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Periphyton Production in an Appalachian Mountain Trout Stream

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 nutritious 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 techniques (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°38′ N lat) and in two tributaries, Glade Brook and Piney Branch. Most of the 19 km$^2$ watershed of Guys Run is located within the Goshen Wildlife Management Area. Overstory vegetation with an understory of rhododendron cm per year with heaviest rains usu (Crockett, 1972). Soils are acidic (aver Devonian shale, sandstone and quartz the minimal disturbance within the angular gravel-rubble beds. Though t 5.0), the basin is within a highly fol limestone layers occasionally occur (B be buffered by such a layer near their chronically acidic (pH 4.7 - 5.7) for features of the three study streams are

Common algae in the streams include Staurosirella pinnata, green algae (C (Europia and Chlorella). Periphyton seasonally by standard techniques (A m$^2$ averaging about 50 mg Chl. a m$^{-2}$)

MATERIALS AND METHODS

Primary production rates of peripl phyton using recirculating chambers and $^{14}$C, approximately three times monthly f period of ice cover and inaccessibi located near the mouths of the tribut waters, just upstream of the mouth c

The recirculating chambers were : et al. (1978) and consisted of 1.9-liter submersible pumps maintained water eriments. Two clear and two opaqu placed at each stream site on each st cobble-sized rocks, were randomly sel from the streambed to the incubation water, sealed and positioned in the subm Three-hr midday incubation periods of $^{14}$C-sodium bicarbonate. Freshly were used as controls. Injections were mained high throughout the incubat were removed from the chambers an

<table>
<thead>
<tr>
<th>Stream length (m)</th>
<th>Mean gradient (m km$^{-1}$)</th>
<th>Mean channel width (m)</th>
<th>Mean midstream depth at study sites (cm)</th>
<th>Mean annual discharge (1 sec$^{-1}$)</th>
<th>Drainage basin area (km$^2$)</th>
<th>Mean pH (range)</th>
<th>Mean phosphate-orthophosphate (mg l$^{-1}$)</th>
<th>Mean nitrate (mg l$^{-1}$)</th>
<th>Mean inorganic carbon (mg l$^{-1}$)</th>
<th>Mean sulfate (mg l$^{-1}$)</th>
<th>Mean hardness (mg l$^{-1}$)</th>
<th>(Ca, Mg, Fe, Zn, Mn)</th>
</tr>
</thead>
</table>

1Address correspondence to J. R. Webster.

1981 HORNICK ET AL.: STR
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 pH, 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 (pH, 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 (pH, 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 (Europia 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 14C. 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 14C- sodium bicarbonate. Freshly broken rock surfaces and formalin-fixed samples were used as controls. Injections were equal within ±4% and 14C 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>
<thead>
<tr>
<th>Stream parameters</th>
<th>Guys Run</th>
<th>Piney Branch</th>
<th>Glade Brook</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stream length (m)</td>
<td>8000</td>
<td>2050</td>
<td>1050</td>
</tr>
<tr>
<td>Mean gradient (m km^-1)</td>
<td>40</td>
<td>86</td>
<td>49</td>
</tr>
<tr>
<td>Mean channel width (m)</td>
<td>5.1</td>
<td>3.0</td>
<td>2.4</td>
</tr>
<tr>
<td>Mean midstream depth at study sites (cm)</td>
<td>20</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>Mean annual discharge (1 sec^-1)</td>
<td>414</td>
<td>51</td>
<td>44</td>
</tr>
<tr>
<td>Drainage basin area (km^2)</td>
<td>19.0</td>
<td>3.3</td>
<td>1.2</td>
</tr>
<tr>
<td>Mean pH (range)</td>
<td>7.4 (6.8 - 7.8)</td>
<td>4.0 (4.7 - 5.4)</td>
<td>6.8 (6.4 - 7.2)</td>
</tr>
<tr>
<td>Mean phosphate-orthophosphate (mg 1^-1)</td>
<td>0.013</td>
<td>0.013</td>
<td>0.011</td>
</tr>
<tr>
<td>Mean nitrate (mg 1^-1)</td>
<td>0.051</td>
<td>0.061</td>
<td>0.029</td>
</tr>
<tr>
<td>Mean inorganic carbon (mg 1^-1)</td>
<td>7.8</td>
<td>1.9</td>
<td>4.8</td>
</tr>
<tr>
<td>Mean sulfate (mg 1^-1)</td>
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<td>3.8</td>
<td>4.4</td>
</tr>
<tr>
<td>Mean hardness (mg 1^-1)</td>
<td>23.6</td>
<td>4.8</td>
<td>18.0</td>
</tr>
</tbody>
</table>

