

Aquatic macrophyte breakdown in an Appalachian river

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Keywords: macrophytes, decomposition, river

Abstract

Weight loss from *Podostemum ceratophyllum*, *Elodea canadensis*, *Potamogeton crispus*, *Justicia americana*, and *Typha latifolia* was measured by exposing air dried leaf material in 15 cm² nylon mesh bags (3 mm octagonal openings). Breakdown rates for these species were 0.037, 0.026, 0.021, 0.016, and 0.007 day⁻¹, respectively. In general, these rates are much faster than reported rates of tree leaf breakdown in streams. Shredders accounted for 35% of the macroinvertebrates found on the leaf bags. However, macroinvertebrate densities on the aquatic macrophyte tissue were well below densities commonly found on leaf bags in small streams. The rapid breakdown of aquatic macrophytes in the New River suggests that organic matter from this source may constitute a significant pulse in the annual energy dynamics of the river.

Introduction

The role of aquatic macrophytes in the energy budgets of stream ecosystems has largely been overshadowed by the dominance of periphyton and watershed derived organic matter in these habitats (e.g., Minshall 1978; Vannote *et al.* 1980). Vannote *et al.* (1980) suggested that, while aquatic macrophytes may be present in the mid-reaches of stream systems, macrophytes are seldom abundant enough to significantly affect stream energy budgets. However, recent evidence (Fisher & Carpenter 1976; Hill & Webster, in press) shows that aquatic macrophytes in streams, as has been found in lakes (e.g., Wetzel *et al.* 1972; Wetzel & Hough 1973), may play a greater role than was formerly suspected. While aquatic macrophytes may not constitute a large organic matter pool, the timing of aquatic macrophyte breakdown makes these plants an important link between periods of high periphyton

production of summer and allochthonous leaf litter input of autumn. Vannote *et al.* (1980) proposed that natural streams should tend towards a temporal uniformity of energy flow. Fisher & Carpenter (1976) and Hill & Webster (in press) proposed that breakdown of aquatic macrophytes could contribute a pulse of organic matter that bridges the energy gap between the two major trophic bases of stream ecosystems. Two major tenets of the proposal are that aquatic macrophytes breakdown rapidly and that this source of organic matter is utilized by the stream community. The purpose of this study was to measure the rate of aquatic macrophyte breakdown in the New River, a sixth-order stream ecosystem, and to determine macroinvertebrate colonization of decaying aquatic macrophyte tissue.

Methods

The New River originates in the Appalachian highlands of North Carolina and flows in a gener-

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ally northward direction through Virginia and West Virginia to join the Ohio River. The river is characterized by a narrow floodplain, steep gradient 2.33 m km^{-1} , and high velocity. The New River passes through two distinct geologic formations, gneiss and limestone/dolomite, which divide the river into softwater ($10 \text{ mg CaCO}_3 \text{ l}^{-1}$) and hardwater ($50 \text{ mg CaCO}_3 \text{ l}^{-1}$) 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, forming a sixth-order stream, downstream 135 km to Allisonia, Virginia, at the head of Claytor Lake (Hill & Webster, in press). This 135 km reach includes both softwater and hardwater sections of the river with sites located in each. Average channel width for the study reach is 167 m. Site 1, the most downstream site, is characterized by hardwater, a channel width of 100 m, and absence of riffles. Substrate at this site is gravel with scattered boulders. Water depths ranged up to 2.0 m. Site 2 is also located in the hardwater section of the river. This site has a channel width of 200 m and flows over bare limestone bedrock. Water depth at this site is less than 0.5 m. Site 3 is located in the softwater reach of the river. Channel width at this site was 125 m, substrate was mostly gravel with some bare gneiss bedrock, and depth was about 1.0 m. This site tended to have more silt accumulation than the other sites. Site 4, also located in the softwater section of the river, had a channel width of 150 m. Substrate at this site was small gravel and sand. Water depths were generally less than 1.0 m. Temperatures measured at each collection time varied from $14 \text{ }^\circ\text{C}$ in October to $0 \text{ }^\circ\text{C}$ in December.

