PERIPHYTON PRODUCTION IN AN APPALACHIAN

MOUNTAIN TROUT STREAM

by

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INTRODUCTION

Over most of the last half century stream studies consisted of
localized tabulations of abiotic characteristics and taxonomic lists
(Hynes 1975). Early watercourse classification systems were descrip-
tively useful but not unifying (Horton 1945; Strahler 1954, 1957;
Leopold et al. 1964; Shreve 1966; Pennak 1971). The transition from
purely taxonomic and structural studies to those concerned with inter-
actions and energetics has gained momentum over the last 15-20 years
from studies in which streams were examined as whole systems (e.g., Teal
1957, Odum 1957, Nelson and Scott 1962, Cummins 1964, Minshall 1967).
Lotic waters are now recognized as true ecosystems. The River Continuum
Theory has given further conceptual support and finally offered a func-
tional linkage, where a physical one has always existed, between head-
water streams and the largest rivers (Cummins 1975).

Many outstanding socio-economic problems are directly associated
with large rivers, but important reasons for studying small streams have
recently been recognized and stressed. Small streams are numerous, with
first to third order streams comprising 85% of all stream miles (Cummins
1975). Furthermore, small streams are now recognized as zones of alloch-
thonous detritus collection and processing as reviewed by Cummins (1975)
and Hynes (1975). Smaller streams may literally feed larger streams and
lakes. They also act as primary mechanisms of nutrient removal from
their watershed ecosystems (Likens et al. 1967, Woodall and Wallace 1975,
Monk et al. 1977). Therefore low order streams predispose major nutrient
and energy aspects of higher order systems (Hynes 1975). Other reasons
for studying small streams are their aesthetic value and recreational

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use. Although there is an emphasis upon maximized resource utilization, the public demands preservation of these areas of special aesthetic and recreational value. Therefore, base-line data studies on small, undisturbed streams offer means to later gage permissible modifications during exploitation such as logging or road building. In addition, small stream ecosystem studies can go beyond preservation and offer possible management techniques for enhancing stream productivity (Harshbarger 1975).

By supplying and delimiting energy to dependent heterotrophic organisms, primary production is a fundamental parameter of any ecosystem (Lindeman 1942). Many studies indicate that allochthonous (terrestrially derived) organic material is the major energy base for low order streams (e.g., Nelson and Scott 1962; Hynes 1963; Maciolek 1966; Minshall 1967; Fisher and Likens 1972, 1973; Cummins 1974). However, a comprehensive study of stream production dynamics must include quantification of autochthonous as well as allochthonous sources of primary consumer nutrition. In a recent review on lotic primary production, Wetzel (1975a) emphasized that in any attempt to effectively evaluate the efficiency and dynamics of a detritus based system, it is essential that the magnitude and fluctuations in autotrophy be measured. In small woodland streams, the autochthonous primary producers are benthic algae, or "periphyton" (Blum 1960, Hynes 1970, Whitton 1975).

In general, reliable quantitative data concerning annual primary production in aquatic ecosystems are scarce (Likens 1975). Of the few measurements made of annual primary production in low order woodland streams nearly all have been of tangential interest within more general

studies, and were usually accomplished by biomass accumulation techniques (e.g., King and Ball 1966). Use of various biomass accumulation techniques to measure photosynthetic rate is considered highly error prone (Wetzel 1975a). Diurnal oxygen curve methods seem to offer more accurate measurements. Hoskin (1959, as cited by Wetzel 1975a) and Hall (1972) used this technique in relatively small streams, but in most low order streams relatively high gradients and turbulence usually precludes using open system oxygen methods. Hansmann (1969), in a study of three small streams, used the oxygen method but employed recirculating chambers to avoid problems produced by turbulence. Chambers seem to offer hope of better measurements in low order woodland streams, but in many cases where primary production is relatively low, accurate measurement requires more sensitive methods than gas exchange techniques. This is especially true if subtle temporal patterns of periphyton production are to be better quantified and related to environmental factors. Carbon-14 methodology is about 50 times more sensitive than gas exchange methods (Wetzel 1975b) and therefore appears to be particularly useful in low order woodland streams.

In the following study I have coupled the advantages of using recirculating chambers and carbon-14 methodology. The primary objective of my research was to investigate carbon fixation rates in a second order Appalachian Mountain trout stream and two of its tributaries. Specific objectives of my study were:

1) To test for differences in primary productivity rates between first and second order streams of the same basin.

2) To investigate seasonal patterns of primary production.

3)   To compare photosynthetic rates in stream sites exposed to full sunlight with sites of varying percentages of shading.

4)   To compare temporal patterns of allochthonous and autochthonous inputs.

5)   To examine possible correlations between primary production rates and important abiotic parameters.

DESCRIPTION OF STUDY AREA

Primary productivity measurements were made on Guys Run and in two tributaries, Glade Brook and Piney Branch. Guys Run is a second order tributary of the Calfpasture River (James River Basin, Rockbridge County, Virginia; 79 39" W longitude, 38 58" N latitude) (Fig. 1). It is approximately 8 km long and has an average discharge of 0.4 m^3/sec. Headwaters of Guys Run originate at 655 m elevation and the stream drops an average of 28.6 m/km to its mouth at 415 m. A majority of the 19 km^2 watershed is located within the Goshen Wildlife Management Area. Overstory vegetation is primarily oaks, hickory, maple, and pine with an understory of rhododendron and mountain laurel. Light logging consisting of small scale firewood thinnings is conducted well away from the streams. Precipitation averages 96 cm per year with heaviest rains usually occurring during spring and late autumn (Crockett 1972). Soils are acidic (average pH of 4.5), derived from lower and middle Devonian shale, sandstone, quartzite (Bick 1960). This relatively inert geology and the minimal disturbance within the basin produces clear, low nutrient streams with angular gravel-rubble beds. Headwater springs issue acidic water (ca. pH 5.0) into these streams. The basin is within a highly folded syncline where local, thin, non-outcropping limestone layers occasionally occur (Bick 1960). Guys Run and Glade Brook seem to be buffered by such a layer near their source, while Piney Branch is not and remains chronically acidic (pH 4.7-5.7) for the entire length. Physical parameters of the three study streams are shown in Table 1.

Diatom dominated epilithic periphyton accounts for most allochthonous production in Guys Run and its tributaries. There are some locally

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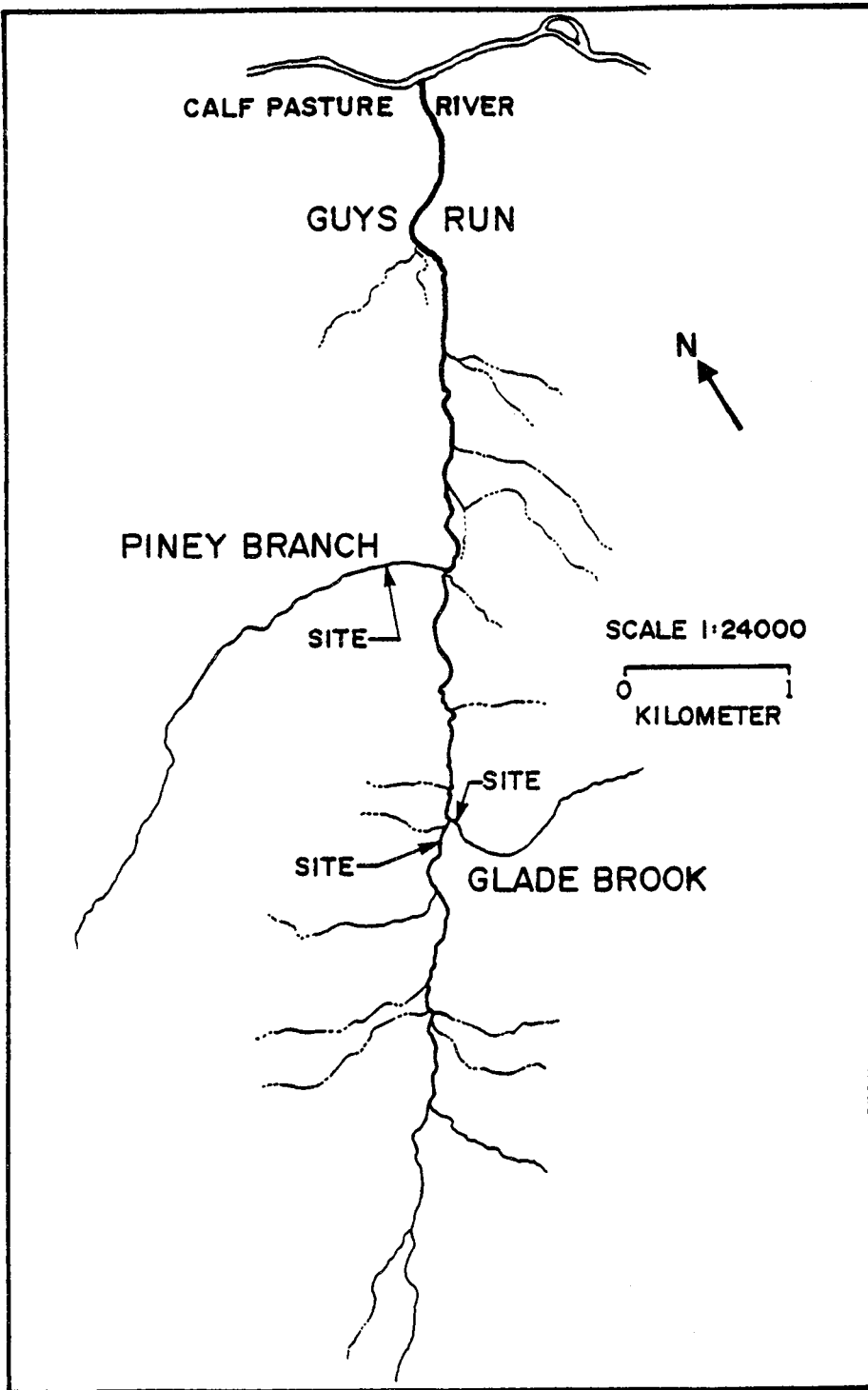
Figure 1. Guys Run drainage

Table 1. Physical stream parameters

Stream	Reach from the mouth	Gradient (m/km)	Channel Width (m)	Average Summer Waters Width (m)	Depth (cm)	Average Discharge (mouth) (ℓ/sec)	Basin (km^2)
Glade	0–500 m	40.5	2.5	1.41	4.7	44	1.2
Brook	500–900 m	56.7	2.2	0.50	2.4		
Piney	0–500 m	70.1	2.9	1.92	8.0	51	3.3
Branch	500–1000 m	70.1	3.0	1.67	6.6		
	1000–1500 m	140.8	3.6	2.00	6.2		
	1500–2000 m	66.4	2.5	1.43	7.4		
Guys	0–1 km	26.2	5.6	3.66	19.0	414	19.0
Run	1–2 km	23.5	6.3	3.68	15.0		
	2–3 km	33.2	6.1	4.36	14.0		
	3–4 km	37.8	6.4	4.07	9.0		
	4–5 km	43.6	5.7	4.02	12.0		
	5–6 km	40.5	5.0	3.34	7.5		
	6–7 km	52.4	3.8	2.20	7.0		
	7–8 km	64.9	2.2	0.98	3.5		

occurring heavy growths of aquatic moss (Foninalaceae) and intermittently

submerged liverwort (Jungermanniales).

MATERIALS AND METHODS

Primary production rates of periphyton on natural substrates were estimated in situ using carbon-14 assimilation within recirculating chambers as outlined by Vollenweider (1974). Experiments at all three stream sites were performed approximately three times per month from April 1977 through April 1978, excluding a period of ice cover and inaccessibility from January-March 1978.

The recirculating chambers were slight modifications of those designed by Rodgers et al. (in press). Chamber bodies were 1.9 liter polystyrene cylinders with lids. Battery powered submersible pumps maintained water circulation (pumping 300 ml/min) during the experiments. I used two clear and two opaque chambers at each stream site on each sampling date. Substrates were typically small cobble size rocks, but some auxiliary sampling of submerged leaves, aquatic moss, liverwort, and fine gravel was conducted for comparison. I selected substrates randomly and with minimal disturbance transferred them from stream to incubation chambers. Chambers were filled with water, sealed, and positioned in the stream with tops just below the water surface. I initiated three hour long mid-day incubation periods by injecting chambers with 1 ml of ^{14}C - sodium bicarbonate from a common working solution (ca. 6.5 μCi, New England Nuclear, NEC - 086H). Syringes were flushed at least three times into each chamber following injection and were always changed between streams. Freshly broken rock surfaces and formalin fixed samples were used as controls. One ml water samples were extracted from several chambers at the beginning, middle, and end of incubation periods to test injection consistency, obtain direct chamber activities,

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and test for potential ^{14}C depletion. Injections were equal within $\pm 4\%$ and ^{14}C concentrations remained high. At the end of incubation substrates were removed from the chambers and placed in marked plastic bags containing water (pH 8.5). They were transferred to the laboratory on ice.

In the laboratory, substrates were processed immediately or frozen until further processing could be accomplished. Two 7 cm^2 periphyton subsamples were taken from each substrate using the sampler shown in Fig. 2. Choice of subsample areas was random beyond the ability to accomodate the clamped-on sampler. The area encompassed by the sampler was scrubbed with a small wire brush to loosen periphyton. Efficiency and consistency of periphyton removal was empirically tested by microscopic examination of the percentage of periphyton coverage before and after sampling. Removal was >95% effective. Loosened material was removed to a 5 ml shell vial via pipette after adding a weak (pH 8.5) sodium hydroxide solution to wash down the sampler walls and brush. Samples were then placed into a fuming chamber. Within the chamber samples were agitated in a 100 C water bath while being exposed to concentrated HCl acid fumes. Acidification by this step eliminated any residual tagged inorganic carbon (Wetzel 1965). I froze the samples until final processing.

