l	mg/l	JTU	umhos/cm		C
7/31	Kg	1	1.078	0.108	4.513	0.128	11.0	615	*	21.0
8/7	Kg	1	0.339	0.080	10.192	0.332	7.9	620	8.2	26.0
8/10	Kg	1	0.211	0.049	8.755	0.254	4.4	540	8.4	22.0
9/6	Kg	2	0.013	0.057	0.462	0.029	8.4	470	7.6	16.0
9/11	Kg	2	0.047	0.073	0.683	0.042	9.4	445	8.1	14.0
9/13	Kg	2	0.032	0.064	0.509	0.057	8.5	*	8.4	21.0
9/20	Kg	3	0.012	0.059	0.324	0.000	11.0	510	7.8	17.0
9/25	Kg	3	0.043	0.119	0.066	0.091	16.0	445	8.2	12.0
9/27	Kg	3	0.016	0.080	0.078	0.037	10.0	520	8.1	9.0
10/4	Kg	4	0.015	0.054	0.080	0.036	8.8	480	7.9	10.5
10/9	Kg	4	0.022	0.052	0.161	0.052	8.3	470	8.0	13.0
10/16	Kg	4	0.148	0.124	0.738	0.050	14.0	440	7.6	12.0
10/23	Kg	5	0.089	0.157	3.829	0.175	6.5	615	8.3	5.0
10/30	Kg	5	0.080	0.057	2.826	0.070	5.2	580	8.7	8.0
11/6	Kg	5	0.250	0.117	7.519	0.033	6.8	650	8.5	3.0
11/13	Kg	6	0.378	0.135	10.113	0.170	4.8	660	8.3	4.0
11/20	Kg	6	0.056	0.050	9.409	0.148	3.3	835	8.3	0.0
11/27	Kg	6	0.199	0.026	7.763	0.074	3.2	630	8.0	4.0
7/31	Sk	1	151.0	0.236	7.713	0.037	13.5	625	8.0	23.0
8/7	Sk	1	88.0	0.130	7.835	0.305	13.0	620	8.0	25.5
8/10	Sk	1	78.0	0.123	6.394	0.289	5.4	600	8.1	24.0
9/6	Sk	2	12.0	0.181	1.243	0.612	13.0	625	7.8	17.0
9/11	Sk	2	15.0	0.198	1.153	0.251	16.0	645	7.9	15.5
9/13	Sk	2	11.0	0.203	1.554	0.481	20.5	680	7.9	16.5
9/20	Sk	3	6.7	0.128	0.454	0.217	10.0	590	8.0	18.5
9/25	Sk	3	24.0	0.132	0.532	0.000	15.0	545	8.1	15.0
9/27	Sk	3	18.0	0.124	0.335	0.315	6.5	625	8.2	11.0