Five species of aquatic macrophytes commonly found in the New River (*Podostemum ceratophyllum* Michx., *Justicia americana* L., *Typha latifolia* L., *Potamogeton crispus* L., and *Elodea canadensis* Michx.) were collected just prior to the onset of senescence in early autumn 1979. These plants were returned to the laboratory for air drying ($22 \text{ }^\circ\text{C}$). Two to five gram samples (air dry weight) of these plants were placed in nylon mesh leaf bags (15 cm^2 , 3 mm octagonal openings), and sets of bags were placed between two layers of wire mesh as a means of holding samples on the river bed (Benfield *et al.* 1979). Each set contained five replicates of each of the five species of aquatic macrophytes. Six sets were anchored to the river bed by concrete blocks at each of the four sites. A seventh set was transported

to each site to determine losses of plant matter from the leaf bags due to handling. This loss was subtracted from the original bag weight before determining % weight loss from subsequent samples. Subsamples of the original plant material were ashed ($525 \text{ }^\circ\text{C}$, 30 min) to determine initial ash free weight (AFDW).

One set of leaf bags was removed from each site after two days, one, four, six, and eight weeks. The leaf bags were returned to the laboratory, air dried ($22 \text{ }^\circ\text{C}$, 5 days), weighed, ashed, and reweighed to determine AFDW remaining. We assumed that breakdown followed an exponential pattern and breakdown rates were calculated using linear regression of log transformed data (Jenny *et al.* 1949; Olson 1963). Analysis of covariance (Sokal & Rohlf 1974) was used to compare breakdown rates among all five species at a single site and for a single species among the four sites.

Four leaf bags (one from each site) of each macrophyte species were removed on four sampling dates to determine macroinvertebrate colonization. These leaf bags were packed separately in plastic bags in the field and placed on ice until they could be sorted later that day or early the next day. Macroinvertebrates collected from the leaf bags were sorted, identified taxonomically, and each taxonomic group placed into a functional category according to Merritt & Cummins (1978) or Edmondson (1959).

Results

Weight loss from decaying aquatic macrophytes was rapid for all species except *T. latifolia*. There were no significant ($p < 0.05$) site differences in breakdown rates and data from all sites were combined to give average values for each of the macrophyte species. Breakdown rates for the five aquatic macrophytes ranged from 0.037 day^{-1} for *P. ceratophyllum* to 0.007 day^{-1} for *T. latifolia*. The other three species were intermediate, with breakdown rates closer to that of *P. ceratophyllum* (Table 1).

Breakdown rates were significantly different between most species ($p < 0.05$). However, some species with structural similarity had comparable breakdown rates. This is probably a reflection of species similarity rather than an overlap in sample variance.

Table 1. Breakdown rates, samples size (n), standard error of the mean (SE), coefficients of determination (r^2), and time required for a 95% loss of leaf material (t_{95} based on exponential model) for five species of aquatic macrophytes in the New River, Virginia. (Vertical bar after breakdown rates indicate no significant difference ($p > .05$) between species.)

Species	n	Breakdown rate (day^{-1}) \pm SE	r^2	t_{95} (days)
<i>Podostemum ceratophyllum</i>	26	0.037 \pm 0.009	0.74	81.1
<i>Elodea canadensis</i>	28	0.026 \pm 0.004	0.84	115.4
<i>Potamogeton crispus</i>	28	0.021 \pm 0.007	0.59	142.8
<i>Justicia americana</i>	28	0.016 \pm 0.003	0.79	187.5
<i>Typha latifolia</i>	28	0.007 \pm 0.002	0.64	428.6

Leaf bags used to determine macroinvertebrate colonization from the four sites were combined and treated as one sample. Shredders represented 35.3% of the total macroinvertebrate fauna collected, filterers 31.6%, scrapers 16.6%, gatherers 10.2%, and predators 6.4% (Table 2). Macroinvertebrate densities increased throughout the study (Fig. 1) but were lower than densities found in small headwater streams in the Appalachian region (e.g., Kirby *et al.*, in press). Maximum densities were generally less than 4.0 animals g^{-1} macrophyte tissue. Patterns of invertebrate colonization were similar for all species except *P. ceratophyllum* (Fig. 1) where densities increased rapidly, then decreased, while densities on other species of leaf bags were still increasing.

Discussion

The average breakdown rates reported for the five species of aquatic macrophytes in this study (Table 1) can be compared to rates reported in other investigations of aquatic macrophyte breakdown (Table 3). Webster & Simmons (1978) reported a rate of 0.010 day^{-1} for *Typha latifolia* in Claytor Lake, a reservoir at the downstream edge of our study area. This is faster than the 0.007 day^{-1} we are reporting for the same species, yet slower than the 0.03 day^{-1} reported by Rodgers *et al.* (in press) for a site in the New River 128 km downstream from our study area and under a similar temperature regime. Boyd (1970) reported a breakdown rate of 0.003 day^{-1} for *T. latifolia* in a pond.