Final sample preparation for liquid scintillation counting involved a wet oxidation technique modified from Shimshi (1969). Frozen samples were placed into scintillation vials containing 2 ml of .25 N NaOH and one to two ml of cool oxidizer (50 g potassium dichromate dissolved in 200 ml of distilled H$_2$0 and brought up to one liter with concentrated
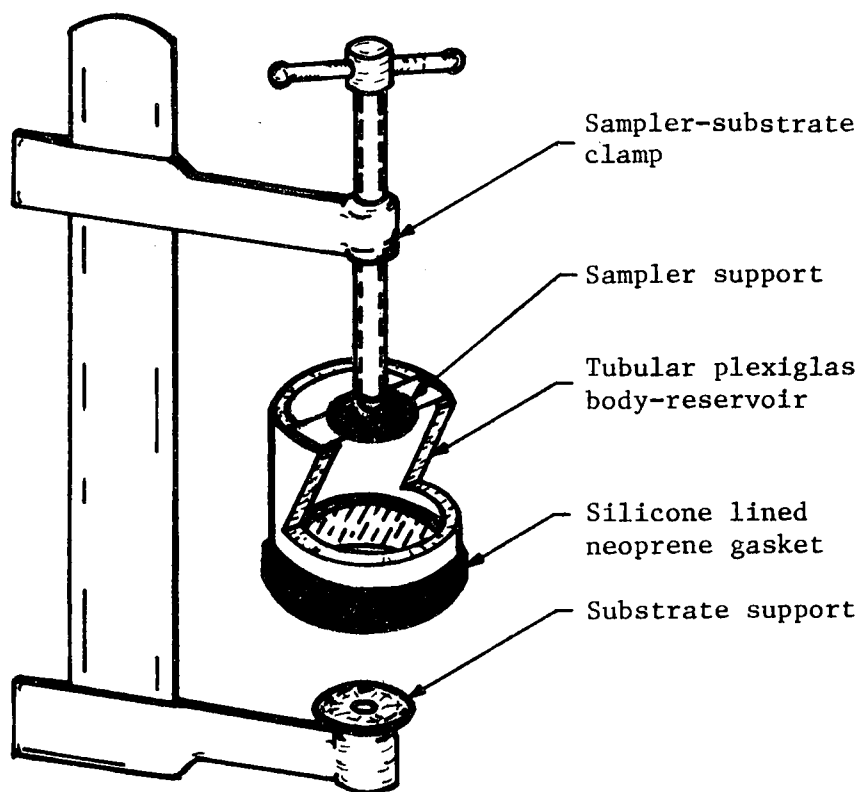
Figure 2. Quantitative sampler for periphyton removal

H_2SO_4 according to Stanley (1976) was added to the sample. The scintillation vials were immediately capped and placed in a boiling water bath for three hours to assure sample oxidation and then placed under refrigeration. Oxidation efficiency, as checked by known additions of ^{14}C, was 86% $\pm 3\%$. Following refrigeration, shell vials were removed and 17 ml of scintillation cocktail (667 ml toluene, 333 ml Triton-X-100, 5.5 g PPO, and 0.1 g POPOP) was added to each scintillation vial. Samples were then refrigerated for at least 72 h to allow chemiluminescence to subside (Patterson and Greene 1965). Samples were counted on a Beckman Instruments Inc. LS3150T. Counting efficiency was accounted for by external channels ratio and internal standard activity additions, and ranged from 86%-100%. Final areal primary productivity was calculated with the following formula based on Vollenweider (1974):

$$P = \frac{^{12}C \times V \times 1.064 \times A \times {}^{14}C_a}{T \times {}^{14}C_i}$$

where:

^{12}C = inorganic carbon concentration

(mg/ℓ determined by infrared carbon analyzer)

V = water volume of incubation chamber (1.6 ℓ $\pm 4\%$)

1.064 = correction factor for ^{14}C heavy isotope

A = factor to correct sampled area to m^2

$^{14}C_a$ = ^{14}C specific activity in sampled organisms (dpm)

T = time (hours)

$^{14}C_i$ = injected ^{14}C specific activity (dpm)

I used two subsample scrapings from each substrate and averaged them to yield two clear and two opaque chamber rates for each stream each sampling date. Light chamber carbon fixation is considered closest to net primary production (Strickland and Parsons 1972) thus only light chamber fixations were used in analysis. Readings of 128 substrates from opaque chambers varied between 0 and an extreme high of 0.7 mg C/m^2/h. A majority of the readings were close to the mean of 0.09 mg C/m^2/h (standard error of the mean = -.01). Dark chamber carbon fixation can be considered to correct somewhat for non-photosynthesizing, labelled and unlabelled carbon exchange, dark production of oxaloacetate from pyruvate, and bacterial carbon fixation (Goldman 1961). Dark uptake need not be subtracted from light, rather the two are slightly overlapping (Hall and Moll 1975). Because dark activity was low, as expected, I simply noted it and used light fixation to describe primary production (Wetzel 1975b).

Statistical analysis of primary production rates and correlations with abiotic parameters were conducted using computerized programs of the Statistical Analysis System - 1976 (SAS - 76) (Barr et al. 1976). Cochran's test failed to prove unequal variances in production rates. In addition, rates appeared to be linearly related and normally distributed although this could not be checked. Therefore a two factor (streams and dates) analysis of variance (ANOVA) (Sokal and Rohlf 1969) was used to test for differences between streams. This analysis also yielded annual mean mid-day hourly rates. I then grouped dates into seasons (defined by forest canopy condition, see Discussion) and used an ANOVA to test for differences between seasons, calculate seasonal means of each

stream, and seasonal means with rates of all streams combined. Correlation of abiotic factors with each other and with primary production rates was analyzed using a one way classification multivariate SAS program. The program checked correlations by approaching the analysis three ways: each stream-season combination with, and then without, assuming equal cell covariance, and finally producing an overall matrix combining all stream-season possibilities.

I collected water samples at each stream site on every primary production sampling date. Samples were analyzed for alkalinity, ammonia, total inorganic carbon (infrared analyzer), chloride, hardness (Ca, Mg, Fe, Zn, Mn), nitrate, dissolved oxygen, sulphate, pH, total phosphate, and orthophosphate using standard methods (APHA 1976). Water temperature as well as notes concerning water clarity, weather, and substrate appearance were also recorded. At Piney Branch air and stream temperature were continuously recorded (T601, Weather Measure Corp.). Parameters selected for multivariate analysis with production rates are presented in Tables 3-9.

A constant flow record was kept on Piney Branch using measurements from a liquid level recorder (F551, Weather Measure Corp.) coupled with a one foot HL flume and calibrated against the discharge through a downstream culvert. The other two study stream flows were estimated relative to Piney Branch based on point flow estimates.

Total scalar, unshaded solar irradiance (300-2600 nm wavelength) was recorded on roll charts by a thermo-electric line pyranometer (R412 Weather Measure Corp.) located in a clearing near the stream sites. I later determined daily insolation by graphic digitizer planimetry.

Auxiliary irradiance data were supplied by one or two mechanical pyrano-graphs (R401, Weather Measure Corp. and 5-3850A, Belfort Instrument Co.) located at sampling sites.

The ratio of photosynthetically active range (PAR, 390-710 nm wave-lengths) light to total solar spectrum is generally found between 0.45 and 0.50 (Reifsnyder and Lull 1965, Gates 1965, Szeicz 1966, 1974). I checked PAR quantity by surveying clearings and shaded stream sites using a PAR quantum sensor and millivolt meter (LI 192S and LI 185A, Lambda Inst. Co.). Quantum to energy conversions were made using $2.77 \pm 0.16 \times 10^{18}$ quanta/sec/watt, a constant independent of sun elevation and meteorological conditions (Morel and Smith 1974). In addition the line pyranometer was calibrated with the PAR meter. I calculated the ratio of PAR light to total solar light to be 0.49.

I monitored solar irradiance penetration of the forest canopy by taking light readings in clearings, at stream sites, and along stream lengths several times per season and during season transitions. A cosine corrected foot-candle was used to compare total and shaded irra-diance because its sensitivity coincides well with the photosynthet-ically active range (Vollenweider 1974). Adjustment factors for cloud cover were calculated for ambient light during incubation period. Actual PAR light quantity (in langleys) to sites during productivity measurements was calculated by:

Site PAR light = 0.49 x (Total irradiance during incubation) x % canopy

penetration x factor for cloud cover

Correlations were also made for water reflectance (6%, Wetzel 1975b), water transmittance (determined with an underwater star pyranometer to

be 96% for depths of 1-15 cm), and chamber transmittance (85±5%, Rodgers 1977).

Allochthonous input was measured for one year starting October 1976. Two 0.1 m^2 vertical litter fall traps and two 0.29 m wide lateral movement traps were located on each bank at five sites. Sites were on Guys Run at 2.6, 5.0, and 7.0 km and Piney Branch at 0.2 and 0.8 km. Material in the traps was collected weekly during autumn and monthly during the rest of the year. Samples were air dried, weighed, and identified, as nearly as possible, to species.

I measured periphyton chlorophyll _a_ (Chl. _a_) concentration once during each season. Periphyton was removed from 7 cm^2 of substrate as described for production rate measurements. Samples were brought to a 96% acetone extraction level (APHA 1976). Well mixed samples were then placed in the dark at 4 C for 24 hours. After centrifuging at 500 G to remove extraneous sediment, samples were spectrophotometrically analyzed (250 Gilford Instruments Co.) for chlorophyll _a_ with phaeophytin correc-tions according to APHA (1976). Values ranged from 7 mg Chl. $\underline{a}/m^2$ to 55 mg Chl. $\underline{a}/m^2$ averaging about 50 mg Chl. $\underline{a}/m^2$.

Taxonomic sampling was done in the summer only for descriptive purposes. Identification was done by G. Seaburg (Biology Dept., VPI&SU). A listing of the most common genera for Guys Run and Piney Branch is as follows:

Guys Run: <u>Cocconeis</u>, 2 spp., <u>Gomphonema</u> sp., <u>Microspora</u> sp., <u>Navicula</u> sp., <u>Nitzschia</u>, 2 spp., <u>Schizothrix</u>, <u>Synedra</u> sp.

Piney Branch: <u>Chlorococcum</u> sp., Coccoid Blue Green, <u>Eunotia</u>, 2 spp., <u>Schizothrix</u>, <u>Stauroneis</u> sp.

RESULTS AND DISCUSSION

Primary Production Rates and Relationships

to Physiochemical Parameters

In the one year experimental period the highest primary production rate for each stream during midday occurred in early July (Fig. 3). Primary production rates in Guys Run ranged between 0.42-7.16 mg $C/m^2/h$ with a mean of 2.27 mg $C/m^2/h$ (+0.37 SE, n = 46). Photosynthetic rates in the two tributaries were consistently lower. Piney Branch exhibited rates between 0.15-5.46 mg $C/m^2/h$, the mean being 1.65 mg $C/m^2/h$ (+0.25 SE, n = 46). Primary production rates in Glade Brook varied between 0.25-3.82 and produced an annual mean of 1.37 mg $C/m^2/h$ (+0.19 SE, n = 46).