(Ca, Mg, Fe, Zn, Mn)
orthophosphate concentrations. They 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 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). Concentrations were generally highest in summer (Fig. 2), though a peak was observed in Guys Run in October. Hydrogen ion concentrations remained fairly constant (8.38 ± 0.37, n = 50) and chamber transmittance (85 ±5%, Rodgers, 1977). Oxidation efficiency, as checked 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 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 clear area 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), the average 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 dates of increasing light penetration (F Fig. 1). Primary production rates. — In the 1- primary production rate for each stream was 2.27 mg C m^-2 h^-1 (±0.37 SE, n = 50) and significantly different (analysis of variance: 0.15 - 11.64 mg C m^-2 h^-2, with a mean in Glade Brook, from 0.25 - 3.82 mg L^-1 (±0.19 se, n = 50). Primary production rates were significantly different during the study.

In all three streams, primary production declined during summer and autum peaks in mid-May were followed by a mid-May peak perhaps due to increased light penetration in the stream, which prevented the stream from receiving light. Production rates were observed in mid-autumn and primary production rates, inorganic orthophosphate concentration and day of covariance. Analyses were made for combined (Table 2). Several general observations were made: slight inverse correlation between daytime PAR (direct for pH), orthophosphate and
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 pro-
duction 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 (±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 (±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
(±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,
than 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 ex-
hibit 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 produc-
tivity were observed in mid-autumn as available light increased due to leaf fall.

Primary production rate, inorganic carbon concentration, pH, 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 com-
bined (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 pH), 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 \( (r = 0.56 \text{ over all seasons and } r = 0.66 \text{ in summer}; n = 18 \text{ and } 12, \text{ respectively}) \). 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 Run in summer. The summer cor stimulatory flow effects on diffusion during low flows, and to the cleansi In a series of experiments compa were higher in unshaded sites (Tab when light levels were extremely lo suggest a correlation between primar keeps light below the saturation leve duction under natural shaded condit significant correlation (Table 2). Gr than NO\(_3\)-N limited primary prod differences in intensity between natura tically lighted sections, with and v thetic rates than naturally lighted set of larger woodland streams or mea have also been able to relate irradian Bott et al., 1978).

![Fig. 2. — Inorganic carbon and pH in the three study streams](image1)

![Fig. 3. — Photosynthetically active r](image2)
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 photosynthesis was calculated as the mean hourly photosynthetic rate plus a fraction of the lower light of the curve. Seasonal primary production was zero during January. Seasonal primary production estimates low primary production in Glade Brook and in its tributaries. Combined spring and annual primary production in the study streams was among the lowest of any system studied. Combined spring and annual primary production in each study stream was among the lowest of any system studied.

TABLE 2. — Partial correlation coefficients

<table>
<thead>
<tr>
<th></th>
<th>Inorganic carbon</th>
<th>Temperature</th>
<th>PAR light</th>
<th>Orthophosphate</th>
<th>Relative discharge</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>14C Fixation</td>
<td>0.337</td>
<td>0.129</td>
<td>-0.052</td>
<td>-0.317</td>
<td>0.178</td>
<td>0.075</td>
</tr>
</tbody>
</table>

TABLE 3. — Results of experiments measuring canopy shading in shaded and unshaded streams

<table>
<thead>
<tr>
<th>Stream</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Piney Branch</td>
<td>23 April</td>
</tr>
<tr>
<td></td>
<td>5 May</td>
</tr>
<tr>
<td></td>
<td>13 June</td>
</tr>
<tr>
<td>Guys Run</td>
<td>23 April</td>
</tr>
<tr>
<td></td>
<td>5 May</td>
</tr>
<tr>
<td></td>
<td>13 June</td>
</tr>
</tbody>
</table>

Fig. 4. — 14C 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

<table>
<thead>
<tr>
<th></th>
<th>Inorganic carbon</th>
<th>Temperature</th>
<th>PAR light</th>
<th>Orthophosphate</th>
<th>Relative discharge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inorganic carbon</td>
<td>0.337</td>
<td>-0.020</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>0.129</td>
<td>-0.052</td>
<td>-0.052</td>
<td>-0.051</td>
<td></td>
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<tr>
<td>PAR light</td>
<td>-0.317</td>
<td>0.178</td>
<td>0.178</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orthophosphate</td>
<td>-0.155</td>
<td>0.075</td>
<td>0.075</td>
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<tr>
<td>Relative discharge</td>
<td>0.118</td>
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<td>-0.100</td>
<td>-0.489</td>
<td>-0.281</td>
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<tr>
<td>pH</td>
<td>0.075</td>
<td>-0.052</td>
<td>-0.027</td>
<td>0.125</td>
<td>0.087</td>
</tr>
</tbody>
</table>