Date	Str	Exp	Dis	TP	NO_3-N	NH_3-N	Tur	CON	pH	TH2O
			m^3/s	mg/l	mg/l	mg/l	JTU	umhos/cm		C
10/4	Sk	4	19.0	0.147	0.338	0.382	7.9	605	8.3	12.0
10/9	Sk	4	30.0	0.185	0.488	0.047	9.0	600	8.2	14.5
10/16	Sk	4	44.0	0.345	0.373	0.041	20.0	625	7.9	13.0
10/23	Sk	5	21.0	0.397	2.764	0.143	7.4	650	8.2	6.0
10/30	Sk	5	18.0	0.270	1.914	0.023	5.4	655	8.5	9.0
11/6	Sk	5	42.0	0.308	6.539	0.072	5.5	650	8.5	4.0
11/13	Sk	6	71.0	0.409	7.645	0.104	6.3	700	8.4	5.0
11/20	Sk	6	36.0	0.219	7.413	0.000	2.6	905	8.3	0.0
11/27	Sk	6	41.0	0.148	6.486	0.189	5.4	715	8.1	5.0
7/31	Sq	1	75.0	0.136	9.370	0.161	10.0	595	8.2	27.0
8/7	Sq	1	38.0	0.082	6.104	0.214	6.2	560	8.0	26.0
8/10	Sq	1	29.0	0.063	4.652	0.013	2.9	490	8.4	29.0
9/6	Sq	2	1.7	0.093	0.228	0.032	9.2	515	8.0	18.0
9/11	Sq	2	3.9	0.151	0.264	0.043	11.5	520	8.1	15.3
9/13	Sq	2	2.4	0.089	0.232	0.101	10.5	*	8.2	21.5
9/20	Sq	3	1.4	0.185	0.089	0.249	13.5	565	7.8	17.0
9/25	Sq	3	41.0	0.215	0.629	0.118	44.0	270	7.8	12.0
9/27	Sq	3	1.8	0.053	0.140	0.140	9.5	475	7.9	10.0
10/4	Sq	4	1.4	0.056	0.188	0.191	6.5	510	8.0	11.5
10/9	Sq	4	2.4	0.074	0.111	0.272	9.2	480	7.8	14.0
10/16	Sq	4	46.0	0.213	0.452	0.000	22.0	340	8.2	11.0
10/23	Sq	5	7.6	0.177	1.617	0.000	4.6	600	8.3	7.0
10/30	Sq	5	5.8	0.061	0.512	0.167	3.7	550	8.5	8.0
11/6	Sq	5	25.0	0.192	4.555	0.137	*	620	8.5	0.0
11/13	Sq	6	39.0	0.288	6.298	0.076	5.1	650	8.4	4.0
11/20	Sq	6	19.0	0.094	5.471	0.159	3.8	860	8.3	0.0
11/27	Sq	6	22.0	0.076	3.848	0.141	5.6	625	8.3	5.0
7/31	Bg	1	0.047	0.101	9.479	0.102	4.5	638	7.7	22.0
8/7	Bg	1	0.025	0.112	6.749	0.086	11.0	690	7.5	23.0
8/10	Bg	1	0.027	0.107	6.149	0.164	5.4	680	7.7	21.5
9/6	Bg	2	0.015	0.188	0.298	0.154	14.5	475	7.7	16.5
9/11	Bg	2	0.017	0.202	0.913	0.054	8.3	510	7.6	15.6
9/13	Bg	2	0.007	0.208	0.424	0.237	17.0	530	7.6	15.5
9/20	Bg	3	0.017	0.143	0.270	0.042	11.0	650	7.8	17.0
9/25	Bg	3	0.076	0.393	1.596	0.027	22.0	290	7.3	12.0
9/27	Bg	3	0.009	0.214	1.570	0.055	23.0	300	7.4	11.0
10/4	Bg	4	0.006	0.121	0.908	0.018	9.8	650	8.0	11.0
10/9	Bg	4	0.010	0.114	0.384	0.033	6.3	635	7.8	13.5
10/16	Bg	4	0.565	0.467	3.609	0.139	26.0	560	7.7	12.0

Date	Str	Exp	Dis	TP	NO_3-N	NH_3-N	Tur	Con	pH	TH2O
			m^3/s	mg/l	mg/l	mg/l	JTU	umhos/cm		C
10/23	Bg	5	0.019	0.146	4.451	0.061	11.5	815	8.1	9.0
10/30	Bg	5	0.014	0.144	4.557	0.003	7.2	790	8.3	8.0
11/6	Bg	5	0.046	0.157	7.551	0.019	3.7	800	8.2	10.0
11/13	Bg	6	0.051	0.114	7.930	0.004	3.4	910	8.0	9.0
11/20	Bg	6	0.041	0.109	7.912	0.018	4.6	1130	7.9	4.0
11/27	Bg	6	0.034	0.127	7.247	0.025	2.9	910	8.0	8.0

APPENDIX 2:

CHLOROPHYLL A VALUES FOR EACH SUBSTRATE

(* denotes missing value. Str=Stream, Exp=Experiment Trt=Treatment, Chl a=Chlorophyll a).

