

Dynamics of Lotic Ecosystems

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13. AQUATIC MACROPHYTE CONTRIBUTION TO THE NEW RIVER ORGANIC MATTER BUDGET

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ABSTRACT

The contribution of aquatic macrophytes to the energy budget of a 135-km reach of the New River was estimated. Production rates were measured by the harvest method and extrapolated to the entire reach on the basis of measurements of cover made by aerial photography. The estimated macrophyte contribution was compared with measurements of periphyton production and model estimated allochthonous inputs. Macrophytes contributed 13.1% of the total input and 28% of the input generated within the reach. Macrophyte input to the New River trophic dynamics occurs as an autumnal pulse of rapidly decomposed detritus. This pulse forms an important link between spring-summer periphyton production and fall-winter allochthonous-based production.

INTRODUCTION

Recent studies of energy flow in lotic ecosystems indicate that streams are strongly dependent on watershed-derived organic matter (Cummins, 1974; Hynes, 1975; Vannote et al., 1980). However, appreciable in situ production of organic matter can occur under favorable conditions of insolation and nutrient availability (Minshall, 1978). Such conditions are

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likely to be met in higher order streams where shading by riparian vegetation is minimal and nutrient levels are generally high (Vannote et al., 1980). In such streams the ratio of photosynthesis to respiration may be greater than one (Minshall, 1978).

Generally the first producers to appear along the length of a stream system are attached periphyton. As stream size increases, autotrophic production by attached benthic algae often decreases in proportion to contributions by other primary producers. Assuming that planktonic forms are rare in swift-flowing, medium-sized rivers (Hynes, 1970; Wetzel, 1975a), the other important primary producers are aquatic macrophytes. Hynes and Wetzel stated that macrophytes (which include bryophytes, macroalgae, and angiosperms) are, as a whole, poorly adapted to lotic conditions. In spite of this, macrophytes can contribute significantly to energy budgets of some streams. Previous studies have shown that aquatic macrophytes contribute between 1.2 and 30% of stream primary production (Odum, 1957; King and Ball, 1967; Mann et al., 1972; Westlake et al., 1972; Fisher and Carpenter, 1976).

Since aquatic macrophytes are not extensively grazed in most aquatic systems (Westlake, 1965; Fisher and Carpenter, 1976), the only avenues for macrophyte input into stream trophic dynamics are excretion of dissolved organic matter (DOM) by living macrophytes and decay of senescent macrophyte tissue. The excretion of DOM by aquatic macrophytes has been extensively studied in lake ecosystems (e.g., Wetzel, 1975b), but little is known of this phenomenon in lotic ecosystems. Apparently, the major contribution by aquatic macrophytes to stream ecosystems comes via death and decay. Aquatic vegetation has been found to decay considerably faster than terrestrial vegetation (Fisher and Carpenter, 1976; Godshalk and Wetzel, 1978; Hill, 1979). Thus, although autumn-shed tree leaves may be an organic energy supply for many months (e.g., Petersen and Cummins, 1974), macrophytic detritus occurs as an autumn pulse in the energy budget.

The purpose of this study was to estimate the relative contribution of aquatic macrophytes to the organic matter budget of the New River. We hypothesized that aquatic macrophytes, although perhaps only secondary as an annual energy source to streams, may contribute a significant organic matter pulse in late summer and autumn and can provide a readily usable carbon source between high summer production by periphyton and the breakdown of autumn-shed allochthonous litter.