**Table 3.** - Results of experiments comparing primary production rates in 1977 for forest canopy shaded and unshaded stream sites

<table>
<thead>
<tr>
<th>Stream</th>
<th>Date</th>
<th>Canopy light penetration (%)</th>
<th>14C fixation rates (mg C m⁻² h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Shaded</td>
</tr>
<tr>
<td></td>
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<td>Unshaded</td>
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<td>Piney</td>
<td>23 April</td>
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<tr>
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<td>4 June</td>
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<td>13 June</td>
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<td>3.02</td>
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<tr>
<td>Guys Run</td>
<td>23 April</td>
<td>50</td>
<td>1.35</td>
</tr>
<tr>
<td></td>
<td>5 May</td>
<td>30</td>
<td>5.82</td>
</tr>
<tr>
<td></td>
<td>4 June</td>
<td>8</td>
<td>2.75</td>
</tr>
<tr>
<td></td>
<td>13 June</td>
<td>7</td>
<td>5.01</td>
</tr>
</tbody>
</table>

**1981 HORNICK ET AL.: STREAM PERiphyton Production**
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 m² 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 yr⁻¹ vertical fall and 113 g m⁻² yr⁻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 yr⁻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

<table>
<thead>
<tr>
<th>Season</th>
<th>Guys Run</th>
<th>Piney Branch</th>
<th>Glade Brook</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>1.58</td>
<td>1.38</td>
<td>0.39</td>
</tr>
<tr>
<td>Summer</td>
<td>4.40</td>
<td>2.28</td>
<td>2.92</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.21</td>
<td>0.23</td>
<td>0.14</td>
</tr>
<tr>
<td>Winter</td>
<td>0.35</td>
<td>0.21</td>
<td>0.26</td>
</tr>
<tr>
<td>Total</td>
<td>6.54</td>
<td>4.10</td>
<td>3.71</td>
</tr>
</tbody>
</table>

### Table 5. — Estimates of average annual (or annual range) net primary production by periphyton in streams. The following conversion factors were used:

<table>
<thead>
<tr>
<th>Study area</th>
<th>Stream flow average (m² sec⁻¹)</th>
<th>Net primary production (g C m⁻² d⁻¹)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morgan's Cr., Ky.</td>
<td>0.010 - 0.260</td>
<td>0.286 x 0.4 kcal per g AFDW (Weslake, 1974; Stockner, 1974; Stockner, 1975; Weslake, 1975)</td>
<td>0.004 - 0.007</td>
</tr>
</tbody>
</table>
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 x g O\(_2\) m\(^{-2}\) (Westlake, 1974; Stockner, 1968; Megard, 1972; Bott et al., 1978); net production = 0.556 x gross production (Westlake, 1974; Likens, 1975); 4.52 kcal per g AFDW (Kevery and Ball, 1965); g C = 0.45 x dry weight (Odum, 1971); and g C = 0.47 x g AFDW (Westlake, 1974)