Str	Exp	Site	Trt	Chl a	Str	Exp	Site	Trt	Chl a
				mg/m^2					mg/m^2
Kg	1	1	C	4.97	Sq	1	1	C	11.56
Kg	1	1	P	20.64	Sq	1	1	P	6.81
Kg	1	1	Am	43.67	Sq	1	1	Am	11.28
Kg	1	1	N	10.79	Sq	1	1	N	10.93
Kg	1	1	Amx	-5.22	Sq	1	1	Amx	5.63
Kg	1	2	C	22.04	Sq	1	2	C	14.86
Kg	1	2	P	4.38	Sq	1	2	P	11.43
Kg	1	2	Am	32.47	Sq	1	2	Am	17.87
Kg	1	2	N	24.35	Sq	1	2	N	18.68
Kg	1	2	Amx	4.22	Sq	1	2	Amx	15.29
Kg	1	3	C	28.27	Sq	1	3	C	20.06
Kg	1	3	P	*	Sq	1	3	P	15.11
Kg	1	3	Am	*	Sq	1	3	Am	17.87
Kg	1	3	N	*	Sq	1	3	N	15.59
Kg	1	3	Amx	4.81	Sq	1	3	Amx	8.06
Sk	1	1	C	35.79	Bg	1	1	C	30.53
Sk	1	1	P	34.90	Bg	1	1	P	31.56
Sk	1	1	Am	50.36	Bg	1	1	Am	15.52
Sk	1	1	N	44.84	Bg	1	1	N	25.90
Sk	1	1	Amx	38.17	Bg	1	1	Amx	27.89
Sk	1	2	C	17.17	Bg	1	2	C	23.17
Sk	1	2	P	28.57	Bg	1	2	P	34.93
Sk	1	2	Am	41.80	Bg	1	2	Am	36.21
Sk	1	2	N	32.34	Bg	1	2	N	22.36
Sk	1	2	Amx	21.73	Bg	1	2	Amx	15.13

Str	Exp	Site	Trt	Chl *a* mg/m^2	Str	Exp	Site	Trt	Chl *a* mg/m^2
Sk	1	3	C	23.39	Bg	1	3	C	33.Ø4
Sk	1	3	P	22.49	Bg	1	3	P	39.72
Sk	1	3	Am	29.19	Bg	1	3	Am	42.76
Sk	1	3	N	19.95	Bg	1	3	N	34.58
Sk	1	3	Amx	18.27	Bg	1	3	Amx	42.86
Kg	2	1	C	6.Ø5	Sq	2	1	C	6.14
Kg	2	1	P	7.57	Sq	2	1	P	3.Ø3
Kg	2	1	Am	1Ø.ØØ	Sq	2	1	Am	7.57
Kg	2	1	N	6.18	Sq	2	1	N	4.93
Kg	2	1	AmP	12.6Ø	Sq	2	1	AmP	3.49
Kg	2	2	C	5.63	Sq	2	2	C	4.97
Kg	2	2	P	6.22	Sq	2	2	P	3.81
Kg	2	2	Am	1Ø.96	Sq	2	2	Am	12.58
Kg	2	2	N	7.4Ø	Sq	2	2	N	6.41
Kg	2	2	AmP	9.43	Sq	2	2	AmP	3.67
Kg	2	3	C	1Ø.32	Sq	2	3	C	4.85
Kg	2	3	P	13.41	Sq	2	3	P	3.51
Kg	2	3	Am	9.98	Sq	2	3	Am	11.68
Kg	2	3	N	8.21	Sq	2	3	N	5.24
Kg	2	3	AmP	16.26	Sq	2	3	AmP	3.79
Sk	2	1	C	3.41	Bg	2	1	C	11.Ø9
Sk	2	1	P	2.83	Bg	2	1	P	9.Ø1
Sk	2	1	Am	3.46	Bg	2	1	Am	8.ØØ
Sk	2	1	N	2.87	Bg	2	1	N	9.46
Sk	2	1	AmP	4.Ø6	Bg	2	1	AmP	9.7Ø
Sk	2	2	C	2.3Ø	Bg	2	2	C	7.96
Sk	2	2	P	3.49	Bg	2	2	P	12.Ø5
Sk	2	2	Am	2.7Ø	Bg	2	2	Am	11.38
Sk	2	2	N	2.63	Bg	2	2	N	12.19
Sk	2	2	AmP	2.85	Bg	2	2	AmP	3.81
Sk	2	3	C	2.34	Bg	2	3	C	5.29
Sk	2	3	P	2.19	Bg	2	3	P	4.83
Sk	2	3	Am	2.Ø3	Bg	2	3	Am	7.92
Sk	2	3	N	1.87	Bg	2	3	N	9.97
Sk	2	3	AmP	2.47	Bg	2	3	AmP	3.15
Kg	3	1	C	1.9Ø	Sq	3	1	C	4.8Ø
Kg	3	1	P	1.86	Sq	3	1	P	5.13
Kg	3	1	Am	2.Ø8	Sq	3	1	Am	8.26
Kg	3	1	N	2.72	Sq	3	1	N	7.12
Kg	3	1	AmP	13.41	Sq	3	1	AmP	1Ø.43

