Periphyton Production in an Appalachian Mountain Trout Stream[1]

L. E. HORNICK, J. R. WEBSTER and E. F. BENFIELD

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg 24061

ABSTRACT: Periphyton primary production was investigated in a second-order Appalachian Mountain stream and two of its tributaries. Using ^{14}C fixation in recirculating chambers, estimates averaged 2.27 mg C m^{-2} h^{-1} in the mainstream and 1.65 and 1.37 mg C m^{-2} h^{-1} in the two tributaries. Abiotic factors most influential on primary production rates were light, streamflow and inorganic carbon. Based on annual budgets, the estimated stream energy input attributable to autochthonous primary production was about 3% of allochthonous inputs. However, because of high nutritive value and timing, autochthony may be more important than indicated by annual budgets.

Introduction

Many studies have indicated that allochthonous organic material is the major energy base for low-order streams (*e.g.*, Nelson and Scott, 1962; Minckley, 1963; Hynes, 1963; Maciolek, 1966; Minshall, 1967; Fisher and Likens, 1972, 1973; Cummins, 1974). However, Minshall (1978) argued that belief in a general dependency of streams on allochthonous organic materials has resulted from a concentration of research effort in small streams in deciduous forests. In studies of such streams, the role of autotrophy has often been disregarded as negligible and not measured. 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 to measure the magnitude and fluctuations of autotrophy.

In general, quantitative measurements of annual primary production in lotic 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. Biomass accumulation techniques as measures of photosynthetic rate are considered error-prone for various reasons (Wetzel, 1975a). Hoskin (1959, as cited by Wetzel, 1975a) and Hall (1972) used the diurnal oxygen curve method in relatively small streams, but in most low-order streams, relatively high gradients and turbulence preclude using open system oxygen methods. Hansmann (1969) studied three streams, using the oxygen method but employing recirculating chambers to avoid problems produced by turbulence. Chambers improve measurements but in many cases, where primary production is relatively low, accurate measurement requires more sensitive methods than gas exchange techniques. Carbon-14 methodology is about 50 times more sensitive than gas exchange methods (Wetzel, 1975b) and therefore is particularly useful in low-order woodland streams. In this study we have coupled the advantages of using recirculating chambers and carbon-14 methodology to investigate carbon fixation rates in a second-order Appalachian Mountain trout stream and two of its tributaries.

Description of Study Area

Primary productivity measurements were made in Guys Run, a second-order tributary of the Calfpasture River (James River Basin, Rockbridge Co., Virginia; 79°39′ W long, 38°58′ N lat) and in two tributaries, Glade Brook and Piney Branch. Most of the 19 km² watershed of Guys Run is located within the Goshen Wildlife

[1]Address correspondence to J. R. Webster.

Management Area. Overstory vegetation is primarily oak, hickory, maple and pine with an understory of rhododendron and mountain laurel. Precipitation averages 96 cm per year with heaviest rains usually occurring during spring and late autumn (Crockett, 1972). Soils are acidic (average *p*H, 4.5) and derived from lower and middle Devonian shale, sandstone and quartzite (Bick, 1960). The relatively inert geology and the minimal disturbance within the basin produce clear, low-nutrient streams with angular gravel-rubble beds. Though the headwater springs issue acidic water (*p*H, ca. 5.0), the basin is within a highly folded syncline where local, thin, nonoutcropping limestone layers occasionally occur (Bick, 1960). Guys Run and Glade Brook seem to be buffered by such a layer near their sources, while Piney Branch is not and remains chronically acidic (*p*H, 4.7 - 5.7) for its entire length. General physical and chemical features of the three study streams are shown in Table 1.

Common algae in the streams included diatoms (*Cocconeis, Gomphonema, Navicula, Stauroneis* and *Synedra*), green algae (*Chlorococcum* and *Microspora*) and blue-green algae (*Eurotia* and *Schizothrix*). Periphyton chlorophyll *a* concentrations were measured seasonally by standard techniques (APHA, 1976) and ranged from 7 - 55 mg Chl. *a* m^{-2} averaging about 50 mg Chl. *a* m^{-2}.

MATERIALS AND METHODS

Primary production rates of periphyton on natural substrates were estimated *in situ* using recirculating chambers and ^{14}C. Experiments in all three streams were performed approximately three times monthly from April 1977 through April 1978, excluding a period of ice cover and inaccessibility from January-March 1978. Study sites were located near the mouths of the tributaries and on Guys Run ca. 3 km from the headwaters, just upstream of the mouth of Glade Brook.

The recirculating chambers were slight modifications of those designed by Rodgers *et al.* (1978) and consisted of 1.9-liter polystyrene cylinders with lids. Battery-powered submersible pumps maintained water circulation (pumping 300 ml/min) during the experiments. Two clear and two opaque chambers, containing natural substrates, were placed at each stream site on each sampling date. Natural substrates, typically small cobble-sized rocks, were randomly selected and, with minimal disturbance, transferred from the streambed to the incubation chambers. Chambers were filled with stream water, sealed and positioned in the stream with the tops just below the water surface. Three-hr midday incubation periods were initiated by injecting chambers with 6.5 μCi of ^{14}C- sodium bicarbonate. Freshly broken rock surfaces and formalin-fixed samples were used as controls. Injections were equal within $\pm 4\%$ and ^{14}C concentrations remained high throughout the incubation periods. At the end of incubation, substrates were removed from the chambers and placed in plastic bags containing stream water

TABLE 1.—Physical and chemical parameters of the three study streams

	Guys Run	Piney Branch	Glade Brook
Stream length (m)	8000	2050	1050
Mean gradient (m km^{-1})	40	86	49
Mean channel width (m)	5.1	3.0	2.4
Mean midstream depth at study sites (cm)	20	8	7
Mean annual discharge (1 sec^{-1})	414	51	44
Drainage basin area (km^2)	19.0	3.3	1.2
Mean *p*H (range)	7.4 (6.8 - 7.8)	4.0 (4.7 - 5.4)	6.8 (6.4 - 7.2)
Mean phosphate-orthophosphate (mg 1^{-1})	0.013	0.013	0.011
Mean nitrate (mg 1^{-1})	0.051	0.061	0.029
Mean inorganic carbon (mg 1^{-1})	7.8	1.9	4.8
Mean sulfate (mg 1^{-1})	4.4	3.8	4.4
Mean hardness (mg 1^{-1}) (Ca, Mg, Fe, Zn, Mn)	23.6	4.8	18.0

adjusted to *p*H 8.5 and transferred to the laboratory on ice.