Reported breakdown rates for *Elodea canadensis* range from a high of 0.12 day^{-1} (Rodgers *et al.*,

in press) to 0.060 day^{-1} for samples exposed in a northern, temperate lake (Hill 1977). The rate we are reporting here, 0.026 day^{-1} , is slower than any reported from previous studies, though it is similar to a breakdown rate of 0.020 day^{-1} for *Vallisneria americana*, another member of the Hydrocharitaceae, in a northern lake (Boylen *et al.* 1975).

Breakdown of *Potamogeton crispus* in this study was generally slower than rates reported for this and other species of *Potamogeton* by other investigators. This may be due to the propensity of this species to form marl deposits on its leaves, which may slow the breakdown process. This hypothesis is not supported by Rodgers *et al.* (in press) who reported a breakdown rate of 0.12 day^{-1} , however, their use of a short (20–30 day) exposure period probably resulted in overestimation of breakdown rates because of overemphasis of the leaching losses during short exposure periods. Other reported breakdown rates are as much as an order of magnitude slower (e.g., Jewell 1971; Boylen *et al.* 1975; Hill 1979; Howard-Williams & Davies 1979). Howard-Williams & Davies (1979) reported a breakdown rate of 0.020 day^{-1} for *Potamogeton pectinatus*, another plant commonly found with marl deposits. This is similar to the breakdown rate of 0.021 day^{-1} for *P. crispus* we found in this study.

Podostemum ceratophyllum, the dominant aquatic macrophyte in the New River, exhibited the fastest breakdown of any of the five species used in this study. Whether this rapid breakdown reflects the fragile nature of this species when dried or is actually a measure of faster biological processing is speculative and needs more study for clarification. In the only other breakdown study of *P. ceratophyllum*, Rodgers *et al.* (in press) measured rates

Table 2. Functional classification of macroinvertebrates found on aquatic macrophyte leaf packs in the New River, Virginia.

Taxonomic group	Number	% of total
Shredders (35.3% of total)		
Plecoptera		
Taeniopterygidae		
<i>Taeniopteryx</i> sp.	52	27.8
Peltoperlidae		
<i>Peltoperla</i> sp.	1	0.5
Diptera		
Tipulidae		
<i>Tipula</i> sp.	1	0.5
Oligochaeta	12	6.4
Collectors: Filterers (31.6%)		
Tricoptera		
Hydropsychidae		
<i>Hydropsyche</i> sp.	46	24.6
<i>Cheumatopsyche</i> sp.	3	1.6
<i>Macronema</i> sp.	1	0.5
<i>Potamyia</i> sp.	1	0.5
Polycentropodidae		
<i>Neureclipsis</i> sp.	3	1.6
Brachycentridae		
<i>Brachycentrus</i> sp.	2	1.1
Ephemeroptera		
Siphonuridae		
<i>Isonychia</i> sp.	3	1.6
Collectors: Scrapers (16.6%)		
Coleoptera		
Elmidae		
<i>Gonielmis</i> sp.	15	8.0
Ephemeroptera		
Heptagoniidae		
<i>Stenonema</i> sp.	3	1.6
Baetiscidae		
<i>Baetisca</i> sp.	1	0.5
Ephemerellidae		
<i>Ephemerella</i> sp.	1	0.5
Amphipoda		
Talitridae		
<i>Hyalella</i> sp.	7	3.7
Gastropoda		
Lymnaeidae		
<i>Lymnea</i> sp.	4	2.1
Collectors: Gatherers (10.2%)		
Diptera		
Chironomidae		
Chironomini	11	5.9
Podonomini	6	3.2
Orthocladini	2	1.1
Predators (6.4%)		
Plecoptera		
Perlodidae		
<i>Isoperla</i> sp.	5	2.7
Odonata		
Coenagrionidae		
<i>Ischnura</i> sp.	3	1.6
Diptera		
Chironomidae		
Macropelopiini	4	2.1

ranging from 0.08 day⁻¹ to 0.05 day⁻¹, the latter being similar to the 0.037 day⁻¹ we are reporting here. *Justicia americana* an emergent species, broke down at a rate considerably faster than the larger emergent, *T. latifolia*, but also much slower than any of the submerged species. This is consistent with the results reported by Rodgers *et al.* (in press). *Justicia* grows to only 1 m in height, whereas *Typha* may attain a height up to 2 m. The reduced need for structural support in *Justicia* may explain its more rapid breakdown between these two emergent species. This supports the hypothesis that leaf species is the most important factor controlling leaf breakdown (Witkamp 1966).