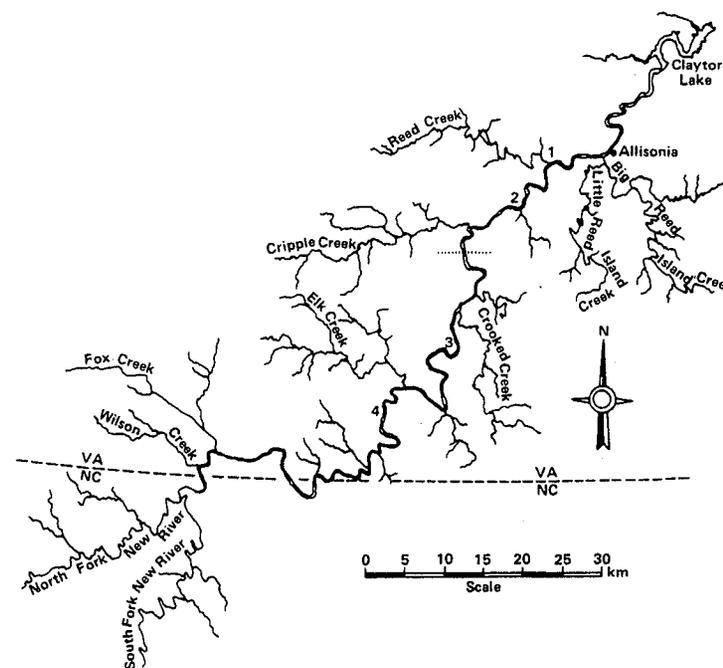


Figure 1. Map of the New River study area. Numbers refer to the sampling locations. The dotted line at the center of the figure separates hardwater (downstream) and soft-water (upstream) sections of the river.

METHODS

Site Description

The New River originates in the Appalachian highlands of North Carolina and flows north through Virginia and West Virginia to the Ohio River. It is characterized by a narrow floodplain, steep gradient (2.33 m/km, average), and high velocity (Kanawha River Basin Coordinating Committee, 1971). The river passes through two distinct geologic formations, gneiss and limestone/dolomite, which divide it into soft and hard-water regions. The section of the New River considered in this study extends from the confluence of the North and South Forks of the New River (forming a sixth-order stream) downstream 135 km to Allisonia, VA, at the upper end of Clayton Lake (Figure 1). Average river width in

this reach is 167 m, and depths are often less than 1 m. Riparian vegetation covers about 47% of the river bank.

Distribution and Production of Aquatic Macrophytes

The distribution and extent of aquatic macrophyte cover in the study area was determined by aerial photography. The Montana method of 35-mm aerial photography (Meyer and Grumstrup, 1978) was used with Ektachrome daylight color transparency film. The film was exposed on October 16, 1979, at an altitude of 305 m above the river surface. After processing, the slides were projected onto a gridded screen for estimation of percent cover by presence or absence of aquatic macrophytes within the squares of the grid. Total area of macrophyte beds and total river area were determined by measuring these areas on the slides with calibration from U. S. Geological Survey 7.5-minute topographic maps.

Production of *Podostemum ceratophyllum* L., *Justicia americana* (L.) Vahl, and *Potamogeton crispus* L. was determined by harvesting above-ground and belowground biomass at monthly intervals throughout the 1979 growing season. Biomass in 0.25 m² plots (0.10 m² for *P. ceratophyllum*) was collected (three to five replicates) from four sites (Figure 1), washed, air-dried, weighed, ashed (525°C for 30 min), and reweighed to determine ash-free dry weight (AFDW). Production rates at these sites were determined by differences in biomass on subsequent sampling dates. Losses of biomass caused by physical and biological processes were assumed to be negligible. Data from all four sites were combined to give a single production value for each species to facilitate extrapolation to the whole river.

Periphyton Contributions

Estimates of New River periphyton production were obtained by extrapolating in-stream measurements of ¹⁴C uptake by periphyton in the New River at Glen Lyn, VA, 128 km downstream from Allisonia (Figure 1) (Rodgers, 1977). In estimating production from this source, we assumed that periphyton cover was 100% in all areas where aquatic macrophytes were absent and that there were no site differences in periphyton production between Glen Lyn and our study reach. Because of the assumption of 100% coverage, our estimate of the periphyton contribution is undoubtedly an overestimate.

Allochthonous Input

Allochthonous particulate organic matter (POM) input as litter fall was estimated by using the New River model developed by Webster et al. (1979). Litter fall was 201.8 g m⁻² year⁻¹ on the stream bank (Hill, 1981), and it decreased linearly to zero at 10 m from the stream bank (Gasith and Hasler, 1976). By solving numerically a partial differential equation relating litter fall to river distance and time, we estimated the upstream and tributary inputs to the study reach and the allochthonous input along the study reach. This estimate of upstream inputs ignores upstream macrophyte and periphyton production. From our observation, ignorance of upstream macrophyte production is probably justified; we have observed few macrophytes in the river upstream from our study reach. We have no information to help us with upstream periphyton production. The model estimate also assumes that allochthonous leaf material is not processed upstream and is, therefore, an overestimate of upstream input. Newbern et al. (1981) estimated that total organic matter transport at a point about halfway through our study reach was 67,400 T/year, of which 24,322 T/year was particulate. This latter value is more than twice the model estimate, 10,962 T/year (see Table 3), which we are using.