In the laboratory, two 7 cm^2 periphyton subsamples were taken with a small wire brush from each substrate from an area defined by a foam-bottomed Plexiglas cylinder. Based on microscopic examination, removal was >95% effective. Loosened material was transferred to a 5 ml shell vial and fumed with concentrated HCL in a 95 C water bath to eliminate residual tagged inorganic carbon (Wetzel, 1965). Samples were frozen until final processing.

Samples were wet-oxidized with potassium dichromate (Shimshi, 1969) and evolved $^{14}CO_2$ was trapped in 0.25 N sodium hydroxide and incorporated into Triton X100 scintillation solution (Rodgers *et al.*, 1978). Oxidation efficiency, as checked by known additions of ^{14}C, was 86% ± 3%. Samples were counted by liquid scintillation. Counting efficiency, measured by external channels ratio and internal standard activity additions, was 85% to 100%. Final areal primary productivity was calculated using the formula given by Vollenweider (1974). The specific activity of ^{14}C in the chambers was calculated from inorganic carbon concentrations measured with an infrared carbon analyzer (Ionics, Inc.). Two subsample scrapings from each substrate were averaged to yield two clear and two opaque chamber rates for each *in situ* incubation. Because dark activity was low, light fixation was used as an estimate of net primary production (Strickland and Parsons, 1972; Hall and Moll, 1975; Wetzel, 1975b).

Water samples were collected at each site on each incubation date. Samples were analyzed for a variety of chemical parameters according to Standard Methods (APHA, 1976). Air and stream temperatures (Weather Measure Corp.) and stream discharge (HL flume) were continuously recorded at Piney Branch and spot-measured at the other two sites. Total unshaded solar irradiance (300-2600 nm wavelength) was recorded by a thermoelectric line pyranometer (Weather Measure Corp.) located in a clearing near the stream sites. Photosynthetically active radiation (PAR, 390-710 nm) was checked by surveying clear and shaded stream sites using a PAR quantum sensor (Lambda Inst. Co.). The ratio of PAR to total solar irradiance was 0.49. Actual PAR light quantity (in langleys) to sites during productivity measurements was calculated as: PAR = 0.49 × total irradiance during incubation × % canopy penetration. Corrections were also made for water reflectance (ca. 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).

RESULTS

Abiotic variables. — Discharge measured in Piney Branch (Fig. 1) was greatest in winter, moderate in spring and low from late June through late October. Summer rainfall in 1977 was 17% below average. Based on USGS measurements of flow in the Maury River just below the confluence with the Calfpasture River (ca. 10 km from Guys Run), annual discharge was about 80% of the average over the last 50 years. During our study, the maximum flow in the Maury River had a return period of 1.5 years. Spot measurements of water temperature showed little difference between temperatures in Guys Run and Glade Brook and the continuous measurements from Piney Branch (Fig. 1). Average annual stream temperature in Piney Branch was 13.5 C ranging from 0 - 19 C.

Inorganic carbon concentrations were low in Piney Branch due to chronic acidity (Table 1). Concentrations were generally highest in summer (Fig. 2), though a peak was observed in Guys Run in October. Hydrogen ion concentrations remained fairly consistent throughout the study (Fig. 2). Orthophosphate concentrations varied between 0.01 and 0.03 mg l^{-1} during the study and concentrations in the three streams were not significantly different (Table 1). Peak concentrations occurred during summer at lowest discharge. Total phosphate concentrations were usually 1.2 to 2.0 times orthophosphate concentrations.

Seasons were defined based on canopy condition. Spring was defined by the change from high winter light penetration to heavy summer shading, and autumn by the five dates of increasing light penetration (Fig. 3). Irradiance was most influenced by forest canopy conditions rather than seasonal day length and light intensity.

Primary production rates. — In the 1-year experimental period, the highest midday primary production rate for each stream occurred in early July (Fig. 4). Primary production rates in Guys Run ranged between 0.42 and 7.16 mg C m^{-2} h^{-1} with a mean of 2.27 mg C m^{-2} h^{-1} ($\pm$0.37 SE, n = 50). Photosynthetic rates in the two tributaries were significantly lower (analysis of variance; α = .05): rates in Piney Branch ranged from 0.15 - 5.46 mg C m^{-2} h^{-1}, with a mean of 1.65 mg C m^{-2} h^{-1} ($\pm$0.25 SE, n = 50), and in Glade Brook, from 0.25 - 3.82 mg C m^{-2} h^{-1}, with a mean of 1.37 mg C m^{-2} h^{-1} ($\pm$0.19 SE, n = 50). Primary production rates in the two tributaries were not significantly different during the study period.

In all three streams, primary production rates peaked in spring and early summer, then declined during summer and autumn (Fig. 4). In Piney Branch and Guys Run, peaks in mid-May were followed by sharp declines coinciding with the "leafing out" of riparian vegetation at the end of May. Primary production in Glade Brook did not exhibit a mid-May peak perhaps due to a N-S channel orientation at the study site which prevented the stream from receiving maximum irradiance. Summer peak values can probably be attributed to increases in available inorganic carbon and higher temperature offsetting the effects of lowered light intensity. Slight increases in productivity were observed in mid-autumn as available light increased due to leaf fall.

Primary production rate, inorganic carbon concentration, *p*H, temperature, PAR, orthophosphate concentration and discharge were compared by multivariate analysis of covariance. Analyses were made for each stream and season and for all samples combined (Table 2). Several general observations emerged from this analysis. There was a slight inverse correlation between discharge and the concentration of hydrogen ions (direct for *p*H), orthophosphate and inorganic carbon. This inverse correlation was

