Periphyton production in an Appalachian river

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Abstract

Periphyton primary production was measured by ^{14}C uptake on natural substrates in two sections of the New River, Virginia, U.S.A. Production ranged from 6.71 ± 0.43 mg C g^{-1} h^{-1} in summer to 1.47 ± 0.22 mg C g^{-1} h^{-1} in late autumn in the hardwater reach and from 1.90 ± 0.10 mg C g^{-1} h^{-1} to 0.12 ± 0.08 mg C g^{-1} h^{-1} in the softwater reach. Production in the hardwater reach was 3–5 times greater than in the softwater reach and significantly correlated with dissolved inorganic carbon (DIC) concentration ($r^2 = 0.506$). No significant correlation was found between periphyton production and photosynthetically active radiation (PhAR). Extrapolation of periphyton production to a 135 km reach of the New River yielded an estimated annual input of 2 252 T AFDW from this source. Estimates of allochthonous (excluding upstream contributions) and aquatic macrophyte inputs to this same reach were 64 T AFDW and 2 001 T AFDW, respectively. While periphyton is not a large source of organic matter, its high food quality and digestibility make it an important component of the New River energy dynamics.

Introduction

While it is widely accepted that most stream ecosystems are heterotrophic, considerable autotrophic production can occur in some streams (e.g., Minshall 1978). Periphyton, generally the most abundant primary producer in stream ecosystems, is often ignored by stream ecologists studying organic matter dynamics. Wetzel (1975a) pointed out the error in this judgement and stated that studies of detritus based ecosystems must also include autochthonous production, as well as allochthonous production, to accurately reflect stream energy budgets.

Rivers of the Appalachian region are usually wide, shallow streams flowing over stable bedrock. Such conditions support high periphyton production. There have been few periphyton production studies of mid-order (4–6 order) streams (e.g., McConnell & Sigler 1959; Duffer & Dorris 1966; King & Ball 1966; Thomas & O'Connell 1966; Flemer 1974), and all have used either biomass accumulation on artificial substrates or gas exchange methods to determine production. Both methods have considerable limitations (Wetzel 1975a). Measurement of ^{14}C uptake by periphyton enclosed in recirculating chambers has greatly improved primary production studies, particularly in systems of low productivity (Hornick *et al.* 1981).

The present study was undertaken to estimate periphyton production in softwater and relatively hardwater reaches of a mid-sized river ecosystem and to extrapolate production data to yield an annual estimate of periphyton inputs to this ecosystem.

Methods

The New River originates in the Appalachian

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highlands of northwestern North Carolina, U.S.A., and flows northward through southwestern Virginia and West Virginia to join the Ohio River. The river is characterized by a steep gradient, swift flow, a wide, shallow, bedrock channel, and a narrow floodplain. The river flows over two geologic formations, gneiss and limestone/dolomite, which divide the river into softwater and relatively hardwater (14.8 and 44.2 mg $CaCO_3$ l^{-1}, respectively, Klarberg 1977) reaches. The section of the New River considered in this study extends from the confluence of the North and South Forks of the New River in North Carolina, where the river becomes sixth-order, downstream 135 km to the head of Claytor Lake, Virginia (Fig. 1).

Four sites were located within the overall study area, two each in the soft and hardwater reaches. Site 1, located near the downstream edge of the study area, is characterized by hardwater, sand and bedrock substrate, 175 m wide channel, and average depth of about 1.5 m during non-storm flows. Most periphyton at this site was located in a bedrock riffle with depths less than 0.5 m. Site 2, also located in the hardwater reach, has a bedrock and sand substrate, 200 m wide channel, and water depth less than 0.5 m. This site is dominated by a