The effect of temperature on aquatic macrophyte breakdown has only recently been investigated (e.g., Gallager 1978; Godshalk & Wetzel 1978; Carpenter & Adams 1979) and results indicate that aquatic macrophytes exhibit a Q₁₀ of 2–3 within a temperature range of 5 to 30 °C. The relatively low temperatures measured in the New River may account for the relatively slow breakdown rates we are reporting for *T. latifolia* and *E. canadensis*.

Generally, breakdown of aquatic macrophytes proceeds more rapidly than breakdown of terrestrial tree leaves though maple (*Acer* spp.) and dogwood *Cornus* spp.) may breakdown faster than some of the slow to intermediate aquatic macrophytes (Hart & Howmiller 1975; Webster & Simmons 1978; Paul *et al.* 1978).

The differential breakdown of species of terrestrial leaf litter along a stream–lake–land continuum, with fastest breakdown rates reported from streams and slowest from land, is well documented (Witkamp & Frank 1969; Thomas 1970; Odum & Heald 1975; Brinson 1977). However, this trend is not apparent from the comparison of aquatic macrophyte breakdown in streams versus lakes. There have been few studies of aquatic macrophyte breakdown in streams (this study; Hill 1979; Hill & Webster, in press; Rodgers *et al.*, in press), and we are unaware of any published reports of direct comparison of aquatic macrophyte breakdown in streams versus lakes. However, comparison of our results with published data for aquatic macrophyte breakdown in lake environments shows no distinct differences.

Macroinvertebrate densities on aquatic macrophyte leaf bags in the New River were at the lower end of the range suggested by the results of other

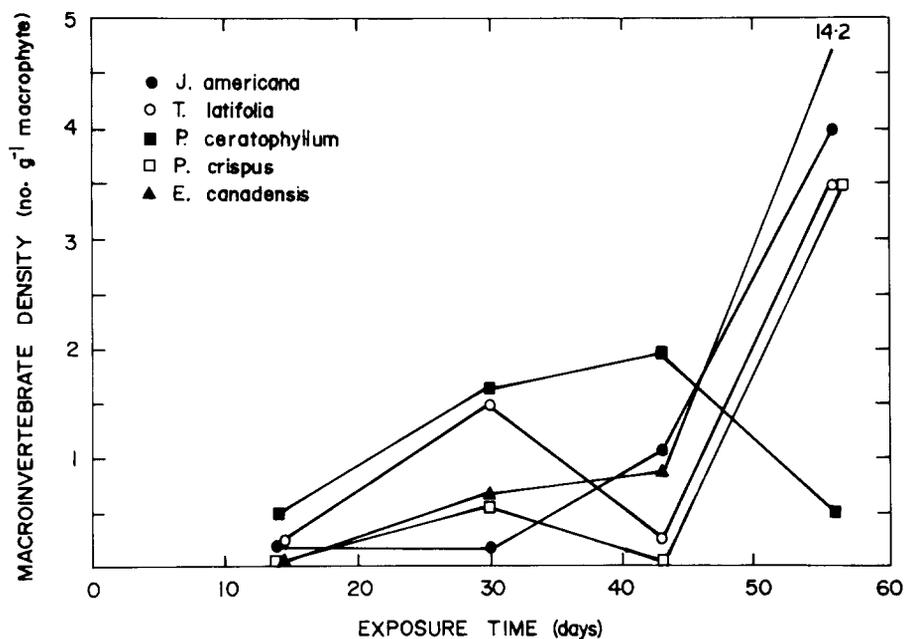


Fig. 1. Macroinvertebrate densities on decomposing aquatic macrophyte leaf bags in the New River.