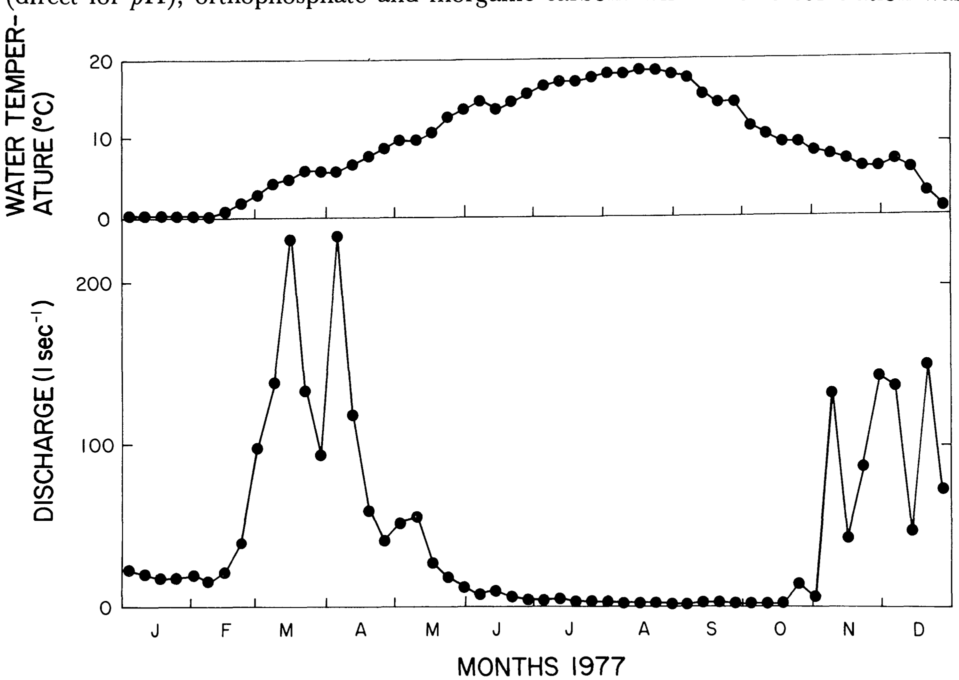

Fig. 1.—Water temperature and discharge in Piney Branch in 1977

probably a result of dilution. The most favorable lighting and temperature conditions were negatively correlated, which contrasts with the synergistic effect of summer light and temperature in unshaded streams. Correlations between primary production rate and nutrient concentrations were variable. Orthophosphate concentrations did not show a direct correlation with primary production rates in any stream.

In Piney Branch, inorganic carbon was significantly correlated with photosynthetic rate (r = 0.56 over all seasons and r = 0.66 in summer; n = 18 and 12, respectively). Piney Branch has chronically low inorganic carbon levels, suggesting that availability of inorganic carbon may, at times, limit primary production.

Although primary production rate and discharge did not appear to be correlated on an annual basis, a significant correlation (r = 0.71, n = 12) was observed in Guys

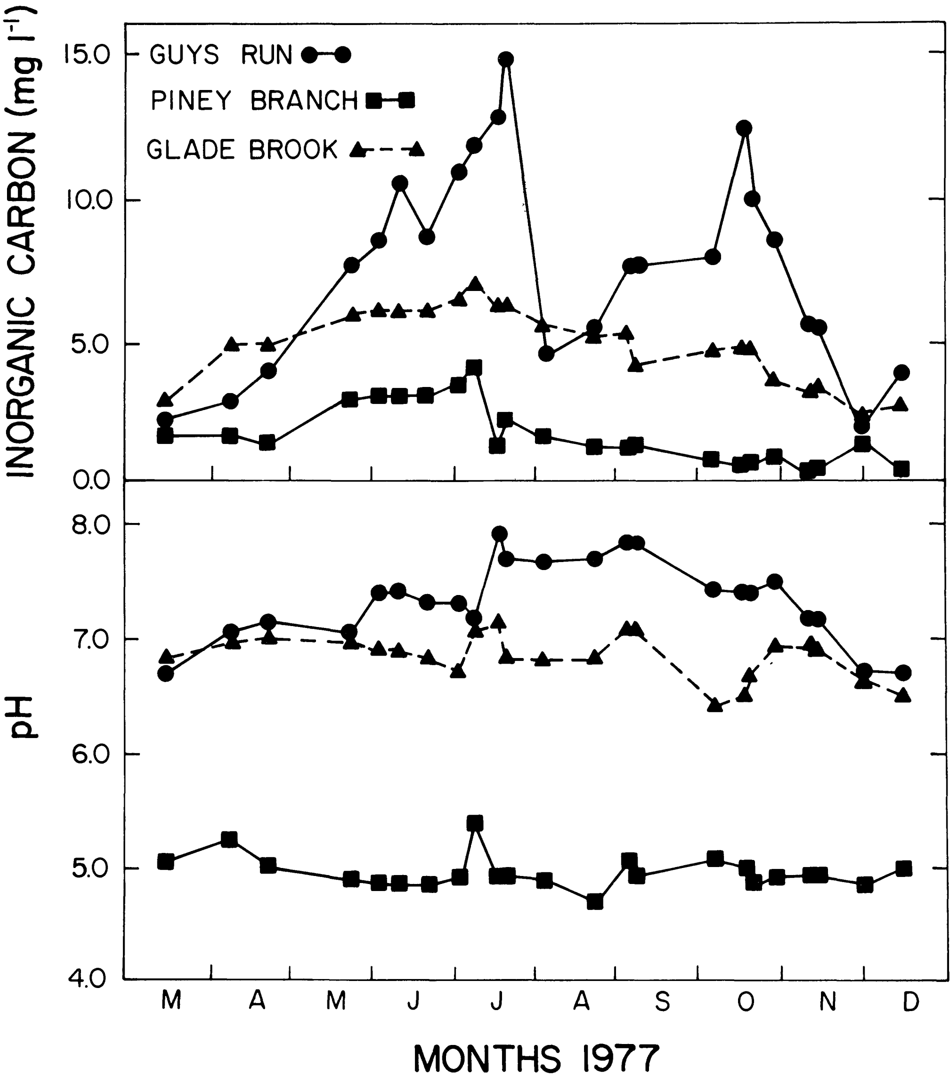

Fig. 2.—Inorganic carbon and *p*H in the three study streams

Run in summer. The summer correlation might have been related to the lack of stimulatory flow effects on diffusion gradients in the immediate vicinity of algal cells during low flows, and to the cleansing effects of high flows (McIntire, 1966 a,b).

In a series of experiments comparing shaded and unshaded sites, ^{14}C fixation rates were higher in unshaded sites (Table 3). Differences were most pronounced in June when light levels were extremely low beneath the forest canopy. These experiments suggest a correlation between primary production and irradiance when canopy shading keeps light below the saturation level. However, in our measurements of primary production under natural shaded conditions, we were unable to demonstrate a statistically significant correlation (Table 2). Gregory (1980) tested the hypothesis that light rather than NO_3-N limited primary production in a small forested stream in Oregon. Differences in intensity between natural light and his artificial light were significant. Artificially lighted sections, with and without NO_3-N, exhibited much higher photosynthetic rates than naturally lighted sections with and without nutrient additions. Studies of larger woodland streams or meadow streams with higher light and nutrient levels have also been able to relate irradiance to primary production rate (*e.g.*, Marker, 1976; Bott *et al.*, 1978).