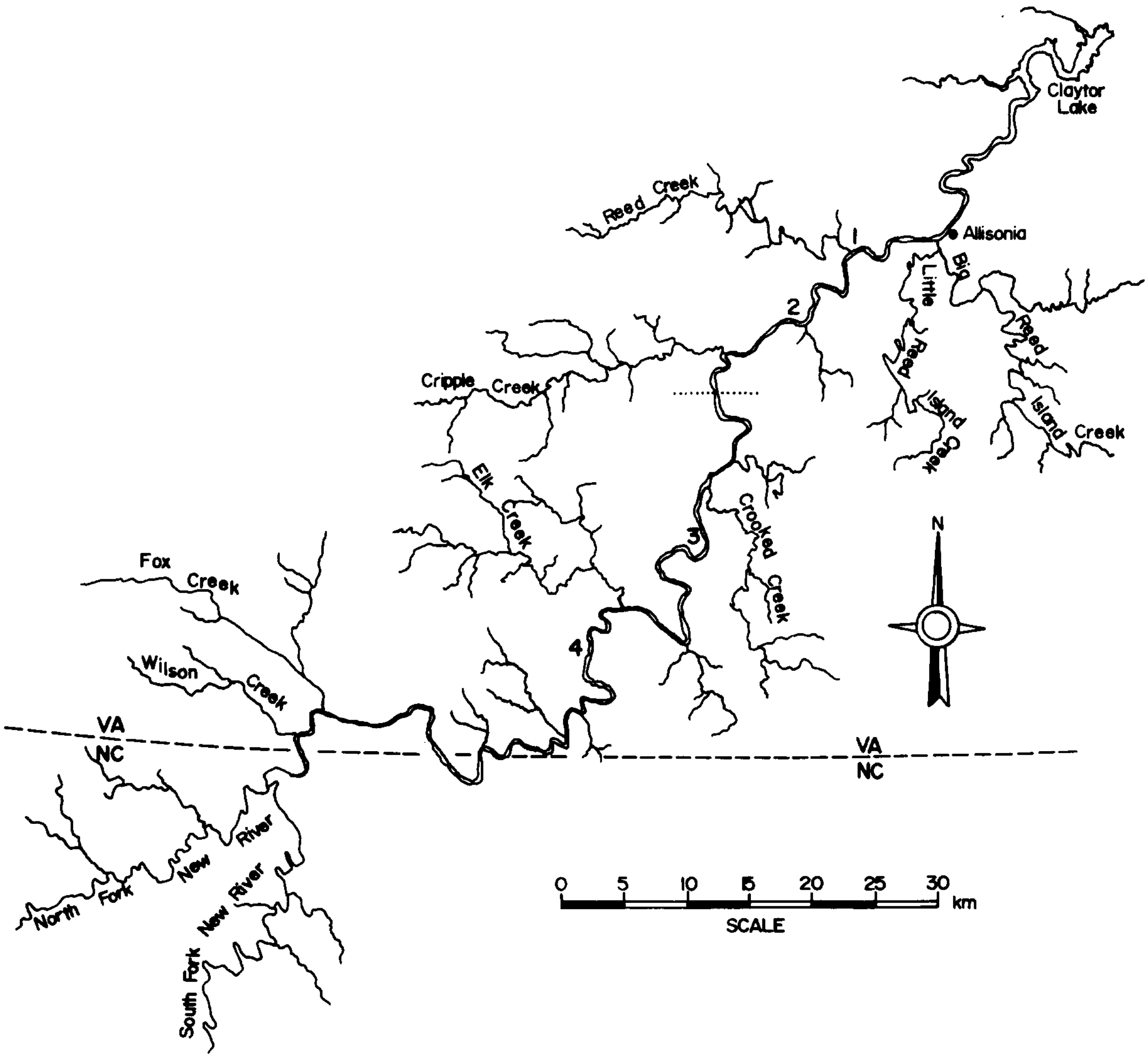

Fig. 1. Map of the New River showing sampling sites and change from softwater to hardwater reaches (dotted line in center of figure).

large bedrock riffle. Site 3, located in the softwater reach, is characterized by bedrock substrate, channel width of 100 m, and an average depth of 0.5 m. Site 4, also located in the softwater reach, has a sand/cobble substrate and an average depth of 0.5 m. Average channel width for the New River study area is 167 m. Water depth averages about 0.5 m.