<table>
<thead>
<tr>
<th>Net primary production (g C m(^{-2}) d(^{-1}))</th>
<th>Study area</th>
<th>Stream flow average or range (m(^3) sec(^{-1}))</th>
<th>Technique</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.004 - 0.007</td>
<td>Morgan's Cr., Ky.</td>
<td>0.005 - 0.350</td>
<td>Biomass change</td>
<td>Minshall, 1967</td>
</tr>
<tr>
<td>0.008 - 0.011</td>
<td>Walker Br., Tenn.</td>
<td>0.015</td>
<td>Biomass change</td>
<td>Elwood and Nelson, 1972</td>
</tr>
<tr>
<td>0.010</td>
<td>Glade Br., Va.</td>
<td>0.044</td>
<td>14C in circulating chambers</td>
<td>This study</td>
</tr>
<tr>
<td>0.011</td>
<td>Piney Br., Va.</td>
<td>0.051</td>
<td>14C in circulating chambers</td>
<td>This study</td>
</tr>
<tr>
<td>0.018</td>
<td>Guys Run, Va.</td>
<td>0.41</td>
<td>14C in circulating</td>
<td>This study</td>
</tr>
<tr>
<td>0.050 - 1.200</td>
<td>Red Cedar R., Mich.</td>
<td>5.7</td>
<td>Biomass change on artificial substrates</td>
<td>King and Ball, 1966</td>
</tr>
<tr>
<td>0.099</td>
<td>Berry Cr., Ore.</td>
<td>0.014</td>
<td>O(_2) changes in circulating chambers</td>
<td>Reese, 1966</td>
</tr>
<tr>
<td>0.14</td>
<td>Lost Cr., Kan.</td>
<td>0.17</td>
<td>Diurnal O(_2) curve</td>
<td>Gelroth and Marzolf, 1978</td>
</tr>
<tr>
<td>0.14 - 0.41</td>
<td>Danube River</td>
<td>&gt;2000</td>
<td>O(_2) changes in chambers with artificial substrates</td>
<td>Ertl and Tomajka, 1973</td>
</tr>
<tr>
<td>0.16</td>
<td>Root Sp., Mass.</td>
<td>0.0005</td>
<td>O(_2) changes in chambers</td>
<td>Teal, 1957</td>
</tr>
<tr>
<td>0.048 - 1.570</td>
<td>9 streams in N.C.</td>
<td></td>
<td>O(_2) changes in upstream - downstream</td>
<td>Hoskin, 1959</td>
</tr>
<tr>
<td>0.25</td>
<td>Fort R., Mass.</td>
<td>1.4</td>
<td>O(_2) changes in circulating chambers</td>
<td>Sumner and Fisher, 1979</td>
</tr>
<tr>
<td>0.30 - 0.46</td>
<td>Drift Cr., Ore.</td>
<td>0.118</td>
<td>O(_2) changes in circulating chambers</td>
<td>Hansmann, 1969</td>
</tr>
</tbody>
</table>
Hynes, 1968; Hargrave, 1969; Iversen, 1969. Recent work by Suberkropp and Iversen demonstrated that leaf detritus is more important in streams and becomes less nutritious downstream.

In contrast to the low quality of leaf detritus, there is a rich lipid and protein content (Currie and Currie, 1979). Assimilation efficiencies are generally less than 50% (Cullough et al., 1979a, b). Chapman also found that 7% of the assimilation efficiency of algal materials used by leaf detritus (generally less than 50%; Cullough and Anderson, 1979; Webber, 1977) in feeding caddisflies in an Appalachian stream was attributable to leaf detritus. More production was attributable to vascular plant detritus, which may have represented the most assimilable detrital material in the stream.

In another stream, much like Guys Brook in the Northeast, periphyton is probably available all year round. During this spring-summer period, almost all the leaf detritus present is low-quality detritus, so that primary production may be significant in providing a high-quality, though limited, food source when available. Many aquatic insects in these streams seem to be feeding periphyton. Chapman's (1966) study of the gut contents of Plecoptera in a small shaded stream near Gatlinburg, Tennessee, found that 7% of the gut contents was of a plant detritus. In most other non-carnivorous insects, the gut contents was often of a plant detritus (Currie and Currie, 1979; Chapman, 1966). In another stream, much like Guys Brook, the detritus had a rich lipid and protein content (Currie and Currie, 1979; Chapman, 1966). In a southern Appalachian stream, much like Hendricks Creek, and in an Inland Fisheries, the research was done at the Southeastern Forest Experiment Station. The research was done at the Southeastern Forest Experiment Station.

Acknowledgments. — Dr. Larry Lee, Soil and Water Conservation Research Station, and Dr. David S. Moxon, Southeastern Forest Experiment Station, provided statistical analyses. Access to the study area was provided by the Forest Service and Inland Fisheries. The research was done at the Southeastern Forest Experiment Station.


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 crop would indicate (Cummins, 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


1981

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An Integrated Multivariate Analysis of Communities of the Great Smoky Mountains National Park

Department of Forest Biology

Abstract: An integrated sequence of vegetation patterns in the Great Smoky Mountains National Park is described from 244 forest stands sampled using a 0.08 ha circular plot. The analyses included cluster analysis and site data from 244 stands. The results are interpreted in the light of the vegetation pattern and forest vegetation patterns reported by previous workers. The study reported here was (1) an integration of several multivariate analyses and (2) to illustrate the importance of soil data on the vegetation pattern. Nineteen forest community types were identified, and the vegetation pattern was most directly related to the soil. However, some soil variables were not as important as others. The Great Smoky Mountains National Park contains large areas of undisturbed mountain forest, and the vegetation pattern is relatively undisturbed. Descriptions of the physiography and vegetation pattern are available elsewhere (Clements and Stupka, 1950; Hoffman, 1967). Whittaker's (1956) monograph on the vegetation pattern was based on data from the park. This paper has two primary purposes: (1) to illustrate the importance of soil data on the vegetation pattern, and (2) to illustrate the importance of soil data on the vegetation pattern.