Table 1. Mean Monthly Aquatic Macrophyte Biomass in the New River*

Species	June	July	August
<i>Justicia americana</i>			
Aboveground	255.5 ± 111.9	341.5 ± 78.5	447.8 ± 123.4
Belowground	886.9 ± 398.8	1568.6 ± 550.1	2076.7 ± 460.0
Combined	1313.8 ± 328.7	1910.1 ± 615.5	2524.5 ± 515.0
<i>Podostemum ceratophyllum</i>	157.0 ± 50.4	251.8 ± 58.4	318.6 ± 156.5
<i>Potamogeton crispus</i>	350.3 ± 87.9	300.3 ± 94.1	269.2 ± 38.0

*Biomass given in g AFDW/m² ± SE.

Table 2. Aquatic Macrophyte Contribution to the New River Study Area

Species	Input, T/AFDW/yr
<i>Podostemum ceratophyllum</i>	1154
<i>Justicia americana</i>	179
<i>Typha latifolia</i>	97
<i>Potamogeton crispus</i>	3
<i>Elodea canadensis</i>	2
Total macrophyte contribution	1435

Table 3. Particulate Organic Matter Inputs to a 135 km Reach of the New River

Source	Input, (T AFDW/yr)	Percent of total input
Allochthonous		
Upstream and tributary	5,893	53.8
Within study area	64	0.5
Autochthonous		
Periphyton	3,570	32.6
Aquatic macrophytes	1,435	13.1
Total POM input	10,962	

Table 4. Breakdown Rates, Sample Size (n), and Coefficient of Determination (r^2) for Five Species of Aquatic Macrophytes in the New River

Species	n	Breakdownrate*	r^2
<i>Podostemum ceratophyllum</i>	26	0.037 ± 0.009	0.74
<i>Elodea canadensis</i>	28	0.026 ± 0.004	0.84
<i>Potamogeton crispus</i>	28	0.021 ± 0.007	0.59
<i>Justicia americana</i>	28	0.016 ± 0.003	0.79
<i>Typha latifolia</i>	28	0.007 ± 0.002	0.64

*Values are rate/d ± SE.

Breakdown of Aquatic Macrophytes

The rate at which aquatic macrophyte organic matter was broken down was measured by the loss of weight from litter bags. Two to five g (air-dried weight) of five species of aquatic macrophytes (*P. ceratophyllum*, *J. americana*, *Typha latifolia* L., *P. crispus*, and *Elodea canadensis* Michx.) were placed in nylon mesh bags (15 by 15 cm, with 3-mm octagonal openings). Five bags of each species were placed between two layers of wire mesh to hold the samples to the river bed. Six sets of samples were anchored at each of four sites, and one set was returned immediately to the laboratory to determine handling loss. The others were removed after 2 days and 1, 2, 4, 6, and 8 weeks. Retrieved samples were air-dried, weighed, ashed, and reweighed to determine loss of AFDW. Breakdown rate coefficients were calculated by using linear regression of log-transformed data (Jenny et al., 1949; Olson, 1963). Analysis of covariance (Sokal and Rohlf, 1969) was used to compare breakdown rates.

RESULTS

Aerial photography indicated that aquatic macrophytes covered about 27% (590 ha) of the New River study area. *Podostemum ceratophyllum*, the dominant aquatic macrophyte in the New River, accounted for 25% of the macrophyte cover. Other species measured were *T. latifolia* (1.4%), *J. americana* (0.9%), *P. crispus* (0.03%), and *E. canadensis* (0.03%). Of these species, only *P. ceratophyllum* and *E. canadensis* occurred throughout the study area. *Justicia* and *P. crispus* were restricted to the hardwater section of the river, and *T. latifolia* occurred mostly in two small impounded areas.

Aquatic macrophyte biomass increased rapidly from late spring to midsummer and then appeared to level off (Table 1). Average production rates were: *J. americana*, 23.3 g AFDW m⁻² day⁻¹ (4.7 g AFDW m⁻² day⁻¹ for aboveground biomass only); *P. ceratophyllum*, 3.4 g AFDW m⁻² day⁻¹; and *P. crispus*, 2.9 g AFDW m⁻² day⁻¹. Maximum standing crops of these three species were 2500 (450 aboveground), 320, and 300 g AFDW/m², respectively. Standing crops for *T. latifolia* and *E. canadensis* were estimated from reported values (McNaughton, 1966; Sculthorpe, 1967; Klopatek and Stearns, 1978) as 2800 (500 aboveground) and 300 g AFDW/m², respectively.