Percentage of light penetration through the forest canopy for each study site on sampling dates is shown in Figure 4. Seasons were defined based on canopy condition. Spring was defined by the change from high winter penetration to heavy summer shading. The five dates of increasing penetration were defined as autumn. The resulting at-site PAR irradiance estimates are graphed in Fig. 5 and included in Appendix Tables A1-A3. Though the number of hours were greater in summer, the hourly intensity under the full leaf canopy was about one third, one fourth, and one fifth of that occurring in spring and early winter for Guys Run, Piney Branch, and Glade Brook, respectively. Average PAR light at shaded study sites during midday in summer was 2.9, 1.9 and 1.1 langleys/ h for Guys Run, Piney Branch, and Glade Brook, respectively. Irradiance was most influenced by forest canopy conditions rather than seasonal day length and light intensity.
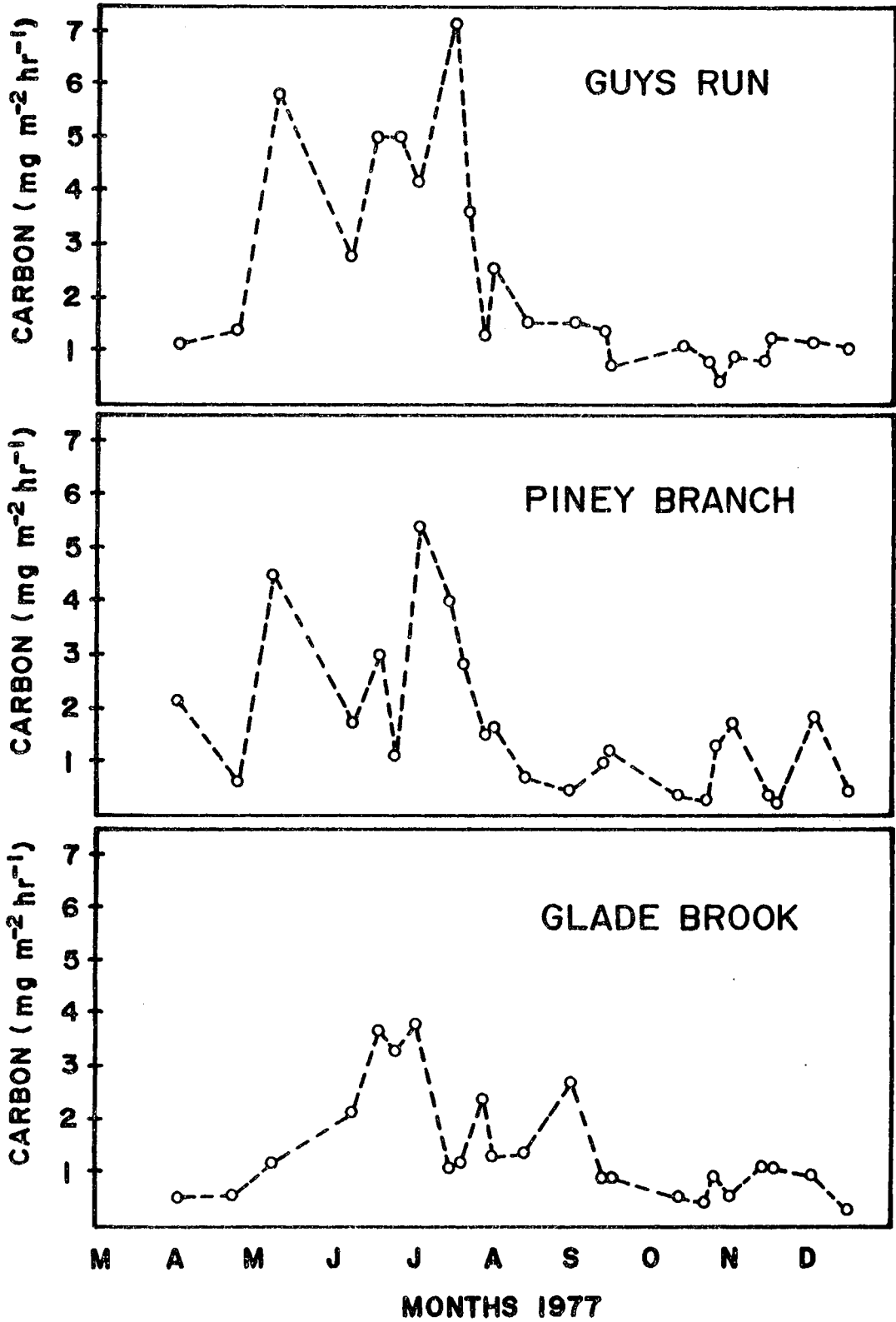
Figure 3 . Carbon fixation rates of study streams
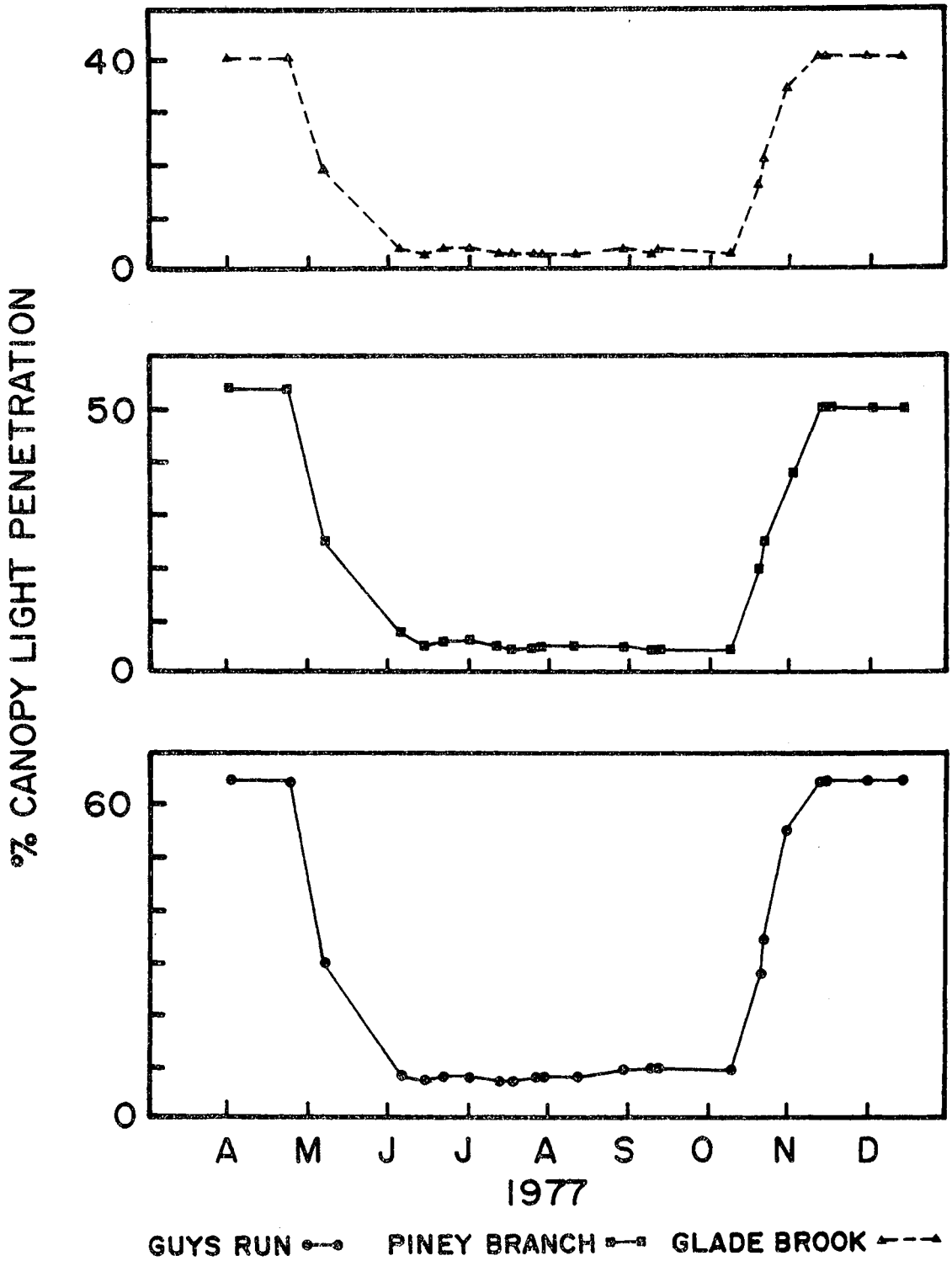
Figure 4. Percentage of light penetration through the forest canopy to the stream study sites
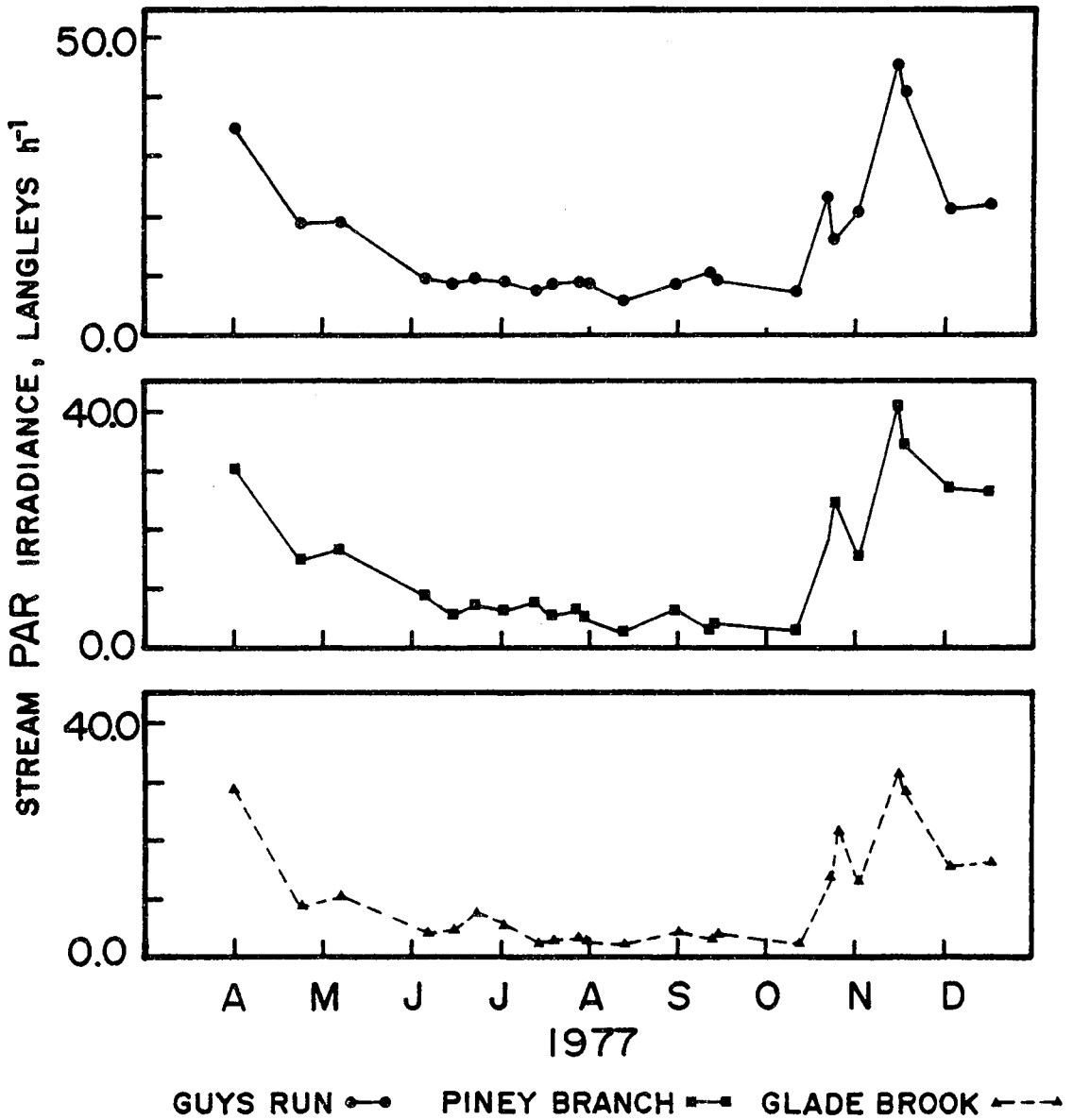
Figure 5. Photosynthetically active range (PAR) irradiance received at study stream sites during primary production measurements

Results of a comparison between primary production rates in shaded and unshaded stream sites on four dates are shown in Table 2. Differences between various degrees of irradiance penetration did not seem to be related to photosynthetic rate in a linear fashion except possibly between 7-25% for Piney Branch and 8-30% for Guys Run. During the lower canopy light penetrations, no particular difference was detectable between the ratios of shaded to unshaded site primary production rate means although the light levels appeared to be below the saturation point of the periphyton. Shade adapted communities have rather low light saturation intensities, well below those of full sunlight. McIntire and Phinney (1965) found that shade adapted periphyton communities reached maximum production rates at a footcandle intensity that is approximately equivalent to 15-25% of full summer sunlight. Saturation values for the periphyton of Guys Run and Piney Branch seemed to be approximately 20-30% of full sunlight. That was evidenced in both streams by the similar ratios of unshaded site to shaded site primary production rates during the two highest, but widely different, light penetration percentages on April 23 and May 5, 1977 (Table 2).

Despite low primary production rates and the inherent patchiness on natural substrates, I had expected to see a correlation between production and ambient irradiance, at least for summer; however, no correlation was observed. That is not to say that primary production was not directly covarying with light. In fact, Gregory (1978) tested the hypothesis that light rather than NO_3-N limited primary productivity in a small, forested stream of the Pacific Northwest. He used four treatments: 1) natural light, 2) increased light (supplied

Table 2. Results of experiments comparing primary production rates for forest canopy shaded and unshaded stream sites.

Stream	Date	Canopy light penetration (%)	C-14 fixation rate (mg C/m^2/h) Shaded site mean	Unshaded site mean	Ratio of unshaded to shaded site rates
Piney Branch	4/23/77	50	0.55	1.05	1.91
	5/ 5/77	25	4.48	9.41	2.10
	6/ 4/77	7	1.74	6.90	3.97
	6/13/77	5	3.02	10.65	3.52
Guys Run	4/23/77	65	1.35	1.89	1.40
	5/ 5/77	30	5.82	8.84	1.52
	6/ 4/77	8	2.75	9.17	3.33
	6/13/77	7	5.01	15.03	3.00

by several fluorescent and incandescent lamps powered by generator),

3) increased light plus nitrate, and 4) natural light plus nitrate.

The intensity difference between the natural light and artificial light

was high. Artificially increased light sections, with and without NO_3-N,

exhibited much higher photosynthetic rates than naturally lighted sec-

tions with and without the nutrient additions. Too high an intensity

has been shown to actually inhibit photosynthesis (Soeder and Stengel

1974, Wetzel 1975b). Therefore, for shade adapted periphyton, it would

seem to be difficult to correctly detect a linear irradiance-photosyn-

thetic rate relationship at either high intensities or low intensities.

It would be especially difficult to measure in situ with other factors

that influence photosynthesis allowed to vary. In the present study,

it is probable that during summer when all other factors affecting

photosynthesis are variable but generally favorable (e.g., higher

nutrient concentrations, less flood scouring, warmer temperatures, and

less acidic conditions), effects of subtly changing weak irradiance are

easily masked. Whitton (1975) noted that other correlated factors

could easily be playing a role in algal variations even in streams that

lacked any marked shading or temperature changes. In addition, Hynes

(1970) mentioned that many diatoms appear to be fairly indifferent to

light intensity. Gregory (1978) was able to resolve irradiance effects

in a heavily shaded stream by artificially supplying steady, well above-

normal light intensities. Blum (1956) also suggested that shade toler-

ant algae might yield different results in relationships between light

and community density than light adapted ones. Examining light adapted

communities at higher irradiances would provide more evident light-

photosynthetic rate relationships. Other studies in larger woodland streams or meadow streams with higher light and nutrient levels were better able to relate irradiance with primary production rate (e.g., Minckley 1963, Marker 1976, Bott et al. 1978). I believe sampling error, processing error, necessity of indirect light estimates, and the matrix of factors affecting primary production concealed any association between available PAR light and primary production rates in the Guys Run system.