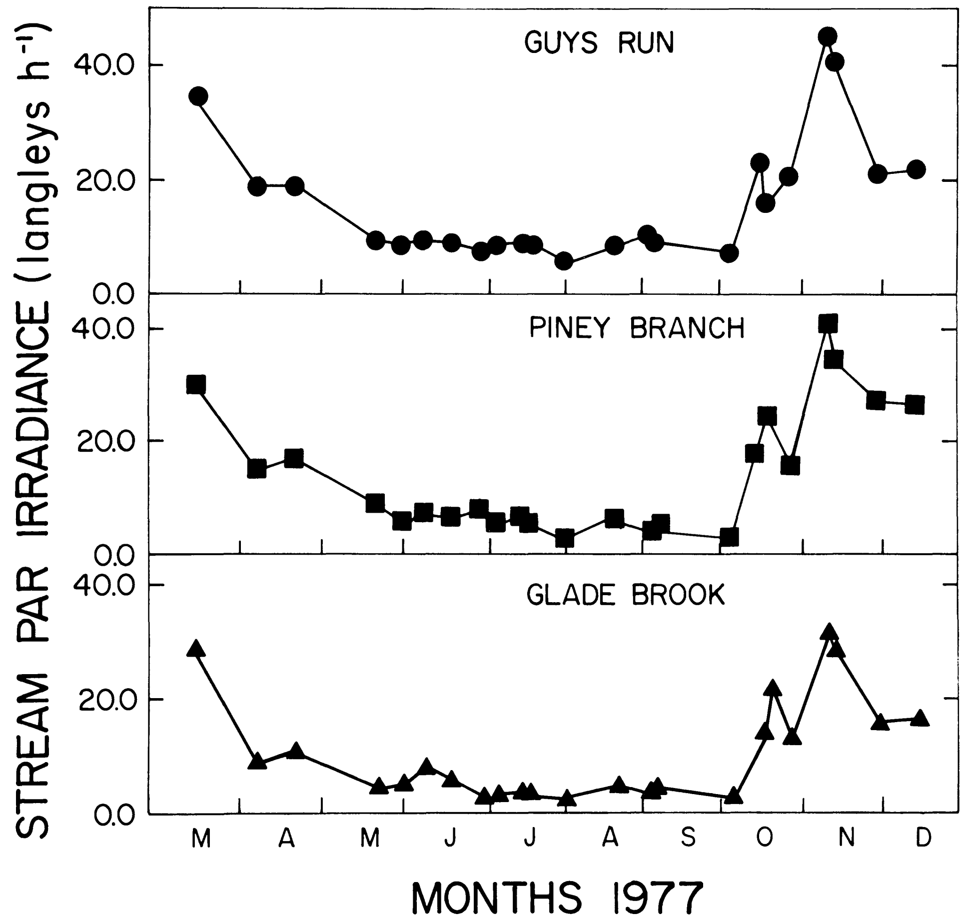

Fig. 3.—Photosynthetically active radiation (PAR) in the three study streams

Annual and seasonal primary production. — The 3-hour measurements of primary production rates were expanded to seasonal and annual estimates by multiplying by the hours of sunlight. This was considered appropriate for several reasons. In lacustrine studies, integrated daily irradiance is routinely used to expand short-term measurements (Vollenweider, 1974; Wetzel, 1975b). However, we found that PAR measured at the stream surface was not a typical bell-shaped curve, but was very flat during most of the day with short tails at morning and evening. Therefore, daily

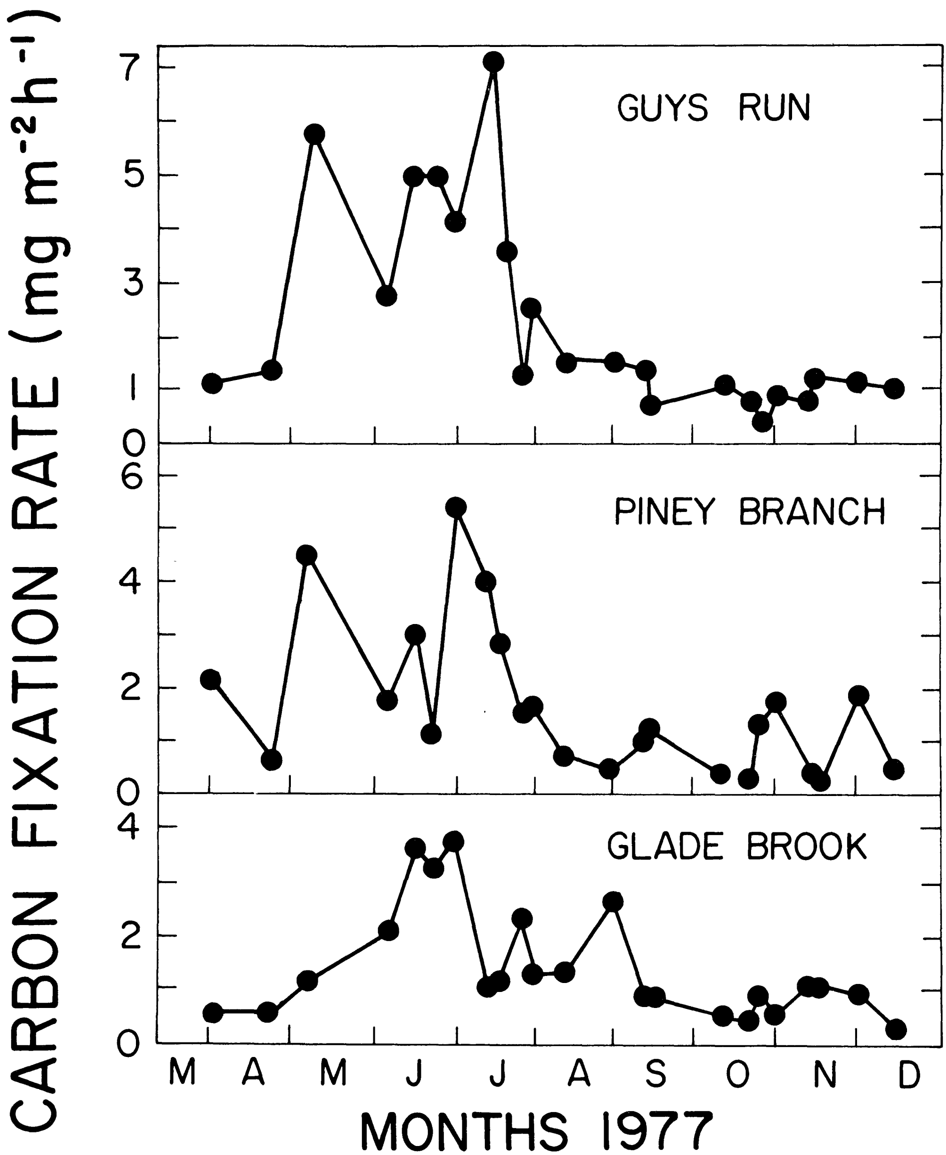

Fig. 4. — ^{14}C measured carbon assimilation rates in the three study streams. Error bars are ±1 SE