The contribution of each macrophyte species to the New River study area was estimated by multiplying the area of coverage by growing season aboveground production or maximum standing crop (*T. latifolia* and *E. canadensis*) (Table 2). Belowground production of *J. americana* and *T. latifolia* was estimated by assuming a belowground biomass turnover of 4.5 years, a rate midway between the values suggested by Westlake (1965) and Sculthorpe (1967). The values in Table 2 can only be considered approximate, especially those for *J. americana* and *T. latifolia*, because of our lack of knowledge concerning belowground dynamics. Because of its wide distribution in the New River, *P. ceratophyllum* was the greatest source of aquatic macrophyte POM, contributing 80% of the macrophyte input. This was followed by *J. americana* (12%), *T. latifolia* (7.7%), *P. crispus* (< 1%), and *E. canadensis* (< 1%) (from Table 2).

Annual periphyton production averaged 0.60 g AFDW m⁻² day⁻¹ (Rodgers, 1977). Extrapolating this value to our study area yielded an estimated organic matter input from this source of 3570 T/year, or roughly twice that of aquatic macrophytes. Upstream and tributary litter-fall inputs were estimated to be 5893 T/year, and in situ allochthonous input contributed 64 T/year to our study area (Table 3).

Breakdown of aquatic macrophytes proceeded rapidly at all sites. Weight loss from litter bags was greatest for *P. ceratophyllum*. Since

there were no overall site effects ($p < 0.05$), all sites were combined to give an average breakdown rate for each species (Table 4).

DISCUSSION

From our estimates, aquatic macrophytes account for at least 13.1% of the total input of particulate organic matter to our study area on the New River (Table 2). They are responsible for nearly one-third (28%) of the POM generated within the study reach, however (autochthonous production plus direct riparian inputs). We feel that the latter number is more significant for two reasons. First, our estimate of upstream and tributary inputs is an overestimate because it assumes no instream utilization. A large portion of the POM entering the New River upstream of our study area is, in fact, used before it enters the study area. Second, the material entering from upstream is low quality, partly because of upstream processing but also because terrestrial leaves generally have lower quality than aquatic macrophyte tissue. Because aquatic macrophytes consist mostly of cellulose and other easily degraded compounds, with little lignin (Sculthorpe, 1967), they break down rapidly (Table 4) in comparison with terrestrial leaves (e.g., Petersen and Cummins, 1974).

The timing of the availability of aquatic macrophytes to aquatic food chains is the key to their importance in the energy dynamics of mid-sized streams. Since aquatic macrophytes are not generally used while living, biomass accumulates through the growing season. In autumn, when the plants die, this material is released as a pulse that is rapidly used by aquatic detritivores. Periphyton production occurs throughout spring, summer, and early fall and probably is the most important trophic base during this period. Allochthonous leaf input occurs in fall and is used by detritivores after a period of conditioning (e.g., Barlocher and Kendrick, 1975). Because some leaves condition and breakdown rapidly and others condition and breakdown slowly, there is a continuum of leaf availability lasting through winter and spring (Petersen and Cummins, 1974).

Vannote et al. (1980) speculated that natural stream ecosystems should tend toward a temporal uniformity of energy flow. In this regard Fisher and Carpenter (1976) and Hill (1979) suggested that the autumn pulse of aquatic macrophyte detritus may be the major energy source during the period when periphyton production is decreasing with decreasing insolation and before allochthonous litter input has become important.

Therefore the role of aquatic macrophytes in rivers should be viewed not only with respect to their organic matter pool or annual production but also with respect to the temporal aspects of stream energy budgets.