Other physiochemical values from primary production sampling dates used in a multivariate correlation analysis are appended in Tables Al-A3 and shown in Figures 6-10 for each stream. Annual means of total inorganic carbon concentrations for Guys Run, Piney Branch, and Glade Brook were 7.7, 1.7 and 5.0 mg/ℓ, respectively. Available inorganic carbon was low in Piney Branch due to chronic acidity with an annual mean pH of 4.9 as compared to 7.4 and 6.8 for Guys Run and Glade Brook, respectively. Inorganic carbon peaked in July. Its concentration rose while hydrogen ion concentration dropped in Guys Run and Glade Brook following heavy precipitation. The opposite was generally the case in Piney Branch. Temperatures during sampling dates ranged from 7.0 to 19.5 C and averaged 13.2 C, the same as average yearly air temperatures (Hynes 1970). Orthophosphate concentrations varied between 0.01-0.03 mg/ℓ annually and peaked during summer at lowest discharge. Phosphate seemed to be washed into the streams with greater concentrations occurring after high discharges from heavy rains had subsided to low summer flows. Total phosphate concentrations were usually 1.2 to 2.0 times those of orthophosphate on any given date for all streams.
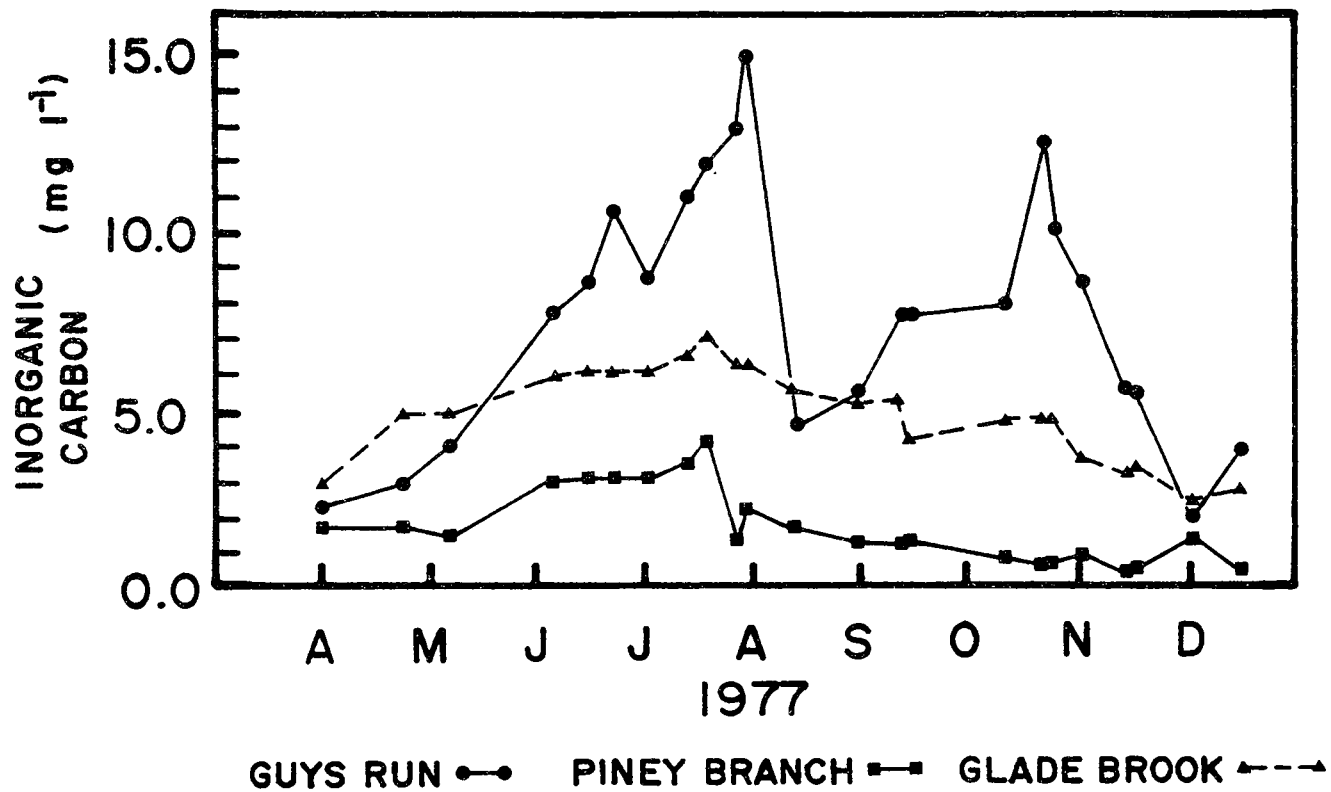
Figure 6. Total inorganic carbon concentrations in the study streams during primary production measurements
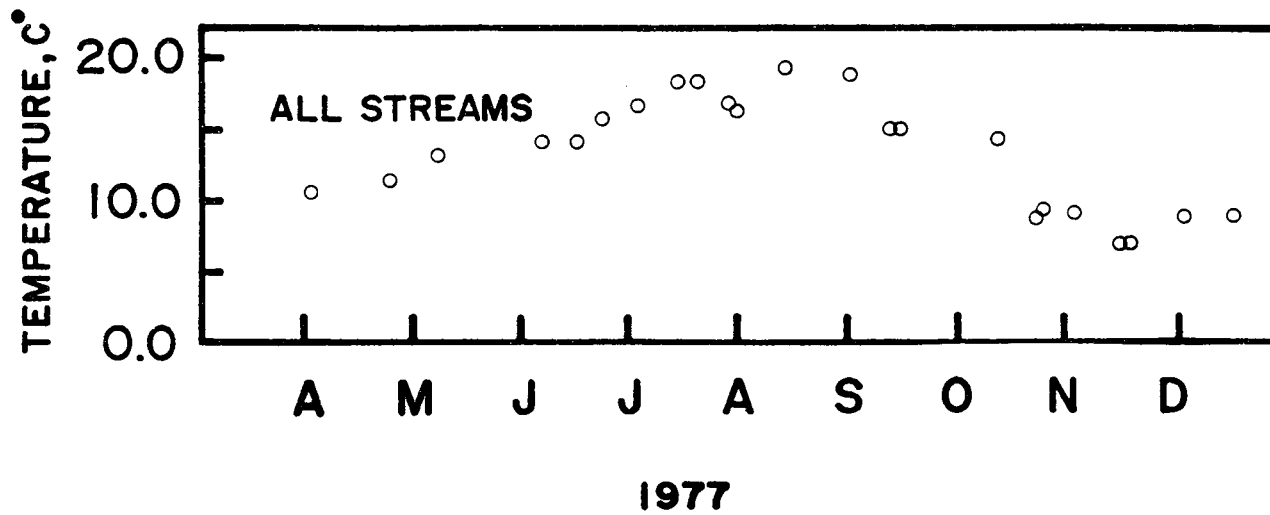
Figure 7. Temperatures of the study streams during primary production measurements
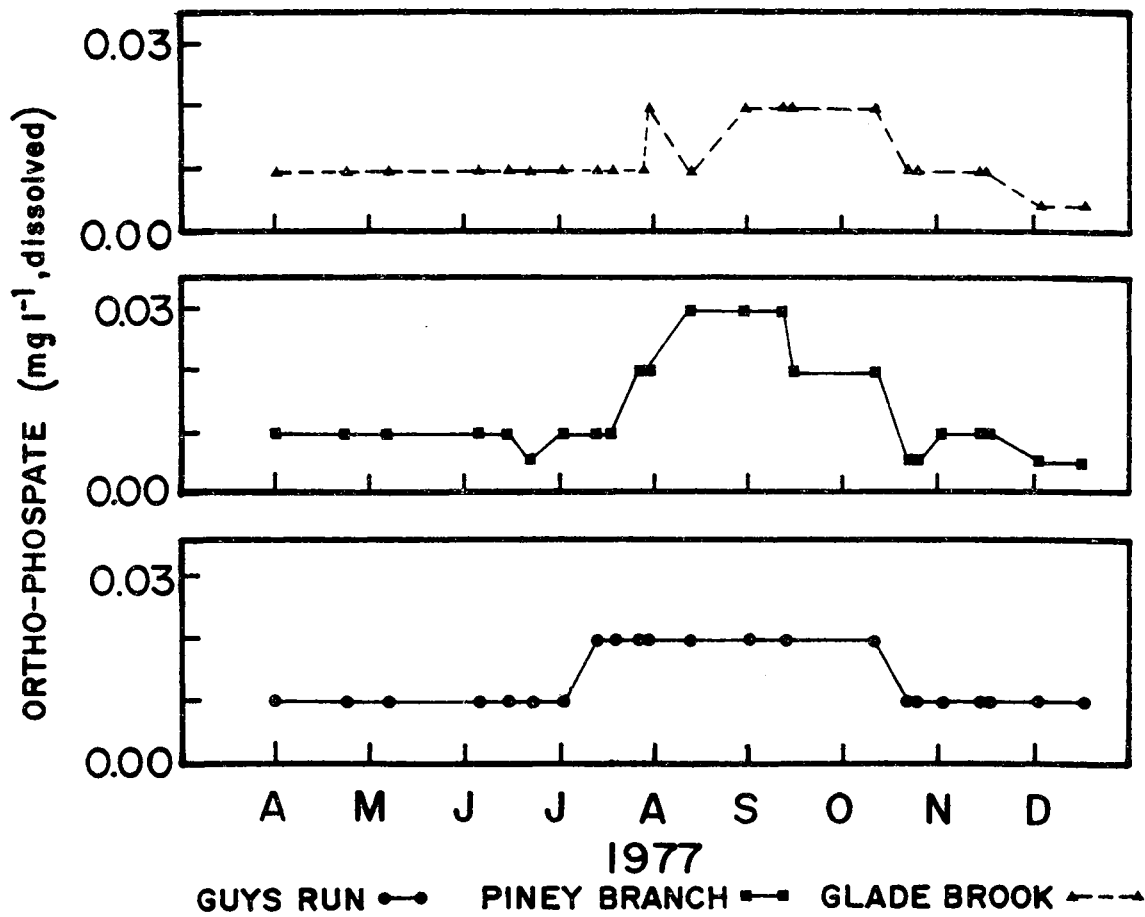
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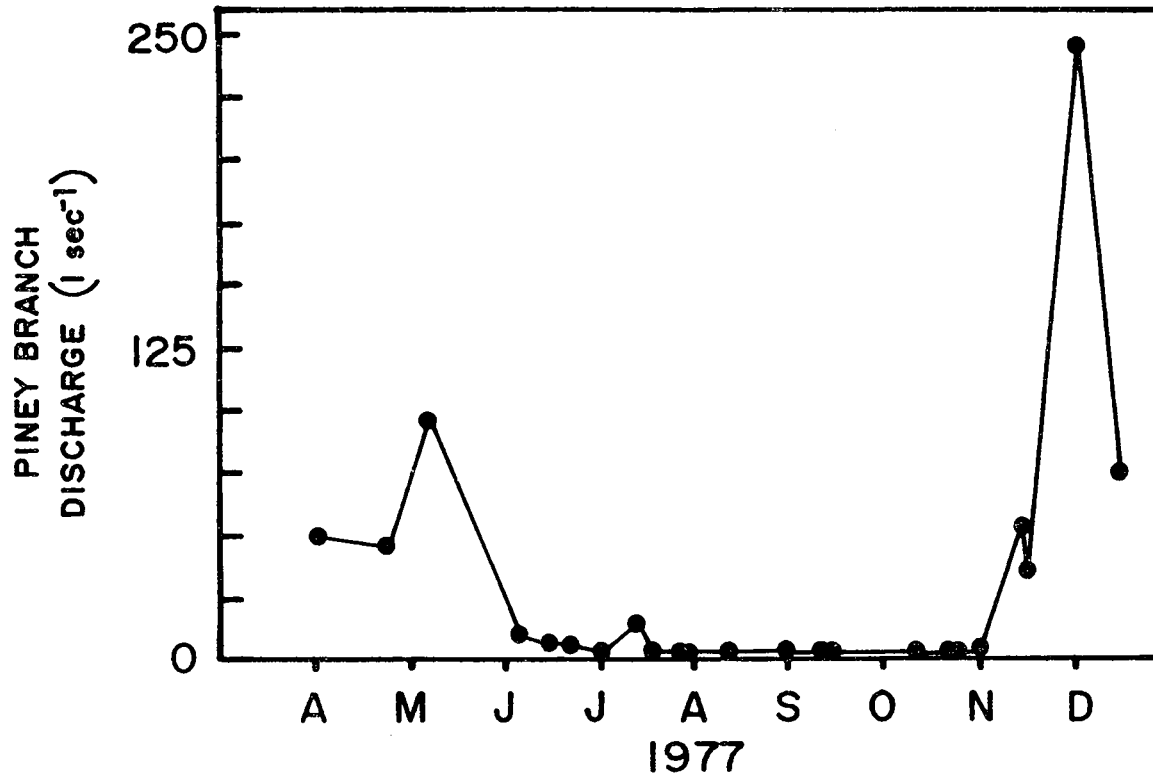
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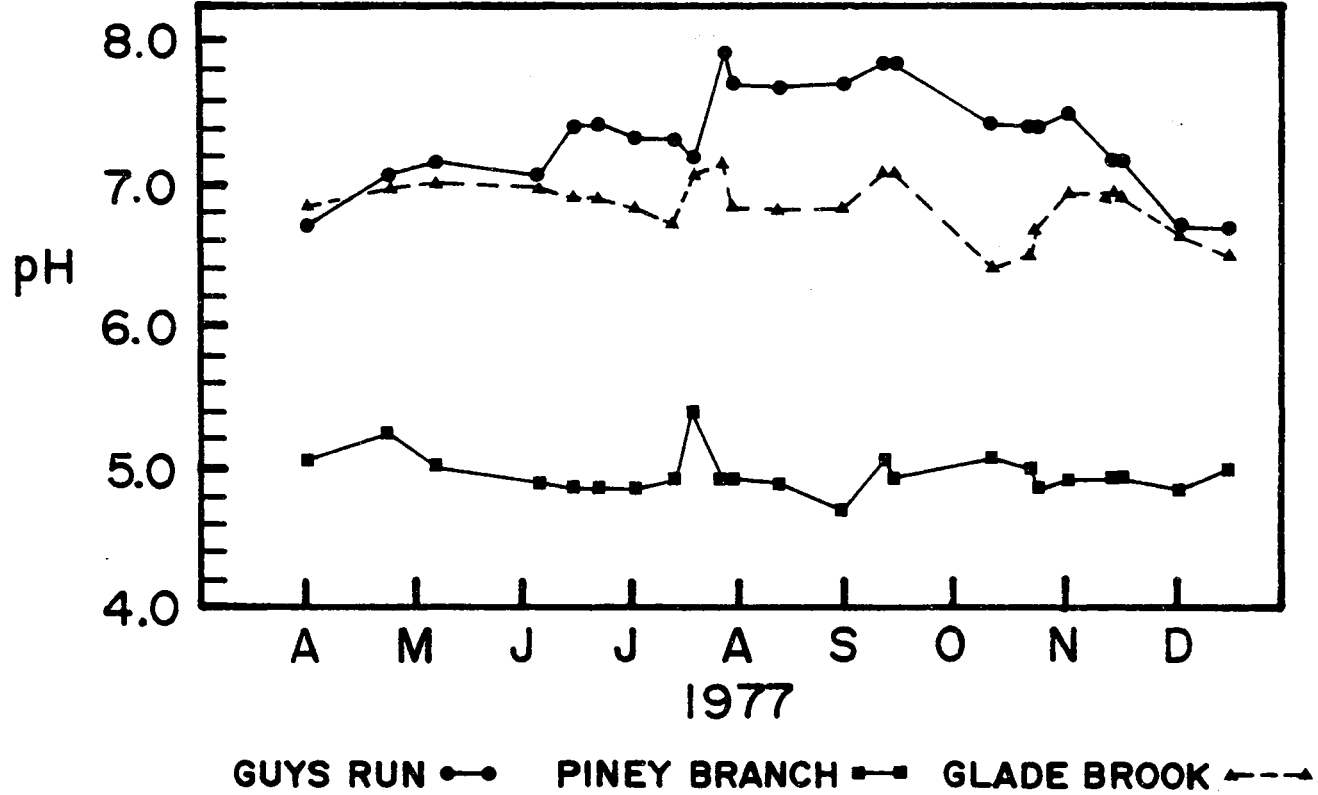
Figure 10. pH of the study streams during primary production measurements