photosynthesis was calculated as the midday rate times the period of constant irradiation plus a fraction of the lower light intensity period estimated by integrating the tails of the curve. Seasonal primary production was calculated by multiplying the total number of daytime hours of a season (adjusted for low light intensity periods) by the mean hourly photosynthetic rate for that season (Table 4). We assumed primary production was zero during January-February when the streams were ice-covered. Seasonal primary production estimates were similar for the three streams except for low primary production in Glade Brook in spring and substantially higher summer primary production in Guys Run. As a result of higher summer primary production, annual primary production in the larger stream exceeded annual primary production in its tributaries. Combined spring and summer production represented ca. 90% of annual primary production in each stream.

DISCUSSION

Direct measurements of *in situ* rates of lotic primary production are confounded by a variety of problems. Problems, other than technical difficulties, are related to variation in physical, chemical and biotic parameters (Hynes, 1970; Wetzel, 1975a). Table 5 is a compilation of periphyton production data from a number of stream studies. Not included in the table are studies of artificial streams (*e.g.*, McIntire and Phinney, 1965), thermal streams (*e.g.*, Naiman, 1976) or streams dominated by macrophytes (*e.g.*, Nelson and Scott, 1962). It is evident from Table 5 that published rates of primary production are extremely variable. The variability is partially a function of the variety of measurement techniques and partially a function of inherent variability among streams.

Although the variability makes it difficult to compare studies listed in Table 5, we can make some general observations. With respect to our study, production rates in Guys Run are among the lowest rates published but are similar to rates measured in

TABLE 2.—Partial correlation coefficients for all streams over all seasons, n = 68

	^{14}C Fixation	Inorganic carbon	Temperature	PAR light	Orthophosphate	Relative discharge
Inorganic carbon	0.337					
Temperature	0.129	-0.020				
PAR light	-0.052	0.125	-0.527			
Orthophosphate	-0.317	-0.155	0.157	0.051		
Relative discharge	0.178	-0.100	0.087	-0.489	-0.281	
*p*H	0.075	-0.052	-0.027	0.0[illegible]8	-0.063	0.142

TABLE 3.—Results of experiments comparing primary production rates in 1977 for forest canopy shaded and unshaded stream sites

Stream	Date	Canopy light penetration (%)	^{14}C fixation rates (mg C $m^{-2}h^{-1}$) Shaded	Unshaded
Piney	23 April	50	0.55	1.05
Branch	5 May	25	4.48	9.41
	4 June	7	1.74	6.90
	13 June	5	3.02	10.65
Guys Run	23 April	65	1.35	1.89
	5 May	30	5.82	8.84
	4 June	8	2.75	9.17
	13 June	7	5.01	15.03

other small, forest-shaded streams (Minshall, 1967; Elwood and Nelson, 1972). In general, there appears to be a relationship between periphyton primary production and stream size: Small forest-shaded streams have low primary production, larger streams have higher primary production. The downstream increase in primary production we observed in Guys Run agrees with this observation. However, the general relationship, which is a fundamental aspect of the river continuum concept (Vannote *et al.*, 1980), is modified by a variety of site-specific factors. For example, periphyton production estimates made for the Danube River by Ertl and Tomajka (1973) are low relative to the size of the river; however, the measurements were made at several meters' depth in fairly turbid water. In contrast, Cushing's (1967) measurements in the Columbia River were made in a large shallow riffle open to full sunlight. As Minshall (1978) observed, some small streams seem to have particularly high primary production for their size, particularly those with high nutrient waters flowing through well-lighted meadows or farmlands (McDiffett *et al.*, 1972; Marker, 1976; Bott *et al.*, 1978). Deep Creek (Minshall, 1978), a well-lighted desert stream, typifies this observation.

Comparing allochthonous and autochthonous inputs to those of streams in the Appalachian Mountain region, the general observation can be made that as stream width increases, light reaching the stream increases and there is a concomitant decrease in allochthonous input to the stream (Vannote *et al.*, 1980). As a result, the ratio of autochthonous to allochthonous inputs increases. Allochthonous inputs to Guys Run and Piney Branch were measured at five sites (three on Guys Run, two on Piney Branch), using 0.1 m^2 litter traps and 0.29 m wide lateral movement (blow-in) traps. There were no statistical differences among sites. Mean allochthonous input at the five sites was 347 g $m^{-2}y^{-1}$ vertical fall and 113 g $m^{-2}y^{-1}$ lateral movement (linear movements converted to area based on average width). Multiplying the total dry weight input by 0.5 g C per g dry weight gives 230 g C $m^{-2}y^{-1}$. If we use this figure, autochthonous primary production accounted for 3% of the total energy input to Guys Run and ca. 2% for Piney Branch and Glade Brook. Autochthonous production may be somewhat higher than these estimates for several reasons: (1) Small rocks were necessarily used in our studies but have been shown to be less productive sites than larger rock surfaces (McConnell and Sigler, 1959; Duffer and Dorris, 1966); (2) photosynthesis was assumed to be zero during much of the winter; (3) subsampled areas were expanded to streambed area without regard to the actual streambed surface area.