investigations of macrophyte and tree leaf breakdown (Petersen & Cummins 1974; Hart & Howmiller 1975; Smock & Stoneburner 1980; Kirby *et al.*, in press). However, the trend of increasing macroinvertebrate colonization with increasing exposure time was similar (Fig. 1), indicating the same macroinvertebrate response to decaying aquatic macrophytes as for decaying terrestrial leaf litter. While delayed colonization of macroinvertebrates may be due simply to random colonization of 'inert' substrates, it may also reflect the time required by microbial populations to condition the leaf material before it is palatable to macroinvertebrates, and suggests that these organisms may be using aquatic macrophytes as a food source after the plants have been conditioned and not solely as a substrate for attachment. Maximum colonization occurred between about 90 and 160 days for terrestrial leaf litter in small streams (Petersen & Cummins 1974; Hart & Howmiller 1975; Kirby *et al.*, in press). For aquatic macrophytes in this study, maximum colonization occurred after 43 days (Fig. 1). The lag in colonization apparently in response to conditioning time,

and the presence of large particle shredders (e.g., *Taeniopteryx* sp.) on aquatic macrophyte leaf bags support the hypothesis that macroinvertebrates use decaying aquatic macrophytes as food.

If the hypothesis that stream ecosystems should tend towards a temporal uniformity of energy flow (Vannote *et al.* 1980) is correct, then there is a gap between the input of organic matter from periphyton production during summer and the autumn input of conditioned allochthonous leaf litter, that needs to be filled. Evidence on the timing of organic matter inputs from aquatic macrophytes (Fisher & Carpenter 1976; Hill 1979; Hill & Webster, in press) suggests that these plants may provide this link in mid-sized stream ecosystems in which aquatic macrophytes are abundant (e.g., the New River, Hill & Webster, in press). The rapid breakdown of aquatic macrophytes comes at a time when other organic matter sources are minimal. The role of aquatic macrophytes in stream energy budgets should not be assessed simply in terms of organic matter pools, but also with respect to the timing of organic matter input from this source.

Table 3. Breakdown rates for some freshwater aquatic macrophytes of the same families as those in our study. Some rates were calculated from reported data.

Species	Rate (day ⁻¹)	Site	Reference
Typhaceae			
<i>Typha latifolia</i>	0.030–0.040 ^a	River	Rodgers <i>et al.</i> (in press)
<i>T. latifolia</i>	0.010	Reservoir	Webster & Simmons (1978)
<i>T. latifolia</i>	0.007	River	This study
<i>T. latifolia</i>	0.003	Pond	Boyd (1970)
Potamogetonaceae			
<i>Potamogeton crispus</i>	0.120–0.210 ^a	River	Rodgers <i>et al.</i> (in press)
<i>P. crispus</i>	0.021	River	This study
<i>P. pectinatus</i>	0.082 ^b	Lake	Carpenter (1980)
<i>P. pectinatus</i>	0.020	Lake	Howard-Williams & Davies (1979)
<i>P. nodosus</i>	0.050	Stream	Hill (1977)
<i>P. nodosus</i>	0.031–0.041	Stream	Hill (1979)
<i>P. nodosus</i>	0.034	Lake	Hill (1977)
<i>P. amplifolius</i>	0.002	Lake	Boylen <i>et al.</i> (1975)
<i>P. robbinsii</i>	0.0002 ^c	Lake	Boylen <i>et al.</i> (1975)
<i>Potamogeton</i> sp.	0.067	Lab	Jewell (1971)
Hydrocharitaceae			
<i>Elodea canadensis</i>	0.120 ^a	River	Rodgers <i>et al.</i> (in press)
<i>E. canadensis</i>	0.087 ^d	Lab	Jewell (1971)
<i>E. canadensis</i>	0.064	Stream	Hill (1977)
<i>E. canadensis</i>	0.060	Lake	Hill (1977)
<i>E. canadensis</i>	0.026	River	This study
<i>E. nutallii</i>	0.120–0.150 ^a	River	Rodgers <i>et al.</i> (in press)
<i>Vallisneria americana</i>	0.164 ^b	Lake	Carpenter (1980)
<i>V. americana</i>	0.025	Lake	Boylen <i>et al.</i> (1975)
Podostemaceae			
<i>Podostemum ceratophyllum</i>	0.050–0.080 ^a	River	Rodgers <i>et al.</i> (in press)
<i>P. ceratophyllum</i>	0.037	River	This study
Acantheraceae			
<i>Justicia americana</i>	0.050–0.080 ^a	River	Rodgers <i>et al.</i> (in press)
<i>J. americana</i>	0.016	River	This study

^a Used exposure period of 20–30 days.

^b Used freeze-dried plant material.

^c Suspected that plants remained alive.

^d Used segmented leaves.

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Received 23 March 1981.