Discharge was greatest in winter, moderate in spring, and extremely low from late June through late October. Discharge in Guys Run at the study site was approximately six times greater than Glade Brook and five times greater than Piney Branch. Over all the primary production measurement days the Guys Run discharge ranged about 0.005-2.000 m^3/sec. The summer of 1977 was considered a drought period with rainfall being 17% below normal (Johnson et al. 1975).

The multivariate analysis for covariance of primary production rate, stream inorganic carbon, hydrogen ion concentration (pH), temperature, ambient PAR lighting, orthophosphate concentration, and discharge did suggest a few relationships (Tables 3-9). The analysis supported the general observations discussed above. There was a slight inverse correlationship between discharge and the concentrations of hydrogen ions and ortho-phosphate. It has often been noted that heavier discharge dilutes concentrations of dissolved matter (Hynes 1970). Light and temperature were always negatively correlated. The most favorable lighting and temperature conditions for photosynthesis were never complimentary in small woodland streams, which contrasts with the synergistic effects of summer light and heat in high order streams. Inorganic carbon concentrations did not show a strong inverse relationship with discharge as might be expected for dissolved salts in general (Hynes 1970). A possible explanation for it not being diluted would be an inorganic carbon loading of the numerous springs by a subterranean calcareous layer. During rains longer resident waters seem to be forced into the streams by displacement (Dunne and Black 1970, Freeze 1972). The spring waters are 'pumped' out and seem to compensate increased discharge with their

Table 3. Partial correlation coefficients from the error SS&CP matrix (upper value) and significance probability (lower number, indicates the probability that the correlation coefficient $\geq$ the one shown and $\neq 0$). DF = 56. For all streams, all seasons.

	^{14}C fixation	Inorganic carbon	Temperature	Available light	Ortho-phosphate	Relative discharge
Inorganic carbon	0.337 0.0098					
Temperature	0.129 0.3356	−0.020 0.8797				
Available light	−0.052 0.6958	0.125 0.3486	−0.527 0.0000			
Ortho-phosphate	−0.317 0.0154	−0.155 0.2458	0.157 0.2378	0.051 0.7061		
Relative discharge	0.178 0.1818	−0.100 0.4552	0.087 0.5177	−0.489 0.0001	−0.281 0.0328	
pH	0.075 0.5757	−0.052 0.6986	−0.027 0.8402	0.048 0.7225	−0.063 0.6384	0.142 0.2864

Table 4. Correlation coefficients (upper number) and significance probability (lower number, indicates the probability that the correlation coefficient $\geq$ the one shown and $\neq 0$). N = 12. For Guys Run, summer.

	^{14}C fixation	Inorganic carbon	Temper-ature	Available light	Ortho-phosphate	Relative discharge
Inorganic carbon	0.372 0.2341					
Temperature	0.268 0.3989	-0.057 0.8598				
Available light	-0.095 0.7695	0.224 0.4846	-0.624 0.0300			
Ortho-phosphate	-0.416 0.1788	0.100 0.7603	0.085 0.7939	-0.244 0.4451		
Relative discharge	0.7125 0.0095	0.090 0.7802	-0.037 0.9101	-0.152 0.6366	-0.229 0.4748	
pH	0.547 0.0656	0.081 0.8027	0.047 0.8844	-0.048 0.8822	-0.600 0.0391	0.527 0.0781

Table 5. Correlation coefficients (upper number) and significance probability (lower number, indicates the probability that the correlation coefficient $\geq$ the one shown and $\neq 0$). N = 12. For Piney Branch, summer.

	14C fixation	Inorganic carbon	Temperature	Available light	Ortho-phosphate	Relative discharge
Inorganic carbon	0.660 0.0196					
Temperature	0.048 0.8613	0.037 0.9090				
Available light	0.394 0.2047	0.512 0.0886	-0.238 0.4663			
Ortho-phosphate	-0.528 0.0777	-0.797 0.0019	0.237 0.4583	-0.722 0.0080		
Relative discharge	0.374 0.2313	0.492 0.1041	-0.112 0.7293	0.693 0.0124	-0.480 0.1140	
pH	-0.094 0.7705	-0.271 0.3940	0.071 0.8265	0.065 0.8407	0.013 0.9688	0.044 0.8921

Table 6. Correlation coefficients (upper number) and significance probability (lower number, indicates the probability that the correlation coefficient $\geq$ the one shown and $\neq$ 0). N = 12. For Glade Brook, summer.

	^{14}C fixation	Inorganic carbon	Temper- ature	Available light	Ortho- phosphate	Relative discharge
Inorganic carbon	0.194 0.5458					
Temperature	-0.085 0.7925	0.333 0.2903				
Available light	0.313 0.3216	-0.080 0.8048	-0.456 0.1362			
Ortho- phosphate	-0.372 0.2343	-0.644 0.0240	-0.299 0.3455	-0.025 0.9377		
Relative discharge	-0.021 0.9475	0.311 0.3245	0.005 0.9885	0.131 0.6851	-0.411 0.1845	
pH	0.204 0.5246	0.156 0.6288	0.426 0.1669	-0.319 0.3125	-0.067 0.8357	0.433 0.1598

Table 7. Partial correlation coefficients from the error SS&CP matrix (upper value) and significance probability (lower number, indicates the probability that the correlation coefficient $\geq$ the one shown and $\neq$ 0). DF = 18. For Guys Run, all seasons.

	^{14}C fixation	Inorganic carbon	Temperature	Available light	Ortho-phosphate	Relative discharge
Inorganic carbon	0.326 0.1609					
Temperature	0.293 0.2102	-0.157 0.5074				
Available light	-0.161 0.4978	0.257 0.2736	-0.566 0.009			
Ortho-phosphate	-0.269 0.2557	0.104 0.6528	0.216 0.3605	0.163 0.4926		
Relative discharge	0.161 0.4970	-0.212 0.3694	0.110 0.8437	-0.552 0.0115	-0.332 0.1521	
pH	0.018 0.9389	-0.185 0.4360	-0.105 0.6592	-0.251 0.2863	-0.496 0.0262	0.511 0.0212

Table 8. Partial correlation coefficients from the error SS&CP matrix (upper value) and significance probability (lower number, indicates the probability that the correlation coefficient $\geq$ the one shown and $\neq$ 0). DF = 18. For Piney Branch, all seasons.

	^{14}C fixation	Inorganic carbon	Temper-ature	Available light	Ortho-phosphate	Relative discharge
Inorganic carbon	0.563 0.0097					
Temperature	0.057 0.8098	0.050 0.8343				
Available light	0.040 0.8665	0.039 0.8709	-0.501 0.024			
Ortho-phosphate	-0.427 0.0601	-0.719 0.0004	0.299 0.2006	-0.109 0.6469		
Relative discharge	0.320 0.1687	0.231 0.3269	0.116 0.6253	-0.438 0.0534	-0.224 0.3431	
pH	0.133 0.5751	-0.163 0.4936	-0.057 0.8097	0.096 0.6887	-0.077 0.7464	0.240 0.3081

Table 9. Partial correlation coefficients from the error SS&CP matrix (upper value) and significance probability (lower number, indicates the probability that the correlation coefficient $>$ the one shown and $\neq$ 0). DF = 18. For Glade Brook, all seasons.

	^{14}C fixation	Inorganic carbon	Temperature	Available light	Ortho-phosphate	Relative discharge
Inorganic carbon	0.185 0.4347					
Temperature	−0.096 0.6880	0.403 0.0784				
Available light	0.075 0.7547	−0.294 0.2085	−0.508 0.0220			
Ortho-phosphate	−0.243 0.3025	−0.245 0.2972	−0.120 0.6138	0.214 0.3647		
Relative discharge	0.021 0.9312	−0.200 0.3986	0.034 0.8873	−0.471 0.0361	−0.367 0.1110	
pH	−0.035 0.8841	0.057 0.8108	0.479 0.0327	−0.333 0.1517	−0.107 0.6540	0.054 0.8220

higher inorganic carbon concentration.

Primary production rate-nutrient correlations ranged from zero to mild. Orthophosphate concentrations did not show a direct correlation with primary production rate in any stream, and in fact exhibited a slight inverse correlation. Again cause-effect cannot be assumed, but phosphate is usually cited as a limiting factor to stream photosynthesis. In Piney Branch, inorganic carbon showed a moderate positive correlation with photosynthetic rate ($r = 0.56$ over all seasons and $r = 0.66$ in summer). Piney Branch, as mentioned above, has especially low inorganic carbon levels suggesting that availability of inorganic carbon may limit primary production. Nitrogen availability did not seem to be limiting in any of the streams. In Piney Branch nitrate ranged between 0.006-0.150 mg/ℓ with most readings near the mean of 0.034 mg/ℓ.

Discharge was included primarily to investigate its effect on periphyton nutrients, but also to observe any possible direct conditioning of the periphyton prior to chamber measurements. Primary production showed a moderate positive correlation with discharge ($r = 0.71$) only in Guys Run during the summer. A possible relationship may come from McIntire (1966a, b) who suggested that the volume of flow effected the diffusion gradients in the immediate vicinity of photosynthesizing cells. He thought that stronger discharges and mixing better penetrated the comglomerations of heterotrophic organisms and dead and decomposing autotrophic forms that were also part of the periphyton. Larger flows appear to cleanse and uncover the better attached autotrophic portion of the periphyton and thereby predispose higher production rates. This appeared to be a possible relationship during the summer in the second order

stream (Guys Run) where finer particulate matter and flocculent material build up when the flow slackens.

Seasonal Patterns of Primary Production Rates

In all three streams greatest primary production rates occurred in the spring and beginning of summer. In general, rates of all three streams diminished from the beginning of summer to reach lowest values in early autumn. A slight rise in rates occurred after the canopy leaves were down (mid-November) but declined by winter (Fig. 3). The general pattern observed in Guys Run drainage is typical for streams with less overstory vegetation (e.g., Ball and Bahr 1975, Marker 1976).

Both Piney Branch and Guys Run showed relatively high production in spring followed by a drop that coincided with the rapid 'leafing-out' of the forest canopy at the end of May. That peak is also generally observed in other streams. Glade Brook did not exhibit a high spring peak which may be attributable to less intense spring irradiance due to its north-south channel orientation. The unusual part of the annual pattern for all three streams was the rising photosynthetic rate through June to maximum values in July. It seems curious that these rises began just after the forest canopy had completely emerged and initiated maximum stream shading. One explanation for this pattern may be an increase of shade adapted periphyton that gradually offset lower irradiance penetration. Coupled with that may be the favorably increasing temperatures and inorganic carbon concentrations at the beginning of summer. McIntire and Phinney (1965) found that periphyton primary production rates in artificial streams with constant illumination intensity rose during June

to a peak in early July, then decreased through the rest of July and August. As in the present study, influences clearly distinct from irradiance had to be affecting photosynthesis. This is another example of a difficult to explain seasonal complex of photosynthesis influences clearly distinct from irradiance. Similar, difficult to explain, photosynthetic rate patterns that exhibited a rise to a July peak have been shown in other forest shaded streams (e.g., Minshall 1967, Hansmann 1969, de la Cruz and Post 1977).