Str	Exp	Site	Trt	Chl a	Str	Exp	Site	Trt	Chl a
				mg/m^2					mg/m^2
Kg	3	2	C	Ø.98	Sq	3	2	C	5.Ø7
Kg	3	2	P	1.14	Sq	3	2	P	4.75
Kg	3	2	Am	3.36	Sq	3	2	Am	6.17
Kg	3	2	N	2.63	Sq	3	2	N	6.34
Kg	3	2	AmP	18.16	Sq	3	2	AmP	8.26
Kg	3	3	C	2.22	Sq	3	3	C	1.99
Kg	3	3	P	2.Ø6	Sq	3	3	P	5.67
Kg	3	3	Am	5.26	Sq	3	3	Am	7.85
Kg	3	3	N	2.58	Sq	3	3	N	3.58
Kg	3	3	AmP	16.22	Sq	3	3	AmP	4.38
Sk	3	1	C	1.16	Bg	3	1	C	8.91
Sk	3	1	P	1.26	Bg	3	1	P	11.4Ø
Sk	3	1	Am	2.57	Bg	3	1	Am	12.12
Sk	3	1	N	2.29	Bg	3	1	N	11.41
Sk	3	1	AmP	2.23	Bg	3	1	AmP	1Ø.98
Sk	3	2	C	1.47	Bg	3	2	C	12.48
Sk	3	2	P	Ø.75	Bg	3	2	P	9.77
Sk	3	2	Am	1Ø.57	Bg	3	2	Am	11.36
Sk	3	2	N	2.39	Bg	3	2	N	11.55
Sk	3	2	AmP	2.37	Bg	3	2	AmP	13.75
Sk	3	3	C	1.61	Bg	3	3	C	9.Ø9
Sk	3	3	P	*	Bg	3	3	P	7.37
Sk	3	3	Am	*	Bg	3	3	Am	1Ø.85
Sk	3	3	N	*	Bg	3	3	N	8.55
Sk	3	3	AmP	1Ø.34	Bg	3	3	AmP	6.86
Kg	4	1	C	2.Ø5	Sq	4	1	C	7.19
Kg	4	1	P	4.2Ø	Sq	4	1	P	6.88
Kg	4	1	Am	12.43	Sq	4	1	Am	5.65
Kg	4	1	N	11.98	Sq	4	1	N	7.34
Kg	4	1	AmP	19.53	Sq	4	1	AmP	6.82
Kg	4	2	C	4.14	Sq	4	2	C	8.11
Kg	4	2	P	6.Ø1	Sq	4	2	P	6.98
Kg	4	2	Am	18.19	Sq	4	2	Am	7.56
Kg	4	2	N	22.6Ø	Sq	4	2	N	5.69
Kg	4	2	AmP	28.61	Sq	4	2	AmP	5.89
Kg	4	3	C	2.62	Sq	4	3	C	4.14
Kg	4	3	P	3.33	Sq	4	3	P	2.73
Kg	4	3	Am	16.6Ø	Sq	4	3	Am	5.73
Kg	4	3	N	19.66	Sq	4	3	N	5.32
Kg	4	3	AmP	22.9Ø	Sq	4	3	AmP	5.45