Periphyton (used here to mean epilithic algae) production at the four sites was measured as ^{14}C uptake by enclosed natural substrates. Measurements were taken twice monthly from June through early November 1980. Randomly selected rock substrates, with periphyton attached, were placed in 1.9 liter, recirculating (battery powered submersible pumps, 300 ml min^{-1}), polystyrene chambers (Hornick *et al.* 1981). The chambers were filled with river water, sealed, and placed in the river at the approximate depth from which the rocks were taken (usually 0.25–0.50 m). Ninety minute, midday incubations were initiated by injecting 5 μCi ^{14}C-sodium bicarbonate into the chambers. Following the incubations, substrates were removed from the chambers, placed in plastic bags, packed on ice, and returned to the laboratory for processing. Depletion of ^{14}C within the chambers was checked by withdrawal of 1 ml samples of chamber water which were transferred to scintillation cocktail. In no instance was ^{14}C depleted within the chambers.

In the laboratory, three 7 cm^2 periphyton subsamples were scraped from each substrate from an area contained by a foam-bottomed cylinder (Hornick *et al.* 1981). Loosened material from two of the scrapings was washed into 7 ml shell vials and fumed with concentrated HCl in a 100 °C water bath to eliminate residual labelled inorganic carbon (Wetzel 1965). Samples were wet oxidized with cold potassium dichromate (Shimshi 1969), and evolved $^{14}CO_2$ was trapped in 0.25 N NaOH and transferred to Aquasol scintillation cocktail. Oxidation efficiency, checked by oxidation of benzoic acid of known activity, was 85%. Counting efficiency, measured by the external channels ratio method and by internal standards, was 96%. Production rate of the samples was calculated using the formula of Vollenweider (1974). Loosened material from the third scraping was dried, weighed, ashed (525 °C, 30 min), and reweighed to determine ash free dry weight (AFDW) of the samples.

Temperature, pH, and alkalinity (titration with 0.2 N H_2SO_4, methyl purple endpoint, 4.5 pH) of river water were determined on each sampling date to estimate dissolved inorganic carbon (DIC). Photosynthetically active radiation (PhAR, 390–710 nm) was measured on eight dates during the study period using a PhAR quantum sensor.

Results

Periphyton production in the New River increased at most sites until late August or early September before declining sharply in the November samples (Fig. 2 and Table 1). Average summer production (±SE) was: Site 1, 4.17 ± 0.95 mg C g^{-1} h^{-1} Site 2, 6.35 ± 0.97 mg C g^{-1} h^{-1} Site 3, 1.22 ± 0.20 mg C g^{-1} h^{-1} Site 4, 1.16 ± 0.17 mg C g^{-1} h^{-1}. Production was generally 3–5 times greater in the hardwater reach of the New River.

Abiotic variables potentially affecting New River periphyton production are given in Table 2. Temperature, PhAR, and pH were similar in both the softwater and hardwater reaches of the New River. Alkalinity, and thus DIC, showed marked differences between the two reaches, with values in the hardwater reach averaging 5 times those of the softwater reach. Average nitrogen and phosphorus concentrations were 1.22 mg NO_3-N l^{-1} and 0.071 mg PO_4-P l^{-1}, respectively (Wright 1976). While Wright (1976) showed that New River periphyton was nutrient limited in static, 6-hour incubations, the constant replenishment of waters containing these concentrations of nitrogen and phosphorus precludes the possibility of limitation

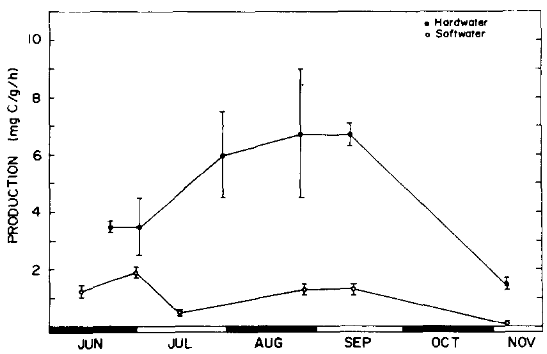

Fig. 2. Periphyton production, as ^{14}C uptake, in the River during 1980. Sites 1 and 2, and 3 and 4 were combined to yield hardwater and softwater estimates, respectively.