Taking into consideration various sampling day conditions, overall low photosynthetic rates, and the patchiness of biotic components in the Guys Run study streams, seasonal fluctuations were within reasonable limits. Even in third order streams of higher light and nutrients, midsummer photosynthetic rates often vary by 60 to 300% between two dates (e.g., Marker 1976, Bott et al. 1978).

Estimation of Annual Primary Production

To estimate annual primary production I expanded single date incubation period measurements to complete seasonal figures for each stream. Of the physiochemical factors measured, most were unvarying on any one date. Irradiance intensity was the only diurnally varying parameter; therefore, I used that as a basis for making expansions beyond measurement periods. Integrated daily irradiance is normally used to expand short term lacustrine incubation periods (Vollenweider 1974, Wetzel 1975b). No diurnal fluctuations in photosynthetic rate have been noted in lotic studies (e.g., Marker 1976). I tested morning and evening incubations and found no detectible differences.

Daily irradiance to lakes typically looks like the upper curve in Fig. 11. However, the PAR irradiance I measured at the stream surfaces was not the typical bell shaped curve, but a very flat curve during most of the day with short tails during morning and evening (lower curve, Fig. 11). Apparently, sun angle is of little significance in determining intensity of the diffuse light that makes up most of the stream lighting. Therefore, diurnal light intensity changes evident in full sunlight areas were less noticeable under the forest canopy. Recent studies have agreed with this generalization (e.g., Hutchison and Matt 1977). In addition, overcast conditions caused less light variation than expected. This occurred because, although clouds did diminish overall light intensity at shaded sites, the effect was moderate. Diffuse light from a cloud cover penetrated the forest canopy at double to triple the percentage of the more intense direct sunlight. Hutchison and Matt (1977) reported that the fraction of total incident radiation penetrating to the forest floor during summer seems to be increased by cloud cover if most canopy openings are directly overhead, as in the case over stream beds. Similarly, McIntire and Phinney (1965) recorded that on cloudy days shaded stream sites received 65-78% of the irradiance they would have on sunny days, while, in contrast, exposed sites received only 16-18% of clear day light intensity.

I used the total solar irradiance records from the pyranometer charts and the lightmeter surveys of unshaded and shaded sites to construct the average daily irradiance for each season (Fig. 11). The central hours of steady light intensity (Area A, Fig. 11) encompassed the ^{14}C incubation times. Therefore, all of the middle hours could be
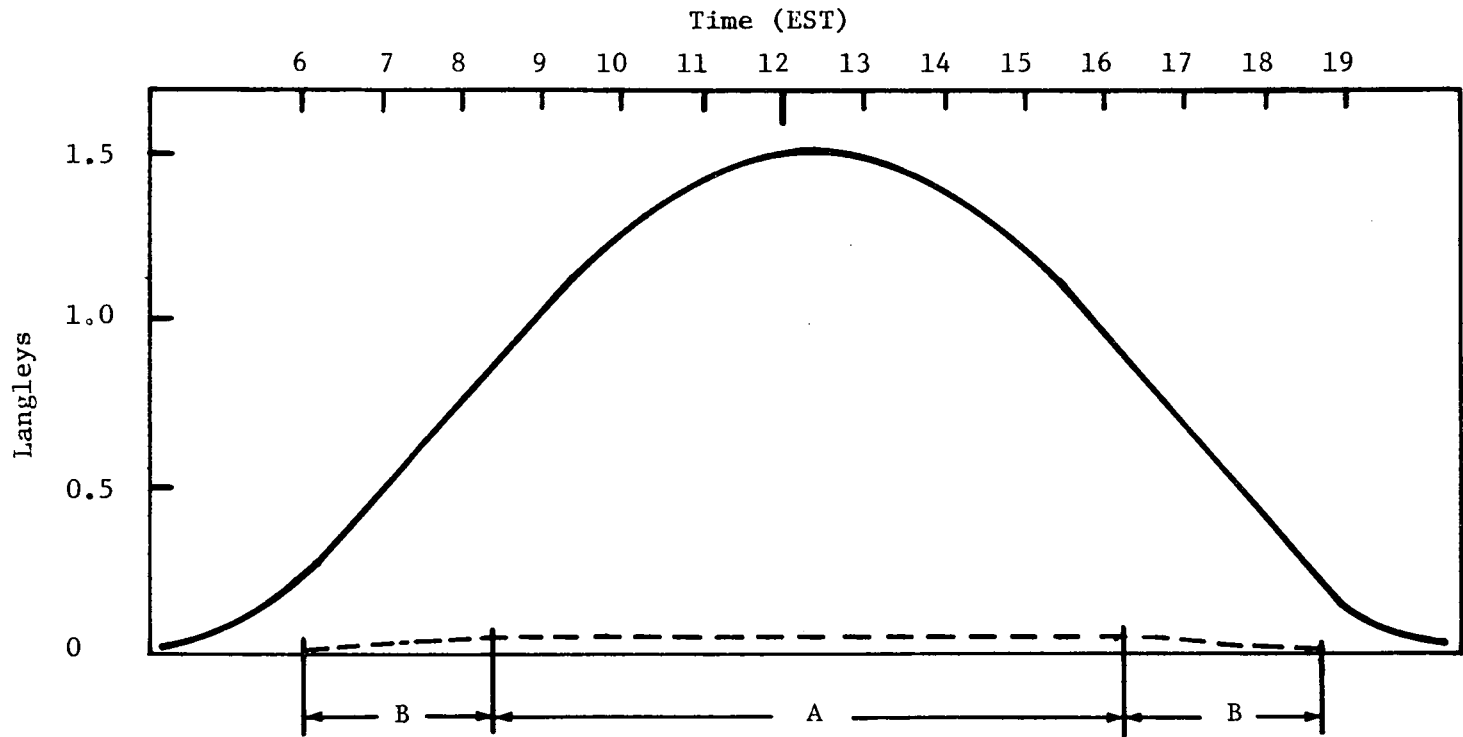
Figure 11. Example of mean daily irradiance for a season (summer shown) in open (━━━) and at Guys Run stream site (━ ━➔). A = central hours; B = tail hours.

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considered time during which the measured primary production rate would
be operating. I found that the midday period of near steady light inten-
sity lasted about the same amount of time on a given day for all sites,
despite their different channel directions. Early and late day hours
were periods of increasing and decreasing irradiance intensity. The
morning hours before and the late afternoon hours increased and
decreased relatively smoothly to the central light maximum. I inte-
grated these hours of lesser light intensity (Areas B, Fig. 11) and
expressed them as a shorter number of hours per day at the midday
incubation irradiance. I added the adjusted number of hours from
the average integrated periods to the average number of central hours
for each season. Multiplying the total number of hours of a season by
the number of days and by the mean hourly photosynthetic rate of that
season yielded estimates of primary production for each season in each
stream.

Calculations of seasonal production and mean midday photosynthetic
rates make evident the ANOVA results that indicated streams differed
most in spring and summer (Table 10). Summer production in Guys Run
was 93% greater than that of Piney Branch and 51% greater than that of
Glade Brook. Combined spring and summer production represented $90\pm1.5\%$
of the annual production for each stream, despite the differing rates
and slightly different production pattern for Glade Brook.

Comparison of Primary Productivity Rates
in First and Second Order Streams

Analysis of variance of primary production rates from 23 sampling

Table 10. Seasonal and annual primary production estimates (excluding 74 days of inaccessibility due to snow and ice).

Season	Number of days	Mean no. of incubation condition h/d	Mean hourly rate (mg C/m^2)			Production (g C/m^2)		
			G.R.	P.B.	G.B.	G.R.	P.B.	G.B.
Spring	71	8.10	2.75	2.41	0.65	1.58	1.38	0.39
Summer	139	10.30	3.01	2.04	2.00	4.40	2.28	2.92
Autumn	32	7.84	0.85	0.92	0.56	0.21	0.23	0.14
Winter	49	6.37	1.11	0.66	0.83	0.35	0.21	0.26
Annual Totals	365	–	–	–	–	6.54	4.10	3.71

G.R. = Guys Run   P.B. = Piney Branch   G.B. = Glade Brook

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dates showed the second order stream (Guys Run) to be significantly

greater (p<.03) than the two tributaries. This result was striking

because it occurred despite the tributaries being sampled near the

mouth, probably the most productive areas, while in contrast Guys Run

was sampled near the upper one third reach. No significant difference

was found between the two tributaries, Glade Brook and Piney Branch.

Season had a significant effect on primary production (p<.01) but the

streams differed from each other most during spring and summer, the

seasons of highest production rates.

Direct measurements of _in situ_ rates of lotic primary production

have always been confounded by a variety of problems. Concerns other

than technical difficulties are problems related to high variations in

physical, chemical, and biotic parameters (Hynes 1970). Periphyton, in

particular, exhibits great spatial and temporal heterogeneity (Blum

1956, Wetzel 1975a, Hall and Moll 1975). Artificial substrates offer a

possible means of reducing variability, but tend to misrepresent, both

qualitatively and quantitatively, natural benthic periphyton (Hansmann

1969, Hynes 1970, Wetzel 1975a). However, despite the variability

encountered, I was able to demonstrate statistically significant dif-

ferences between primary productivity in Guys Run and its tributaries.

An increase in primary productivity from first to second order streams

is implied within the river continuum concept proposed by Dr. Robin

Vannote of the Stroud Water Research Center. From headwaters to large

rivers, lotic community composition proceeds through transitions that

are dictated by changing basin factors. An increase in basin width,

paralleling an increase in stream order, results in greater light energy

input but less allochthonous organic input by riparian vegetation relative to increased stream bottom. From lowest to highest stream orders the major primary organic matter sources shift from adjacent terestrial input, to autochthonous production, and finally to organic matter imported from upstream. Accordingly streams begin as heterotrophic systems. Fourth, fifth, and sixth order reaches are typically autotrophic but eventually converge into the highest orders that are, again, heterotrophic due to their greater depth and higher turbidity. One predicted biological change from low to middle stream orders then is an increase in autochthonous primary production from a minor to a major organic matter source (Cummins 1975). My finding of a distinct increase in periphyton productivity with one increase in lowest stream orders compliments the river continuum concept.

Comparison of Temporal Patterns
of Autochthonous and Allochthonous Inputs

Estimates of annual allochthonous input were 347 ± 17 g/m^2/y for vertical fall and 113 ± 23 g/m^2/y for lateral blow-ins (linear measurements converted to area based on average stream width). This total dry weight input of 460 g/m^2/y multiplied by a factor of 0.5 g C/g dry wt (Odum 1971) gives 230 g C/m^2/y. Composition of the allochthonous input is shown in Table 11. Therefore, annually the periphyton, considered on a plane m^2 basis, accounted for 3% of the total energy budget of Guys Run and about 2% for Piney Branch and Glade Brook.

Macroinvertebrates in woodland streams depend mostly on allochthonous materials for food (e.g., Teal 1957, Nelson and Scott 1962, Darnell

Table 11. Species contribution to allochthonous input, leaf litter-
fall and blow in. Data from J. R. Webster and E. F. Benfield.

Species	Percent
Chestnut oak (Quercus prinus)	41.3
Northern red oak (Q. rubra)	14.0
White oak (Q. alba)	13.5
Pine (Pinus spp.)	4.8
Scarlet oak (Q. coccinea)	4.4
*Witch hazel (Hamamelis virginiana)	3.9
*Mountain laurel (Kalmia latifolia)	3.3
*Alder (Alnus sp.)	3.2
Red maple (Acer rubrum)	2.8
*Dogwood (Cornus florida)	2.6
Birch (Betula spp.)	1.8
Yellow poplar (Liriodendron tulipifera)	1.5
*Rhododendron (Rhododendron maximum)	0.6
Miscellaneous	2.5

*
Understory species

1964, Minshall 1967, Hynes 1970, Cummins 1973, Anderson and Grafius 1975, Wallace et al. 1977). However, Vannote (1969) suggested that autochthonous production in woodland streams may often account for one third of the annual energy requirements of primary consumers. A greater importance of periphyton input appears when food quality and seasonal availability rather than annual budgets are considered. The terms of energy flow in ecosystem analysis often tend to oversimplify the relationships between organisms and their food (Boyd and Goodyear 1971). The efficiency of food utilization by stream herbivores and detrivores depends on the chemical composition and nutritive value of ingested material. Most hardwood trees withdraw a major portion of the nutrients, particularly N, from the leaves before abcission (Zimka and Stachurski 1976). Much of the allochthonous material is not directly digestible by the macroinvertebrates (Hynes 1975), but is made available via aquatic fungi and bacteria that colonize and digest it (Kaushik and Hynes 1968, Hargrave 1969, Iverson 1973, Barlocher and Kendrick 1975). Some leaf types are more easily attacked by decomposers and these in turn seem to be selected for by macroinvertebrates (Kaushik and Hynes 1971, Triska 1970). It appears that initial leaching and microbial colonization of leaves is greatest for the first month. The longer the terrestrial input remains in the water then the greater of its remains are refractory and the less its percentage of viable microbial biomass (Suberkroff and Klug 1976). Ward and Cummins (in press) showed that fresh oak and hickory leaves emerged in stream water for several weeks had higher decomposer activity than natural leaf detritus taken from a stream where it had been for months. They also showed that with one detrivore the

individuals fed fresh leaf particules had a growth rate 2 to 5 times

greater than individuals fed only natural detritus. This emphasizes

the low food quality of decay-resistant particulate organic matter (POM)

found in streams in late spring, summer, and early fall. Guys Run had

a POM standing crop of 64.4 g dry weight/m^2 as measured in three areas

once a month from July to early October (Benfield and Meschter, personal

communication). A visual inspection shows this POM to be composed

mostly of leaf stems, veins, and woody debris. Probably by June less

than 30% of even the most decay-resistant particulate organic matter is

left in the streams (Petersen and Cummins 1974). Therefore in summer

when the terrestrially derived detritus is poorest in quantity and quali-

ty, the periphyton is producing the majority of its annual input. Peri-

phyton is high in food quality (Ward and Cummins in press). Also,

because of its somewhat rapid turnover rate it can support high consumer

standing crops relative to its own. McIntire (1973) suggested that

stream algae might support fifteen times their own standing crop of

consumers. This means that most of what is photosynthetically produced

in the stream is stationary and available in contrast to particulate

organic matter which is often moving and must be captured. In addition,

in this study flat subsampled areas were expanded to plane m^2 of stream

bed to enable comparison with litter input/m^2. Complexity of the stream

bottoms allowed for much greater periphyton habitat than a flat m^2.