REFERENCES

- Barlocher, F., and B. Kendrick, 1975, Leaf-Conditioning by Microorganisms, *Oecologia*, 20: 359-362.
- Cummins, K. W., 1974, Structure and Function of Stream Ecosystems, *Bio-Science*, 24: 631-641.
- Fisher, S. G., and S. R. Carpenter, 1976, Ecosystem and Macrophyte Primary Productivity of the Fort River, Massachusetts, *Hydrobiologia*, 47: 175-187.
- Gasith, A., and A. D. Hasler, 1976, Airborne Litterfall as a Source of Organic Matter in Lakes, *Limnol. Oceanogr.*, 21: 253-258.
- Godshalk, G. L., and R. G. Wetzel, 1978, Decomposition of Aquatic Angiosperms. II. Particulate Components, *Aquat. Bot.*, 5: 301-327.
- Hill, B. H., 1979, Uptake and Release of Nutrients by Aquatic Macrophytes, *Aquat. Bot.*, 7: 87-93.
- , 1981, Organic Matter Inputs to Stream Ecosystems: Contributions of Aquatic Macrophytes to the New River, Ph. D. Thesis, Virginia Polytechnic Institute and State University, Blacksburg.
- Hynes, H. B. N., 1970, *The Ecology of Running Waters*, University of Toronto Press, Toronto.
- , 1975, The Stream and Its Valley, *Verh. Internat. Verein. Limnol.*, 19: 1-15.
- Jenny, H., S. P. Gessel, and F. T. Bingham, 1949, Comparative Study of Decomposition Rates of Organic Matter in Temperate and Tropical Regions, *Soil Sci.*, 68: 419-432.
- Kanawha River Basin Coordinating Committee, 1971, *Kanawha River Comprehensive Basin Study*. Vol. I, Main Report, U. S. Department of Agriculture, Washington, DC.
- King, D. L., and R. C. Ball, 1967, Comparative Energetics of Polluted Streams, *Limnol. Oceanogr.*, 12: 27-33.
- Klopatek, J. M., and F. W. Stearns, 1978, Primary Productivity of Emergent Macrophytes in a Wisconsin Freshwater Marsh Ecosystem, *Am. Midl. Nat.*, 100: 320-332.
- Mann, K. H., R. H. Britton, A. Kowalczewski, J. J. Lack, C. P. Matthews, and I. McDonald, 1972, Productivity and Energy Flow at all Trophic Levels in the River Thames, England, in Z. Kajak and A. Hillbricht-Ilkowska (Eds.), *Productivity Problems of Freshwaters*, IBP/UNESCO Symposium, pp. 579-596, PWN Polish Scientific Publishers, Warszawa-Krakow.
- McNaughton, S. J., 1966, Ecotype Function in the Typha Community Type, *Ecol. Monogr.*, 36: 297-325.
- Meyer, M. P., and P. G. Grumstrup, 1978, *Operating Manual for the Montana 35 mm Aerial Photography System*, Sec. Rev., Remote Sensing Laboratory, College of Forestry and Agricultural Experiment Station, University of Minnesota, St. Paul.
- Minshall, G. W., 1978, Autotrophy in Stream Ecosystems, *BioScience*, 28: 767-771.

- Newbern, L. A., J. R. Webster, E. F. Benfield, and J. H. Kennedy 1981, Organic Matter Transport in an Appalachian Mountain River, Virginia, U.S.A., *Hydrobiologia*, 83: 73-83.
- Odum, H. T., 1957, Trophic Structure and Productivity of Silver Springs, Florida, *Ecol. Monogr.*, 27: 55-112.
- Olson, J. S., 1963, Energy Storage and the Balance Between Producers and Decomposers in Ecological Systems, *Ecology*, 44: 322-332.
- Petersen, R. C., and K. W. Cummins, 1974, Leaf Processing in a Woodland Stream, *Freshwater Biol.*, 4: 343-368.
- Rodgers, J. H., 1977, Aufwuchs Communities of Lotic Systems—Nontaxonomic Structure and Function, Ph.D. Thesis, Virginia Polytechnic Institute and State University, Blacksburg.
- Sculthorpe, C. D., 1967, *The Biology of Aquatic Vascular Plants*, Edward Arnold, Ltd., London.
- Sokal, R. R., and F. J. Rohlf, 1969, *Biometry*, W. H. Freeman and Co., San Francisco.
- Vannote, R. L., 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.
- Webster, J. R., E. F. Benfield, and J. Cairns, Jr., 1979, Model Predictions of Effects of Impoundment on Particulate Organic Matter Transport in a River System, in J. V. Ward and J. A. Stanford (Eds.), *The Ecology of Regulated Streams*, pp. 339-364, Plenum Press, New York.
- Westlake, D. F., 1965, Some Basic Data for the Investigation of the Productivity of Aquatic Vascular Plants, *Mem. Ist. Ital. Idrobiol.*, 18: 229-248.
- , H. Casey, H. Dawson, M. Ladle, R. K. H. Mann, and A. F. H. Marker, 1972, The Chalk Stream Ecosystem, in Z. Kajak and A. Hillbrict-Ilkowska (Eds.), *Productivity Problems of Freshwater*, IBP/UNESCO Symposium, pp. 615-635, PWN Polish Scientific Publishers, Warszawa-Krakow.
- Wetzel, R. G., 1975a, Primary production, in B. A. Whitton (Ed.), *River Ecology*, pp. 230-247, University of California Press, Berkeley.
- , 1975b, *Limnology*, W. B. Saunders Co., Philadelphia.

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