Table 1. Periphyton production in the New River during the 1980 sampling season (mg C/g/h) (±SE).

Date	Site 1	Site 2	Site 3	Site 4
11, 21 June	1.41 ± 0.10	5.54 ± 3.56	0.92 ± 0.28	1.54 ± 0.17
1, 2 July	1.73 ± 0.28	5.27 ± 0.05	1.90 ± 0.10	
17 July			0.51 ± 0.15	0.60 ± 0.02
30 July	8.60 ± 0.59	3.31 ± 0.40		
26, 27 Aug.	10.51 ± 0.55	2.83 ± 0.22	1.52 ± 0.42	1.08 ± 0.28
12, 13 Sept.	7.12 ± 0.65	6.31 ± 0.60	1.64 ± 0.41	0.99 ± 0.28
5, 6 Nov.	1.85 ± 0.02	1.10 ± 0.13	0.12 ± 0.01	0.13 ± 0.01

Table 2. Abiotic variables affecting periphyton production in the New River (June–September 1980).

Variable	Mean ± SE	Range	n
pH			
softwater	7.5 ± 0.2	7.0–7.8	11
hardwater	7.7 ± 0.4	7.2–8.2	13
Alkalinity (mg $CaCO_3$/l)			
softwater	7.5 ± 0.8	6.0–0.8	11
hardwater	37.3 ± 2.8	34.0–42.0	13
Dissolved inorganic carbon (mg/l)			
softwater	2.0 ± 0.2	1.5–2.3	11
hardwater	9.5 ± 0.9	8.2–11.3	13
Temperature (°C)	24.8 ± 2.0	20.0–30.0	24
PhAR (μEin/m^2/s)	1830.2 ± 334.5	1078.1–2222.5	24

of periphyton production due to macronutrient deficiencies.

Product moment correlations (Sokal & Rohlf 1974) were significant (*t*-test, $p < 0.05$) for comparisons of production and DIC (Fig. 3), alkalinity, and temperature. No significant correlations (*t*-test, $p > 0.05$) were found for comparisons of pH and PhAR with productivity.

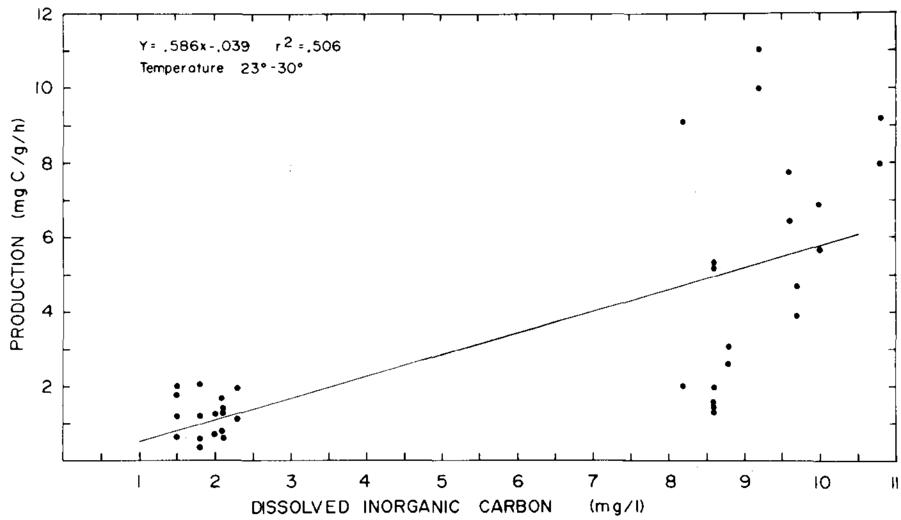

Fig. 3. Periphyton production in response to available dissolved inorganic carbon in the New River during 1980.