Estimates of the relative importance of autochthonous to allochthonous inputs to streams probably greatly underestimate the importance of autochthonous production to consumers. Leaf litter is a low-quality food source. Most hardwood trees withdraw a major portion of the nutrients, particularly nitrogen, from leaves before abscission (*e.g.*, Zimka and Stachurski, 1976), and much of the remaining carbonaceous material is not directly digestible by macroinvertebrates (Hynes, 1975) but is only made available through colonization by aquatic fungi and bacteria (e.g., Kaushik and

TABLE 4.—Seasonal and annual primary production in the three study streams

	Primary production (g C m^{-2})		
Season	Guys Run	Piney Branch	Glade Brook
Spring	1.58	1.38	0.39
Summer	4.40	2.28	2.92
Autumn	0.21	0.23	0.14
Winter	0.35	0.21	0.26
Total	6.54	4.10	3.71

TABLE 5. — Estimates of average annual (or annual range) net primary production by periphyton in streams. The following conversions were used: g C m^{-2} = 0.286 × g O_2 m^{-2} (Westlake, 1974; Stockner, 1968; Megard, 1972; Bott *et al.*, 1978); net production = 0.556 × gross production (Westlake, 1974; Likens, 1975); 4.52 kcal per g AFDW (Kevern and Ball, 1965); g C = 0.45 × dry weight (Odum, 1971); and g C = 0.47 × g AFDW (Westlake, 1974)

Net primary production (g C m^{-2} d^{-1})	Study area	Stream flow average or range (m^3 sec^{-1})	Technique	Reference
0.004 - 0.007	Morgan's Cr., Ky.	0.005 - 0.350	Biomass change	Minshall, 1967
0.008 - 0.011	Walker Br., Tenn.	0.015	Biomass change	Elwood and Nelson, 1972
0.010	Glade Br., Va.	0.044	^{14}C in circulating chambers	This study
0.011	Piney Br., Va.	0.051	^{14}C in circulating chambers	This study
0.018	Guys Run, Va.	0.41	^{14}C in circulating	This study
0.050 - 1.200	Red Cedar R., Mich.	5.7	Biomass change on artificial substrates	King and Ball, 1966
0.099	Berry Cr., Ore.	0.014	O_2 changes in circulating chambers	Reese, 1966
0.14	Lost Cr., Kan.	0.17	Diurnal O_2 curve	Gelroth and Marzolf, 1978
0.14 - 0.41	Danube River	>2000	O_2 changes in chambers with artificial substrates	Ertl and Tomajka, 1973
0.16	Root Sp., Mass.	0.0005	O_2 changes in chambers	Teal, 1957
0.048 - 1.570	9 streams in N.C.	———	O_2 Upstream - downstream O_2 changes	Hoskin, 1959
0.25	Fort R., Mass.	1.4	O_2 changes in circulating chambers	Sumner and Fisher, 1979
0.30 - 0.46	Drift Cr., Ore.	0.118	O_2 changes in circulating chambers	Hansmann, 1969

0.30 - 1.02	Bere St., England	0.7	O_2 changes in circulating chambers	Marker, 1976
0.33 - 1.43	New Hope Cr., N.C.	0 - 8.1	Diurnal O_2 curve	Hall, 1972
0.41 - 1.40	Raritan R., N.J.	0.25	Upstream - downstream O_2 changes	Flemer, 1974
0.73	R. Thames, England	———	O_2 changes in plastic domes	Berrie, 1972
0.78	Buffalo, Cr., Pa.	———	Upstream - downstream O_2 changes	McDiffert *et al.,* 1972
1.11	Logan R., Utah	———	Chlorophyll *a*	McConnell and Sigler, 1959
1.18	Deep Cr., Idaho	0.09 (baseflow)	Upstream - downstream O_2 changes	Minshall, 1978
1.85	Catahoula Cr., Miss.	0.007	Upstream - downstream O_2 changes	de la Cruz and Post, 1977
0.75 - 2.62	Truckee R., Nev.	7.7	O_2 changes in circulating chambers with artificial substrates	Thomas and O' Connell, 1966
0.9 - 2.0	Madison R., Wyo.	13	Upstream - downstream O_2 changes	Wright and Mills, 1967
2.22	White Clay Cr., Pa.	0.13 (baseflow)	Average of 5 methods using O_2 and CO_2 changes upstream - downstream and in circulating chambers	Bott *et al.,* 1978
0.44 - 3.28	Blue R., Okla.	1.1	Upstream - downstream O_2 changes	Duffer and Dorris, 1966
0.16 - 5.14	Cedar Cr., Kan.	1.5	Upstream - downstream O_2 changes	Prophet and Ransom, 1974
2.34 - 33.90	Columbia R., Wash.	———	Biomass change on artificial substrates	Cushing, 1967

Hynes, 1968; Hargrave, 1969; Iverson, 1973; Bärlocher and Kendrick, 1975). Also, recent work by Suberkropp and Klug (1976) and Ward and Cummins (1979) demonstrated that leaf detritus is most nutritious during the 1st month of residence in streams and becomes less nutritious thereafter.

In contrast to the low quality of leaf detritus, periphyton is high in food quality with a rich lipid and protein content (Cummins and Wuycheck, 1971; Naiman and Sedell, 1979). Assimilation efficiencies are relatively high (30-60%; Cummins, 1975; McCullough *et al.*, 1979 a,b) compared to the low assimilation efficiencies of terrestrial leaf detritus (generally less than 50%; Cummins, 1969; McDiffett, 1970; Vannote, 1969; Grafius and Anderson, 1979; Webster and Patten, 1979). In their study of filter-feeding caddisflies in an Appalachian stream, Benke and Wallace (1980) estimated that more production was attributable to algae than to vascular plant detritus even though vascular plant detritus was more abundant in the seston. The difference was the higher assimilation efficiency of algal material. Grafius and Anderson (1979) pointed out that growth and production of shredders may be limited by the lack of high-quality food. More polyphagous insects can supplement their protein requirement by ingesting algae when available. Many aquatic insects of shaded first- and second-order woodland streams seem to ingest periphyton, usually diatoms, to a greater extent than the algal standing crops would indicate (Chapman, 1966; Mecom, 1972; Moore, 1977). Chapman (1966) showed that the gut contents of 27% of Ephemeroptera and 32% of Plecoptera in a small shaded stream in Oregon were 50-90% algal on an annual basis. Most other noncarnivores in the stream contained 5-40% algae on an annual basis. Chapman also found that 7% of the total salmonid energy intake on an annual basis was indirectly attributable to algae, though the streams were as shaded as Guys Run. In another stream, much like Guys Run, algae were found to constitute 17-21% of the macroinvertebrate food supply (Coffman *et al.*, 1971).

In the generally mild climatic region of the southern Appalachian Mountains, periphyton is probably available all year long, but particularly in late spring and summer. During this spring-summer period, there is little input of new leaf material, and the leaf detritus present is low-quality, decay-resistant material. Autochthonous primary production may be of significant importance to low-order stream ecosystems in providing a high-quality, though limited-quantity, food resource during spring and summer when the quantity and quality of leaf detritus are low.