Therefore, actual autochthonous contributions may be about 1.5-2.0 times

as great as I have conservatively calculated. Stream dwellers are oppor-

tunistic feeders (Hynes 1975). Therefore, at least from a management

standpoint, the spring-summer periphyton input may assume even more

importance when considering the macroinvertebrate community and their consumers. Many of the Ephemeroptera, Plecoptera, and Trichoptera of shaded first and second order woodland streams seem to select periphyton, usually diatoms, beyond what their apparent abundance might suggest (Chapman 1966, Mecom 1972, Moore 1977). In a small, cool, shaded stream in Oregon, Chapman (1966) showed that 27% of Ephemeroptera and 32% of all Plecoptera in the stream had mean annual gut contents of 50-90% algae. Even most of the other non-carnivores contained 5-40% algae on an annual basis. In a stream much like Guys Run algae (diatoms) was found to be 17-21% of the macroinvertebrate food supply (Coffman et al. 1971). Chapman (1966) also found that 7% of the total salmonoid energy intake, even on an annual basis, was indirectly attributable to algae, though the streams were as shaded as Guys Run.

In food quality and consumer production it appears that the periphyton compliments, at least in summer, the allochthonous matter in a fashion beyond that indicated by annual dry weight inputs. Harshbarger (1975) suggested the possibility of admitting more light to the stream as an improvement to the trout food chain. Keeping in mind the above observations and referring back to the results of my shaded vs. unshaded production rates (Table 2), it would seem that some trout stream management techniques could be aimed at increasing periphyton productivity. Even though I ran only several trials, it was evident that stream sites receiving full sunlight showed no more than about double the photosynthetic rate of sites receiving only about 7% irradiance. The periphyton was obviously light saturated at a low percentage of sunlight. McIntire and Phinney (1965) found that a shade adapted periphyton community,

including many diatoms, was saturated at about 800-1200 footcandles. According to my footcandle surveys that would be an intensity associated with about 17-22% canopy penetration. It may be possible by judiciously thinning mid-height canopy that many sections of Guys Run could be provided with 20% summer light penetration instead of 7% and thereby nearly double their autochthonous primary productivity. This would seem advantageous in improving the trout prey standing crop during summer, a season of high fish tissue elaboration. Understory regrowth would make the effect somewhat temporary. But thinning only enough to increase light penetration by about 15% and leaving the major understory vegetation would maximize the time of periphyton productivity enhancement. A minor thinning would leave enough overhanging vegetation to maintain the allochthonous input and the important trout forage of terrestrial insects that drop into the stream. Nitrogen fixing species, such as _Alnus_, could be left and herbaceous legumes encouraged. Heat input has been an obvious aftereffect of clearcutting (Hansmann 1969). A controlled minimal thinning would avoid that outcome. In all, by admitting only one fifth of the total solar irradiance, maximized autochthonous primary production may be gained without the disadvantages of frequent maintenance, overheating, or litter input loss.

Comparison of Primary Production Rates in Lotic Waters

In the present study, primary production was estimated _in situ_ using ^{14}C assimilation rates in light and dark chambers equipped with circulating systems. More often used methods for primary productivity estimation in lotic waters include biomass accumulation, relating

photosynthetic rates to chlorophyll a measurements; open water gas

exchange differences upstream-downstream or diurnal changes at a single

point (O_2, CO_2, or CO_2 indicated by pH); and gas exchange or carbon-14

uptake within clear and opaque bottles or chambers (Odum 1971). The

different methods vary in sensitivity and error sources, and while

their results are theoretically comparable, the different methods do

not measure identical parameters.

Measurement of chlorophyll a is a simple procedure and can, to a

degree, be related to standing crop biomass (Strickland and Parsons

1972). But efforts to relate chlorophyll a density and light data to

photosynthetic rates have been less successful. In general, primary

production rates vary due to the type of organisms present, light

quality, and efficiency of light energy utilization. Therefore,

although estimates by chlorophyll a have been performed they are not

recommended for estimating primary production (Hall and Moll 1975).

Biomass methods involve taking a temporal series of weight measure-

ments to estimate growth and thereby net primary production. Variables

affecting final weights include mortality, grazing, new colonization,

decomposition, and accumulation of organic detritus. Many of these are

difficult to measure, therefore biomass accumulations are considered

crude approximations of net primary productivity (Wetzel 1975a).

Dissolved gas exchange procedures are direct estimates of primary

production rate and have been widely used (Table 12). Oxygen production

is reported as gross primary productivity, while CO_2 analysis by infrared

gas analysis or titration is reported as net primary production. These

methods have the advantage of being able to estimate net community

Table 12. Estimates of net primary production of periphyton in flowing waters

Rate expressed as g C/m²/d	Study area	Reference	Technique
0.020–0.031 (i) 0.011–0.018 (j)	Piney Branch and Guys Run First and second order ~0.002–1.000 m³/sec	Hornick 1978	This study, ^{14}C in light and dark circulating chambers
0.004–0.008 (d,g)	Morgan's Creek Woodland 0.005–0.350 m³/sec	Minshall 1967	Biomass change – Approximation
0.008–0.011 (f,i)	Walker Branch Appalachian woodland ~0.015 m³/sec	Elwood and Nelson 1972	Biomass change AFDW
0.050–1.200 (i)	Red Cedar R., Mich. ~5.7 m³/sec	King and Ball 1966	Biomass (AFDW) Artificial substrate
0.14 –0.41 (c,j)	Danube River Littoral areas	Ertl and Tomajka 1973	Light and dark O_2 Artificial substrate
0.16 –0.34 (c,k)	Blue River Mountain Forge River, Oklahoma	Hornuff 1957	O_2 changes
~0.18 (d,j)	Cold spring, shaded pool, low current	Teal 1957	O_2 changes
0.048–1.570 (c,h,1)	9 streams, N.C. Summer, 0.3–2.5 m depth	Hoskin 1959	O_2 changes

Rate expressed as $g\ C/m^2/d$	Study area	Reference	Technique
~0.28 (approx. mean) (j)	Artificial streams and substrates – open sun, some perturbed	Rodgers 1977	^{14}C circulation chambers Artificial substrates
0.28 (c,1)	Artificial streams	Kevern and Ball 1965	O_2 changes
~0.30–0.46 (c,i)	Drift Creek Oregon coast mountains Second order streams, Shaded, ~0.118	Hansmann 1969	O_2 changes Circulating chambers
0.30–1.02 (c,i)	Bere Stream, England Open, chalk streams	Marker 1976	O_2 light and dark, Circulation chamber
0.44 (d,g,j)	Woodland stream Riffle only	Coffman et al. 1971	Biomass estimate
0.33–1.43 (c,i)	New Hope Creek 10 m wide, 0.5 m deep	Hall 1972	O_2 changes
0.41–1.40 (c,i)	Rapitan River, upper reach Open ~0.25 m^3/sec	Flemer 1974	O_2 changes
0.51–1.17 (d,g,1)	Model streams Shaded	McIntire and Phinney 1965	O_2 changes
0.72–1.83 (d,g,1)	Unshaded	McIntire and Phinney 1965	O_2 changes

Rate expressed as g $C/m^2/d$	Study area	Reference	Technique
0.73 (c,j)	River Thames, England Periphyton	Berrie 1972	O_2 changes in perspex domes
0.78 (c,i)	Buffalo Creek Hard water; third order	McDiffett 1972	Diurnal O_2 on two dates
1.11 (b,h,j)	Logan River, Utah Open	McConnell and Sigler 1959	Community metabolism, related Chlorophyll a to photosynthesis
1.85 (c,j) (0.64-4.50)	Catahoula Creek Coastal plain, Miss. Woodland; second order	de la Cruz 1977	O_2 changes
0.75-2.62 (c,1)	Truckee River Some sewage 7.7 m^3/sec	Thomas and O'Connell 1966	O_2 in flexible circulating chambers Artificial substrates
0.9 -2.0 (c,i)	Madison River, Wyoming	Wright and Mills 1967	pH change to estimate CO_2
2.22 (a,i)	White Clay Creek Hard water; open Third order	Bott et al. 1978	Value is an average from 5 methods using O_2 and CO_2 changes
0.44-3.28 (b,h,j)	Blue River Hard water, open ~1.1 m^3/sec	Duffer and Dorris 1966	O_2 changes

Rate expressed as g C/m^2/d	Study area	Reference	Technique
2.35–33.90 (e,1)	Columbia River Open riffle	Cushing 1967	Biomass change

[a] 0.286 (g O_2/m^2) = g C/m^2, average of conversions by Westlake (1974), Stockner (1968), Megard (1972), Bott et al. (1978)
[b] 0.556 ✕(Gross production) = net production, average of conversions by Westlake (1974) and Likens (1975)
[c] a and b combined
[d] 8.40 kcal = g C, derived from Odum (1971)
[e] 0.45 dry wt = g C, Odum (1971)
[f] 0.47 ash free dry wt = g C, Westlake (1974)
[g] reported by Mann (1975)
[h] reported by Wetzel (1975a)
[i] summer average, approx.
[j] approximate annual average
[k] reported by de la Cruz (1978)
[l] reported as mean daily rate x 365, probable over estimate, most measurements from summer

productivity, community respiration, and gross primary productivity with one sampling procedure (Odum 1971). Also, open stream methods integrate community metabolism over a large area and avoid possible errors arising from enclosing the organisms (Bott et al. 1978). A detracting concern of the oxygen method is that, although it expresses gross primary production, it ignores photorespiration and could have considerable error (Mann 1975). Gas exchange methods are affected by variations in metabolic rates, water temperature, and chemistry changes. Open gas exchange is restricted to non-turbulent waters so corrections for diffusion rates can be accurately estimated (Bott et al. 1978).

Restrictions imposed by variable diffusion rates upon the gas exchange methods can be circumvented by enclosing the community in bottles or chambers (Odum 1971). However, serious errors in estimating photosynthetic rates may occur when lotic communities are confined in static systems. Enhancement of primary productivity by current has been demonstrated in a number of studies (e.g., Whitford 1960, McIntire 1966 a, b, Pfiefer and McDiffet 1975, Rodgers and Harvey 1976). Several productivity studies in a wide range of flowing waters have combined various continuous current chambers with gas exchange and pH methods for favorable results (McIntire et al. 1964, Thomas and O'Connell 1966, Bombowna 1972, Cushing and Rose 1970, Hansmann, Lane and Hall 1971, Ertl and Tomajka 1973, Pfeifer and McDiffett 1975, Marker 1976, Rodgers 1977, Bott et al. 1978).

Carbon-14 fixation closely approximates net primary productivity. Carbon-14 methods also necessitate community enclosure. Techniques in lentic waters using stationary light and dark bottles without internal

circulation are acceptable and standardized (Goldman 1961, Vollenweider 1974, APHA 1976). Some lotic studies have also utilized light and dark bottles with no provision for current (McConnell and Sigler 1959, Woods 1965, Kobayasi 1961), but the practice has been discouraged as unrealistic (Hynes 1970, Wetzel 1975a). A few studies previous to mine have used ^{14}C with a water circulating chamber and artificial substrates (Backhaus 1967, 1968, 1969, cited by Wetzel 1975a; Rodgers and Harvey 1976; Rodgers 1977).

For comparison with other study methods, advantages and disadvantages of my methodology should be pointed out. Continuous water circulation has already been discussed. Hynes (1970) pointed out that direct in situ measurements in chambers provided with current offer the best determinations of periphyton primary productivity. As previously mentioned, natural substrates are much preferred over artificial substrates (Hynes 1970, Hall and Moll 1975, Wetzel 1975a, Brown 1976). For low productivity systems, ^{14}C methods offer a sensitivity 50-100 times greater than gas exchange methods (Wetzel 1975b). The usual difficulties viewed as offsetting the sensitivity of the ^{14}C method are artificiality of enclosure, effects of incubation time and conditions, formation of extracellular photosynthetic products, extracellular ^{14}C deposition, and counting techniques. I believe that in my study these problems were minimized by large water circulation chambers; midday incubations that were short enough to avoid extensive bacterial growth; acid fuming to rid samples of extracellular ^{14}C, and maximizing counting efficiency by sample oxidation. In addition, algae under low light and in flowing water release little, if any, photosynthetic products

(Hellebust 1974).

In Table 12 I have compiled a number of lotic primary production studies that included measurement of periphyton production. From Table 12 it is obvious that my results approach some of the lowest primary production rates. Some primary production rates (i.e., Minshall 1967, Elwood and Nelson 1972) were lower than those in the Guys Run system, although the streams of each study were similar in size and woodland setting. An explanation for this may come from loss errors that, as I have mentioned, are common to biomass accumulation methods (used in the other studies).