Str	Exp	Site	Trt	Chl a	Str	Exp	Site	Trt	Chl a
				mg/m^2					mg/m^2
Sk	4	1	C	5.75	Bg	4	1	C	8.36
Sk	4	1	P	4.43	Bg	4	1	P	8.46
Sk	4	1	Am	7.28	Bg	4	1	Am	8.09
Sk	4	1	N	7.75	Bg	4	1	N	14.83
Sk	4	1	AmP	4.66	Bg	4	1	AmP	8.47
Sk	4	2	C	4.05	Bg	4	2	C	6.72
Sk	4	2	P	3.64	Bg	4	2	P	5.32
Sk	4	2	Am	6.43	Bg	4	2	Am	9.18
Sk	4	2	N	3.33	Bg	4	2	N	11.26
Sk	4	2	AmP	5.63	Bg	4	2	AmP	5.88
Sk	4	3	C	*	Bg	4	3	C	8.52
Sk	4	3	P	3.34	Bg	4	3	P	5.45
Sk	4	3	Am	8.68	Bg	4	3	Am	11.10
Sk	4	3	N	*	Bg	4	3	N	12.04
Sk	4	3	AmP	*	Bg	4	3	AmP	7.65
Kg	5	1	C	1.61	Sq	5	1	C	1.67
Kg	5	1	P	1.96	Sq	5	1	P	2.45
Kg	5	1	Am	0.87	Sq	5	1	Am	1.79
Kg	5	1	N	1.88	Sq	5	1	N	4.24
Kg	5	1	AmP	0.76	Sq	5	1	AmP	2.85
Kg	5	2	C	0.41	Sq	5	2	C	3.29
Kg	5	2	P	0.21	Sq	5	2	P	2.42
Kg	5	2	Am	1.06	Sq	5	2	Am	1.99
Kg	5	2	N	1.71	Sq	5	2	N	1.55
Kg	5	2	AmP	4.55	Sq	5	2	AmP	2.58
Kg	5	3	C	0.67	Sq	5	3	C	3.01
Kg	5	3	P	1.56	Sq	5	3	P	3.75
Kg	5	3	Am	3.21	Sq	5	3	Am	2.38
Kg	5	3	N	2.48	Sq	5	3	N	3.43
Kg	5	3	AmP	0.89	Sq	5	3	AmP	8.68
Sk	5	1	C	2.42	Bg	5	1	C	11.65
Sk	5	1	P	1.40	Bg	5	1	P	15.24
Sk	5	1	Am	1.98	Bg	5	1	Am	8.00
Sk	5	1	N	3.78	Bg	5	1	N	11.79
Sk	5	1	AmP	1.06	Bg	5	1	AmP	23.68
Sk	5	2	C	1.35	Bg	5	2	C	6.80
Sk	5	2	P	3.01	Bg	5	2	P	-2.47
Sk	5	2	Am	0.79	Bg	5	2	Am	8.91
Sk	5	2	N	3.15	Bg	5	2	N	4.97
Sk	5	2	AmP	0.31	Bg	5	2	AmP	8.15

Str	Exp	Site	Trt	Chl a	Str	Exp	Site	Trt	Chl a
				mg/m^2					mg/m^2
Sk	5	3	C	1.54	Bg	5	3	C	9.01
Sk	5	3	P	1.12	Bg	5	3	P	7.90
Sk	5	3	Am	0.74	Bg	5	3	Am	5.89
Sk	5	3	N	2.32	Bg	5	3	N	7.62
Sk	5	3	AmP	0.80	Bg	5	3	AmP	6.49
Kg	6	1	C	0.97	Sq	6	1	C	8.78
Kg	6	1	P	1.34	Sq	6	1	P	6.17
Kg	6	1	Am	1.51	Sq	6	1	Am	2.60
Kg	6	1	N	3.40	Sq	6	1	N	10.37
Kg	6	1	AmP	0.69	Sq	6	1	AmP	5.79
Kg	6	2	C	3.45	Sq	6	2	C	4.06
Kg	6	2	P	3.61	Sq	6	2	P	6.45
Kg	6	2	Am	3.88	Sq	6	2	Am	6.78
Kg	6	2	N	1.53	Sq	6	2	N	2.41
Kg	6	2	AmP	3.84	Sq	6	2	AmP	1.59
Kg	6	3	C	0.42	Sq	6	3	C	1.87
Kg	6	3	P	0.90	Sq	6	3	P	1.12
Kg	6	3	Am	0.42	Sq	6	3	Am	5.11
Kg	6	3	N	0.33	Sq	6	3	N	-1.15
Kg	6	3	AmP	1.48	Sq	6	3	AmP	-1.87
Sk	6	1	C	4.31	Bg	6	1	C	-5.14
Sk	6	1	P	-0.04	Bg	6	1	P	2.62
Sk	6	1	Am	1.92	Bg	6	1	Am	11.79
Sk	6	1	N	0.02	Bg	6	1	N	3.45
Sk	6	1	AmP	3.12	Bg	6	1	AmP	20.69
Sk	6	2	C	4.61	Bg	6	2	C	7.48
Sk	6	2	P	0.30	Bg	6	2	P	8.89
Sk	6	2	Am	1.44	Bg	6	2	Am	0.25
Sk	6	2	N	3.70	Bg	6	2	N	9.18
Sk	6	2	AmP	4.12	Bg	6	2	AmP	12.93
Sk	6	3	C	2.05	Bg	6	3	C	9.05
Sk	6	3	P	0.25	Bg	6	3	P	9.47
Sk	6	3	Am	1.93	Bg	6	3	Am	3.16
Sk	6	3	N	2.56	Bg	6	3	N	9.01
Sk	6	3	AmP	2.28	Bg	6	3	AmP	3.96