Acknowledgments.—Dr. Larry Lee, Statistics Department, Virginia Tech, assisted with the statistical analyses. Access to the study area was provided by the Virginia Commission of Game and Inland Fisheries. The research was supported by a grant from the U.S. Forest Service, Southeastern Forest Experiment Station.

LITERATURE CITED

AMERICAN PUBLIC HEALTH ASSOCIATION. 1976. Standard methods for the examination of water and wastewater, 14th ed. Am. Publ. Health Assoc., Washington, D.C. 1193 p.

BARLOCHER, F. AND B. KENDRICK. 1975. Dynamics of the fungal populations on leaves in a stream. *J. Ecol.*, **62**:761-791.

BENKE, A. C. AND J. B. WALLACE. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology*, **61**:108-118.

BERRIE, A. D. 1972. Productivity of the River Thames at Reading, p. 69-86. *In:* R. W. Edwards and D. J. Garrod (eds.). Conservation and productivity of natural waters. Symp. Zool. Soc. Lond.

BICK, K. F. 1960. Geology of the Lexington Quadrangle Virginia report of investigation 1. Va. Division of Mineral Resources, Charlottesville. 40 p.

BOTT, T. L., J. T. BROCK, C. E. CUSHING, S. V. GREGORY, D. KING AND R. C. PETERSEN. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. *Hydrobiologia*, **60**:3-12.

CHAPMAN, D. W. 1966. The relative contributions of aquatic and terrestrial primary producers to trophic relationships of stream organisms p. 116-129. *In:* K. W. Cummins, C. A. Tryon Jr. and R. T. Hartman (eds.). Pymatuning symposium in ecology. Edwards Bros., Ann Arbor, Michigan.

COFFMAN, W. P., K. W. CUMMINS AND J. C. WUYCHECK. 1971. Energy flow in a woodland stream ecosystem: I. Tissue support and trophic structure of the autumnal community. *Arch. Hydrobiol.*, **68**:232-276.

CROCKETT, C. W. 1972. Climatological summaries for selected stations in Virginia. Virginia Water Resources Center, Virginia Polytechnic Institute and State University, Blacksburg. 164 p.

CRUZ, A. DE LA AND H. A. POST. 1977. Production and transport of organic matter in a woodland stream. *Arch. Hyrobiol.*, **80**:227-238.

CUMMINS, K. W. 1969. Energy budgets, p. 31-37. *In:* The stream ecosystem. Technical Report Number 7, Institute of Water Research, Michigan State University, East Lansing.

______. 1974. Structure and function of stream ecosystems. *BioScience,* **24**:631-641.

______. 1975. The ecology of running waters, theory and practice, p. 277-293. *In:* D. B. Baker, W. B. Jackson and B. L. Prater (eds.). Proc. of the Sandusky River Basin Symposium. May 2-3, 1975, Heidelberg College, Tiffin, Ohio.

______ AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Int. Ver. Theor. Angew. Limnol.*, **18**:1-158.

CUSHING, C. E. 1967. Periphyton productivity and radionuclide accumulation in the Columbia River, Washington. *Hydrobiologia,* **24**:125-139.

DUFFER, W. R. AND T. C. DORRIS. 1966. Primary productivity in a southern Great Plains stream. *Limnol. Oceanogr.*, **11**:143-151.

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**:295-305.

ERTL, M. AND J. TOMAJKA. 1973. Primary production of the periphyton in the littoral of the Danube. *Hydrobiologia,* **42**:429-444.

FISHER, S. G. AND G. E. LIKENS. 1972. Stream ecosystem: organic energy budget. *BioScience,* **22**:33-35.

______ AND ______. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecol. Monogr.*, **43**:421-439.

FLEMER, D. A. 1974. Primary productivity in the North Branch of the Raritan River, New Jersey. *Hydrobiologia,* **35**:273-293.

GELROTH, J. V. AND G. R. MARZOLF. 1978. Primary production and litter decomposition in natural and channelized portions of a Kansas stream. *Am. Midl. Nat.*, **99**:238-243.

GRAFIUS, E. AND N. H. ANDERSON. 1979. Population dynamics, bioenergetics, and role of *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) in an Oregon Woodland stream. *Ecology,* **60**:433-441.

GREGORY, S. V. 1980. Effects of light, nutrients and grazing on periphyton communities in streams. Ph.D. Dissertation Oregon St. Univ., Corvallis. 165 p.

HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. *Ecology,* **53**: 585-604.

______ AND R. MOLL. 1975. Methods of assessing aquatic primary productivity, p. 19-52. *In:* H. Lieth and R. H. Whittaker (eds.). Primary productivity of the biosphere. Springer-Verlag, New York.

HANSMANN, E. W. 1969. The effects of logging on periphyton communities of coastal streams. Ph.D. Dissertation, Oregon St. Univ., Corvallis. 133 p.

HARGRAVE, B. T. 1969. Epibenthic algal production and community respiration in the sediments of Marion Lake. *J. Fish. Res. Board Can.*, **26**:2003-2026.

HOSKIN, C. M. 1959. Studies of oxygen metabolism of streams of North Carolina. *Publ. Inst. Mar. Sci. Univ. Tex.*, **6**:186-192.

HYNES, H. B. N. 1963. Imported organic matter and secondary productivity in streams. *Int. Congr. Zool.*, **16**:324-329.

______. 1970. The ecology of running waters. Univ. Toronto Press, Toronto. 555 p.

______. 1975. The stream and its valley. *Verh. Int. Verein. Limnol.*, **19**:1-15.

IVERSON, T. M. 1973. Decomposition of autumn-shed beech leaves in a springbrook and its significance to the fauna. *Arch. Hydrobiol.*, **73**:305-312.

KAUSHIK, N. K. AND H. B. N. HYNES. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. *J. Ecol.*, **56**:229-243.

KEVERN, N. R. AND R. C. BALL. 1965. Primary productivity and energy relationships in artificial streams. *Limnol. Oceanogr.*, **10**:74-87.

KING, D. L. AND R. C. BALL. 1966. A qualitative and quantitative measure of aufwuchs production. *Trans. Am. Microsc. Soc.*, **85**:232-240.

LIKENS, G. E. 1975. Primary production of inland aquatic ecosystems, p. 185-202. *In:* H. Leith and R. H. Whittaker (eds.). Primary productivity of the biosphere. Springer-Verlag, New York.