Discussion

Periphyton production in the New River is divided into two distinct productivity classes which correlate significantly with DIC. The relationship between DIC and primary production in lakes has long been recognized (e.g., Birge & Juday 1911), but has received little attention from stream ecologists. Wright & Mills (1967) found increased net photosynthesis with increased free CO_2 in a stream community dominated by aquatic macrophytes. The phenomenon of increased secondary production in hardwater streams is well documented (e.g., Hynes 1970). Availability of DIC in the New River is related to the geology of the underlying bedrock. In the upstream, softwater reach of the river, DIC is about 5 times less than in the hardwater reach and this is reflected by production which is about 5 times less than concomitant rates in the hardwater reach. Since labelled bicarbonate was not depleted within the production chambers, the limited production of the softwater periphyton suggest that New River periphyton may be unable to use HCO_3^-, and use only dissolved CO_2, as a carbon source in photosynthesis. Limitation due to CO_2 depletion appears to be the result of photosynthetic uptake of CO_2 occurring faster than dehydroxylation of HCO_3^- to CO_2 (Gavis & Ferguson 1975; Burris *et al.* 1981). This is particularly a problem at higher pH where the chemical equilibrium of inorganic carbon species is shifted towards HCO_3^- (Wetzel 1975). At the near neutral to slightly alkaline pH of the New River, dissolved CO_2 appears to be dependent on the size of the HCO_3^- pool, as well as the rate of dehydroxylation of HCO_3^- to CO_2, and explains the greater periphyton production in the hardwater reach.

Use of ^{14}C to measure primary production is widely accepted, though the argument over whether the method measures gross or net primary production is unresolved. Most investigators (e.g., Wetzel 1975a; Petersen 1980) agree that ^{14}C uptake is close to net primary production in incubations less than several hours. Use of the ^{14}C method for periphyton production in the New River (9.3–1,059.0 mg C m^{-2} d^{-1}) gave rates similar to those reported for some stream ecosystems (Wetzel 1975a; Fisher & Carpenter 1976; Hornick *et al.* 1981) though somewhat lower than rates reported for most rivers (King & Ball 1966; Flemer 1974; Duffer & Dorris 1966; Berrie 1972; Thomas & O'Connell 1966; McConnell & Sigler 1959; Cushing 1967). The lower periphyton production in New River, compared to the rivers sited above, may be due to differences in levels of nutrient enrichment, for example the Red Cedar River (King & Ball 1966) is highly enriched, or to differences in site conditions or methods.

Average annual periphyton production in the New River was determined from production measurements for June through November 1980. Periphyton production from December through May was estimated by extrapolating between November and June values. Extrapolation of average annual periphyton production, weighted for production in the softwater (70% of the study area) and hardwater reaches, was based on an average width of 167 m throughout the 135 km study area. Estimated periphyton net primary production input to the New River was 2251.9 T AFDW (825.5 T from the softwater reach, 1423.4 T from the hardwater reach) to the New River. This estimate assumes 100% periphyton cover in all areas not inhabited by aquatic macrophytes (Hill & Webster 1982), an assumption that is reasonable in light of the shallow mean depth of the New River. However, the occurrence of large sandy areas would decrease annual input from periphyton because of reduced substrate available for periphyton colonization.

We can compare this estimate of periphyton input to the 135 km reach of the New River with estimates for other sources. Hill (1981) estimated aquatic macrophyte production by the harvest method for emergent macrophytes and by ^{14}C uptake for submerged macrophytes. Allochthonous input was estimated by measuring leaffall from riparian vegetation (Hill 1981) and includes only input directly to the study reach, not transport from tributaries or upstream. Periphyton input to the New River was 19.5% of total inputs, aquatic macrophyte and allochthonous input represented 20.5% and 60.4%, respectively (Hill 1981). It has been suggested that, while periphyton POM input and production is small in stream ecosystems, it is higher in food quality and digestibility than allochthonous POM (McCollough *et al.* 1979a, 1979b; Naiman & Sedell 1979; Ward & Cummins 1979; Benke & Wallace 1980; Hornick *et al.* 1981). While this input of organic matter is smaller than estimated allochthonous organic matter inputs, its high food quality and digestibility make it an important component of the New River organic matter dynamics.

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