The relationship between primary production rate and stream order (or size) is not simple or uniform. Variations result from an assortment of factors that affect the primary producers. One must consider such individual stream aspects as nutrient or light levels, sampling depth and turbidity, riffle currents versus pool situations, and man's effects. As an example, the littoral zone periphyton production of the Danube River (Ertl and Tomajka 1973) may seem low when matched to that system's size, until one realizes that samples came from depths of several meters and that the fine sediment loads are heavier in such high order flowing waters. This agrees with the river continuum prediction of diminishing autochthonous production from middle to highest stream orders. In contrast, the Columbia River was sampled by Cushing (1967) in a large shallow riffle open to full sunlight and it had substantial carbon fixation. Artificial streams are usually ideal habitats and show relatively high photosynthetic rates (e.g., McIntire and Phinney 1965) unless average primary productivity is lowered by including experiments

in which carbon fixation was suppressed by additions of copper, chloride, or other perturbants (Rodgers 1977). Coffman et al. (1971) showed high rates for a small woodland stream, but their estimates were based on biomass accumulation from one riffle where high primary production is expected (Hynes 1970). Other streams seem to have particularly high primary productivity for their sizes, but usually these are high nutrient waters flowing through well lighted meadows or farmlands (e.g., McDiffett 1972, Marker 1976, Bott et al. 1978). To summarize the lotic water studies collected in Table 12, the general descriptions of the River Continuum concept seem to apply as a generality, but individual site differences determine the final productivity level.

Streams, and low order streams in particular, are individualistic (Margalef 1960, Hynes 1975). However, Minshall (1969) pointed out that the more alike two streams are in size, type, and local climate, the more similar will be their community structure. Considering relationships among abiotic factors, Miller (1961) found uniform water quality regardless of basin size in an area of quártzite and sandstone. Steep gradient, fluctuating discharge, acute bank slopes, mixed hardwood canopy, rhododendron-mountain laurel understory, and soft, low alkaline water resulting from valleys underlain by sandstones, quartzites, slate, and shale are common characteristics of Appalachian streams from Georgia to Pennsylvania (Cooper et al. 1962, McFadden and Cooper 1962, McFadden et al. 1965, Wydoski and Cooper 1966, Cooper and Scherer 1967, Lennon 1967, Dunson and Martin 1973, Lotrich 1973, Hoopes 1975). Guys Run and its tributaries typify many of these soft water Appalachian streams. Combining primary production results from both stream orders in the

present study, I estimate a mean primary production rate during midday in summer of 2.35 mg C/m^2/h ($\pm$0.53 SE, n = 72) for similar Appalachian streams.

SUMMARY AND CONCLUSIONS

1. Periphyton production was measured in Guys Run, a second order western Virginia trout stream, and two of its tributaries. Allochthonous input and physiochemical parameters were also measured.

2. In the one year experimental period, mean photosynthetic rates at midday were 2.27 ± 0.37 SE, 1.65 ± 0.25 SE, and 1.37 ± 0.19 SE (n = 46) for Guys Run, Piney Branch, and Glade Brook, respectively.

3. Highest photosynthetic rates occurred in early July following the emergence of the forest canopy. No irradiance-photosynthetic rate correlation was observed. This implied that other factors obscured that relationship and favored the early summer peak rates.

4. One tributary, Piney Branch, exhibited a chronically low pH (mean = 4.9) and low inorganic carbon concentration. Multivariate analysis suggested that, other than irradiance, periphyton production in this stream may be limited by available inorganic carbon.

5. Due to the surrounding forest, daily irradiance intensity at the stream surfaces was not found to be a bell shaped curve typical of areas open to full sunlight. Irradiance monitored at stream sites produced a rather flat curve during central daylight hours with short tails during morning and evening.

6. Tests comparing photosynthetic rates between variously shaded and completely unshaded stream sites suggested light saturations for the periphyton at approximately 20-30% of full sunlight.

7. Irradiance intensity was the only diurnally varying parameter on days of primary production measurement. It was used as a basis for expanding photosynthetic rate measurements to seasonal periphyton

productions for each stream. Annual autochthonous productions, calculated on a flat m^2 basis, were estimated at 6.54, 4.10 and 3.71 g C/y for Guys Run, Piney Branch, and Glade Brook, respectively.

8. Allochthonous input was 230 g $C/m^2/y$. Therefore autochthonous production represented about 3% of the annual energy budget of Guys Run and 2% for Piney Branch and Glade Brook. These percentages were slightly higher than suggested by many previous studies for woodland streams of first and second orders.

9. Time of year had a significant (p < 0.01) effect on primary production. 90 ± 1% of all autochthonous production occurred during late spring and summer for all three streams.

10. In summer when terrestrially derived detritus was poorest in quantity and quality, the periphyton was producing the majority of its annual input. Current theory, which states that periphyton contributes little to consumer production in low order woodland streams, is based upon generalized annual budgets. I suggest that because of the timing and high nutritional quality of periphyton, its importance may be greater than revealed in gross annual budgets. Reevaluation and refinement of the role of allochthonous input and periphyton production on a seasonal basis is called for.

11. Because of the importance of summer periphyton production, selective forest canopy thinning as a periphyton production enhancement technique was proposed. By admitting one fifth of the total solar irradiance, maximized autochthonous primary production might be gained without the disadvantages of frequent maintenance, overheating, or litter input loss.

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APPENDIX

Table A1. Primary production rates and selected physiochemical
parameters of Guys Run.

Date	Primary production rate (mg C/m^2/h)	Inorganic carbon (mg/l)	pH*	C^o	At site PAR light (langleys)	Ortho-phosphate (mg/l)	Discharge** (l/sec)
4/1/78	1.09	2.4	200	9.5	35.0	0.01	50.0
4/23/77	1.35	3.0	79	13.0	18.9	0.01	45.2
5/5/77	5.82	4.0	63	13.0	19.0	0.01	91.7
6/4/77	2.75	7.7	79	14.0	10.1	0.01	8.3
6/13/77	5.01	8.6	44	16.0	9.1	0.01	6.1
6/21/77	5.07	10.7	44	16.0	9.8	0.01	4.8
7/1/77	4.18	8.6	50	19.5	9.0	0.01	<1.8
7/12/77	7.16	11.0	50	18.0	7.4	0.02	14.6
7/17/77	3.65	12.0	63	18.0	8.5	0.02	<1.8
7/26/77	1.32	12.9	13	17.5	9.6	0.02	<1.8
7/28/77	2.66	15.0	25	15.0	9.1	0.02	<1.8
8/11/77	0.59	4.5	25	18.0	5.2	0.02	<1.8
8/30/77	1.61	5.4	20	18.0	8.8	0.02	<1.8
9/11/77	1.46	7.7	16	14.0	11.4	0.02	<1.8
9/12/77	0.72	7.7	16	15.0	9.9	0.02	<1.8
10/10/77	1.21	8.0	44	14.0	7.1	0.02	<1.8
10/21/77	0.80	12.3	44	8.0	23.5	0.01	<1.8
10/23/77	0.42	10.0	44	9.5	16.0	0.01	<1.8
11/1/77	0.96	8.5	32	9.0	21.6	0.01	2.2
11/13/77	0.83	5.6	63	7.0	46.2	0.01	54.4
11/15/77	1.27	5.4	63	7.0	41.4	0.01	36.8
12/2/77	1.21	2.0	200	8.0	21.3	0.01	246.0
12/13/77	1.13	4.0	160	8.0	22.3	0.01	75.0

*
 pH is expressed as moles per liter of hydrogen ions multiplied by 10^9 to
 eliminate decimals.
**
 Piney Branch discharge used as relative values.

Table A2. Primary production rates and selected physiochemical
parameters of Piney Branch.

Date	Primary production rate (mg C/m^2/h)	Inorganic carbon (mg/ℓ)	pH*	C^o	At site PAR light (langleys)	Ortho-phosphate (mg/ℓ)	Discharge** (ℓ/sec)
4/1/78	2.19	1.8	7,940	11.0	30.0	0.01	50.0
4/23/77	0.55	1.8	5,250	12.0	14.3	0.01	43.2
5/5/77	4.48	1.5	10,000	13.0	16.8	0.01	91.7
6/4/77	1.74	3.0	12,590	14.0	9.1	0.01	8.3
6/13/77	3.02	3.2	15,850	14.0	5.5	0.01	6.1
6/21/77	1.09	3.2	15,850	16.0	7.1	<0.01	4.8
7/1/77	5.46	3.2	15,850	17.0	6.2	0.01	<1.8
7/12/77	4.01	3.6	12,590	18.0	8.3	0.01	14.6
7/17/77	2.79	4.3	3,980	18.0	5.1	0.01	<1.8
7/26/77	1.47	1.1	12,590	17.0	6.4	0.02	<1.8
7/28/77	1.59	2.4	12,590	16.5	5.9	0.02	<1.8
8/11/77	0.70	1.8	15,850	19.0	2.4	0.03	<1.8
8/30/77	0.43	1.2	19,950	18.0	7.1	0.03	<1.8
9/11/77	0.97	1.2	7,940	15.0	3.5	0.03	<1.8
9/12/77	1.24	1.2	12,590	15.0	3.9	0.02	<1.8
10/10/77	0.37	0.9	7,940	14.0	2.7	0.02	<1.8
10/21/77	0.25	0.6	10,000	8.0	18.3	<0.01	<1.8
10/23/77	1.33	1.2	15,850	9.5	25.0	<0.01	<1.8
11/1/77	1.73	0.9	12,590	9.0	15.2	0.01	2.2
11/13/77	0.38	0.3	12,590	7.0	41.2	0.01	54.4
11/15/77	0.15	0.2	12,590	7.0	34.8	0.01	36.8
12/2/77	1.73	1.2	15,850	8.0	22.1	<0.01	246.0
12/13/77	0.40	0.3	10,000	8.0	22.1	<0.01	75.0

*pH is expressed as moles per liter of hydrogen ions multiplied by 10^9 to
eliminate decimals.

Table A3. Primary production rates and selected physiochemical
parameters of Glade Brook.

Date	Primary production rate (mg C/m²/h)	Inorganic carbon (mg/ℓ)	pH*	C°	At site PAR light (langleys)	Ortho-phosphate (mg/ℓ)	Discharge** (ℓ/sec)
4/1/78	0.47	3.0	160	10.0	28.0	0.01	50.0
4/23/77	0.48	5.0	100	12.0	9.6	0.01	45.2
5/5/77	1.02	5.0	100	12.0	10.5	0.01	91.7
6/4/77	2.06	6.0	100	14.0	3.9	0.01	8.3
6/13/77	3.70	6.1	130	14.5	4.3	0.01	6.1
6/21/77	3.20	6.1	130	16.0	7.1	0.01	4.8
7/1/77	3.82	6.1	160	17.5	5.6	0.01	<1.8
7/12/77	1.05	6.5	200	18.5	2.2	0.01	14.6
7/17/77	1.09	7.0	63	18.0	2.6	0.01	<1.8
7/26/77	2.31	6.2	63	17.0	2.6	0.01	<1.8
7/28/77	1.25	6.2	160	15.5	2.2	0.02	<1.8
8/11/77	1.26	5.7	160	19.0	1.1	0.01	<1.8
8/30/77	2.77	5.4	160	18.0	4.6	0.02	<1.8
9/11/77	0.92	5.4	79	14.5	2.3	0.02	<1.8
9/12/77	0.81	4.1	79	15.0	3.0	0.02	<1.8
10/10/77	0.41	4.7	400	14.0	1.4	0.02	<1.8
10/21/77	0.37	4.1	320	8.0	13.3	0.01	<1.8
10/23/77	0.95	4.1	200	9.5	18.0	0.01	<1.8
11/1/77	0.50	3.8	130	9.0	12.6	0.01	2.2
11/13/77	1.10	3.2	130	7.0	31.4	0.01	54.4
11/15/77	1.06	3.5	160	7.0	27.1	0.01	36.8
12/2/77	0.91	2.3	200	8.0	15.2	<0.01	246.0
12/13/77	0.25	2.9	320	7.0	16.2	<0.01	75.0

*pH is expressed as moles per liter of hydrogen ions multiplied by 10^9 to eliminate decimals.
**Piney Branch discharge used as relative values.

PERIPHYTON PRODUCTION IN AN APPALACHIAN MOUNTAIN
TROUT STREAM

by

Lawrence Ernest Hornick

(ABSTRACT)

Temporal production patterns for periphyton have been poorly quantified in small woodland streams. In this study periphyton production on natural substrates was measured in a second order, western Virginia trout stream and two of its tributaries. Measurements were taken about three times monthly from April 1977 through April 1978 excluding 74 days of inaccessibility due to snow. Primary production rates were estimated _in situ_ using ^{14}C assimilation in light and dark chambers equipped with circulating systems. Allochthonous input and physiochemical parameters were measured concurrently.

Annual mean photosynthetic rates at midday were 2.27 $\pm$ 0.37 SE, 1.65 $\pm$ 0.25 SE, and 1.37 $\pm$ 0.19 SE (n = 46) for Guys Run (main stream), Piney Branch, and Glade Brook, respectively. No relationship between the irradiance and photosynthetic rates was observed. Highest photosynthetic rates occurred in early July following the full emergence of the shading forest canopy. Tests comparing primary production rates between variously shaded and unshaded stream sites suggested periphyton light saturation to be about 20-30% of full sunlight. Mean daily irradiance for each season was calculated from light monitored at stream sites and used to estimate seasonal periphyton production in each stream.

Annual autochthonous production, on a flat m^2 basis, was 6.54, 4.10, and

3.71 g C/y for Guys Run, Piney Branch, and Glade Brook, respectively.

Compared to allochthonous input the periphyton contributed 3% of the

total energy budget of the main stream and about 2% for the tributaries.

Of the total autochthonous production, 90 $\pm$ 1% occurred during late

spring and summer for all streams. In summer when terrestrially derived

detritus was poorest in quantity and quality, periphyton was producing

a majority of its annual input. Current concepts, which consider con-

tributions by periphyton to consumer production to be extremely small

in low order woodland streams, are based upon annual energy budgets.

Because of the seasonal timing and high nutritional quality of periphy-

ton, its true importance in low order streams may be greater than

typically indicated in gross annual budgets. The roles of periphyton

production and allochthonous input need to be reevaluated and better

resolved on a seasonal basis.