MACIOLEK, J. A. 1966. Abundance and character of microseston in a California mountain stream. *Verh. Int. Verein. Limnol.,* **16**:639-645.

MARKER, A. F. H. 1976. The benthic algae of some streams in southern England. 11. The primary production of the epilithon in a small chalk-stream. *J. Ecol.,* **64**:359-373.

MCCONNELL, W. J. AND W. F. SIGLER. 1959. Chlorophyll and productivity in a mountain river. *Limnol. Oceanogr.,* **4**:335-351.

MCCULLOUGH, D. A., G. W. MINSHALL AND C. E. CUSHING. 1979a. Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. *Ecology,* **60**:585-596.

______, ______ AND ______. 1979b. Bioenergetics of a stream "collector" organism, *Tricorythodes minutus* (Insecta: Ephemeroptera). *Limnol. Oceanogr.,* **24**:45-58.

MCDIFFETT, W. F. 1970. The transformation of energy by a stream detritivore *Pteronarcys scotti* (Plecoptera). *Ecology,* **51**:995-998.

______, A. E. CARR AND D. L. YOUNG. 1972. An estimate of primary productivity in a Pennsylvania trout stream using a diurnal oxygen curve technique. *Am. Midl. Nat.,* **87**:564-570.

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

______. 1966b. Some factors affecting respiration of periphyton communities in lotic environments. *Ecology,* **47**:918-930.

______ AND H. K. PHINNEY. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. *Ecol. Monogr.,* **35**:237-258.

MECOM, J. O. 1972. Feeding habits of Trichoptera in a mountain stream. *Oikos,* **23**:401-407.

MEGARD, R. O. 1972. Phytoplankton, photosynthesis, and phosphorus in Lake Minnetonka, Minnesota. *Limnol. Oceanogr.,* **17**:68-87.

MINCKLEY, W. L. 1963. The ecology of a spring stream, Doe Run, Meade County, Kentucky. *Wildl. Monogr.,* **11**:1-124.

MINSHALL, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology,* **48**:139-149.

______. 1978. Autotrophy in stream ecosystems. *BioScience,* **28**:767-771.

MOORE, J. W. 1977. Some factors affecting algal consumption in subarctic Ephemeroptera, Plecoptera and Simuliidae. *Oecologia (Berl.),* **27**:261-273.

NAIMAN, R. J. 1976. Primary production, standing crop, and export of organic matter in a Mohave desert thermal stream. *L:imnol. Oceanogr.,* **21**:60-73.

______ AND J. R. SEDELL. 1979. Characterization of particulate organic matter transport by some Cascade Mountain streams. *J. Fish. Res. Board Can.,* **36**:17-31.

NELSON, D. J. AND D. C. SCOTT. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. *Limnol. Oceanogr.,* **7**:396-413.

ODUM, E. P. 1971. Fundamentals of ecology, 3rd ed. Saunders, Philadelphia. 574 p.

PROPHET, C. W. AND J. D. RANSOM. 1974. Summer stream metabolism values for Cedar Creek, Kansas. *Southwest. Nat.,* **19**:305-308.

REESE, W. H. 1966. Physiological ecology and structure of benthic communities in a woodland stream. Ph.D. Dissertation, Oregon State Univ., Corvallis. 144 p.

RODGERS, J. H. 1977. Aufwuchs communities of lotic systems-nontaxonomic structure and function. Ph.D. Dissertation. Virginia Polytechnic Institute and State University, Blacksburg. 336 p.

______, K. L. DICKSON AND J. CAIRNS, JR. 1978. A chamber for *in situ* evaluation of periphyton productivity in lotic systems. *Arch. Hydrobiol.,* **84**:389-398.

SHIMSHI, D. 1969. A rapid field method for measuring photosynthesis with labelled carbon dioxide. *J. Exp. Bot.,* **20**:381-401.

STOCKNER, J. G. 1968. Algal growth and primary production in a thermal stream. *J. Fish. Res. Board Can.,* **25**:2037-2058.

STRICKLAND, J. D. H. AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. 2nd ed. *Fish. Res. Board Can. Bull. No. 167.* 310 p.

SUBERKROPP, K. AND M. J. KLUG. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology,* **57**:707-719.

SUMMER, W. T. AND S. G. FISHER. 1979. Periphyton production in Fort River, Massachusetts. *Freshwater Biol.,* **9**:205-212.

TEAL, J. M. 1957. Community metabolism in a temperature cold spring. *Ecol. Monogr.* **27**:283-302.

THOMAS, N. A. AND R. L. O'CONNELL. 1966. A method for measuring primary production by stream benthos. *Limnol. Oceanogr.,* **11**:386-392.

VANNOTE, R. L. 1969. Detrital consumers in natural systems, p. 20-23. *In:* The stream ecosystem. Tech. Rep. No. 7, Institute of Water Research, Michigan State University, East Lansing.

______, G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL AND C. E. CUSHING. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.,* **37**:130-137.

VOLLENWEIDER, R. A. ED. 1974. A manual on methods for measuring primary production in aquatic environments, 2nd ed. IBP Handbook No. 12. Blackwell, London. 285 p.

WARD, G. M. AND K. W. CUMMINS. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). *Ecology,* **60**:57-64.

WEBSTER, J. R. AND B. C. PATTEN. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. *Ecol. Monogr.,* **49**:51-72.

WESTLAKE, D. F. 1974. Symbols, units and comparability, p. 137-141. *In:* R. A. Vollenweider (ed.). A manual of methods for measuring primary production in aquatic environments, 2nd ed. IBP Handbook No. 12. Blackwell, London.

WETZEL, R. G. 1965. Necessity of decontamination of filters in ^{14}C measured rates of photosynthesis on freshwaters. *Ecology,* **46**:540-541.

______. 1975a. Primary production, p. 230-247. *In:* B. A. Whitten (ed.). River Ecology. Univ. of Calif. Press, Los Angeles.

______. 1975b. Limnology. Saunders, Philadelphia. 743 p.

WRIGHT, J. C. AND J. K. MILLS. 1967. Productivity studies on the Madison River, Yellowstone National Park. *Limnol. Oceanogr.,* **12**:568-577.

ZIMKA, J. R. AND A. STACHURSKI. 1976. Regulation of C and N transfer to the soil of forest ecosystems and the rate of litter decomposition. *Bull. Acad. Pol. Sci. Ser. Sci. Biol.,* **24**:127-132.

SUBMITTED 16 JUNE 1980 ACCEPTED 10 OCTOBER 1980