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PRODUCTIVITY OF *PODOSTEMUM CERATOPHYLLUM* IN THE NEW RIVER, VIRGINIA¹

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ABSTRACT

Productivity of *Podostemum ceratophyllum*, the dominant aquatic macrophyte in the New River, was measured at four sites representing soft- and hardwater reaches of the river. Available dissolved inorganic carbon (DIC) was 4-5 times greater in the hardwater reach. The difference in available DIC was reflected in standing crop and productivity of *P. ceratophyllum*. Maximum standing crops of *P. ceratophyllum* at the two hardwater sites (Sites 1 and 2) were 244.8 ± 30.7 g ash-free dry wt (AFDW) m^{-2} and 193.8 ± 18.7 g AFDW m^{-2} compared to 128.5 ± 14.9 g AFDW m^{-2} and 101.3 ± 6.9 g AFDW m^{-2} for the softwater sites (Sites 3 and 4). Productivity, based on differences in standing crops, was: Site 1, 1.08 ± 0.12 g C $m^{-2} d^{-1}$; Site 2, 0.86 ± 0.08 g C $m^{-2} d^{-1}$; Site 3, 0.58 ± 0.06 g C $m^{-2} d^{-1}$; Site 4, 0.45 ± 0.03 g C $m^{-2} d^{-1}$. Corresponding values for productivity as ¹⁴C uptake were: 2.77 ± 0.44 g C $m^{-2} d^{-1}$; 2.10 ± 0.45 g C $m^{-2} d^{-1}$; 0.34 ± 0.04 g C $m^{-2} d^{-1}$; 0.28 ± 0.03 g C $m^{-2} d^{-1}$. Productivity/biomass (P/B) based on ¹⁴C uptake and standing crop revealed that *P. ceratophyllum* productivity was inhibited at the softwater sites perhaps due to carbon limitation. Because of its abundance and its high productivity, *P. ceratophyllum* is hypothesized to contribute significantly to the New River organic matter budget.

LIKE MANY RIVERS of the Appalachian region, the New River supports a large, productive aquatic macrophyte community. The dominant aquatic macrophyte in the New River is *Podostemum ceratophyllum*, a species well suited to the swift-flowing, shallow, bedrock riffles common to rivers of this region. Because of its abundance, productivity of *P. ceratophyllum* dominates the primary productivity and particulate organic matter (POM) input from aquatic macrophytes to the New River. (Hill and Webster, 1983).

Standing crop and ¹⁴C uptake studies of aquatic macrophyte productivity are well documented for lake ecosystems (e.g., Wetzel, 1964a, b; Wetzel and Hough, 1973; Adams and McCracken, 1974; McCracken et al., 1975; Adams, Guilizzoni and Adams, 1978; Adams, Titus, and McCracken, 1974). Aquatic macrophyte productivity, especially as ¹⁴C uptake, in lotic ecosystems has received far less attention.

Use of chambers for aquatic macrophyte productivity studies is not meant to mimic field conditions but rather to allow the investigator controlled conditions in the field. However, there are some problems associated with the use of chambers that may obscure the actual

productivity of aquatic macrophytes (Wetzel, 1974; Moeller, 1978). Such problems as oxygen accumulation, dissolved inorganic carbon (DIC) depletion, and other environmental changes within the chambers may inhibit photosynthesis of enclosed aquatic macrophytes.

This study was undertaken to compare productivity estimates for *P. ceratophyllum* based on differences in standing crop and ¹⁴C uptake and to determine potential POM contribution from *P. ceratophyllum* to the New River. *Podostemum ceratophyllum* Michx. (Podostemaceae: Angiospermae) is a small aquatic plant characteristic of riffles in tropical and subtropical rivers and extending into temperate regions of North America as far north as New Brunswick and Ontario. This plant lacks roots, but attaches itself to substrate with holdfasts, an adaptation which allows the plant to attach to large cobbles, boulders, and bedrock in swift riffles.

The New River originates in the Appalachian highlands of western North Carolina and flows northward through Virginia and West Virginia. The river is characterized by a narrow floodplain, swift flow, and steep gradient. It flows in the channel of the ancient River Teays, reported to be the second oldest river in the world (Janssen, 1953). This ancient channel of exposed bedrock remains relatively free of silt because of the swift flow and is quite shallow for its width. The river passes through two geologic provinces, gneiss and limestone/do-

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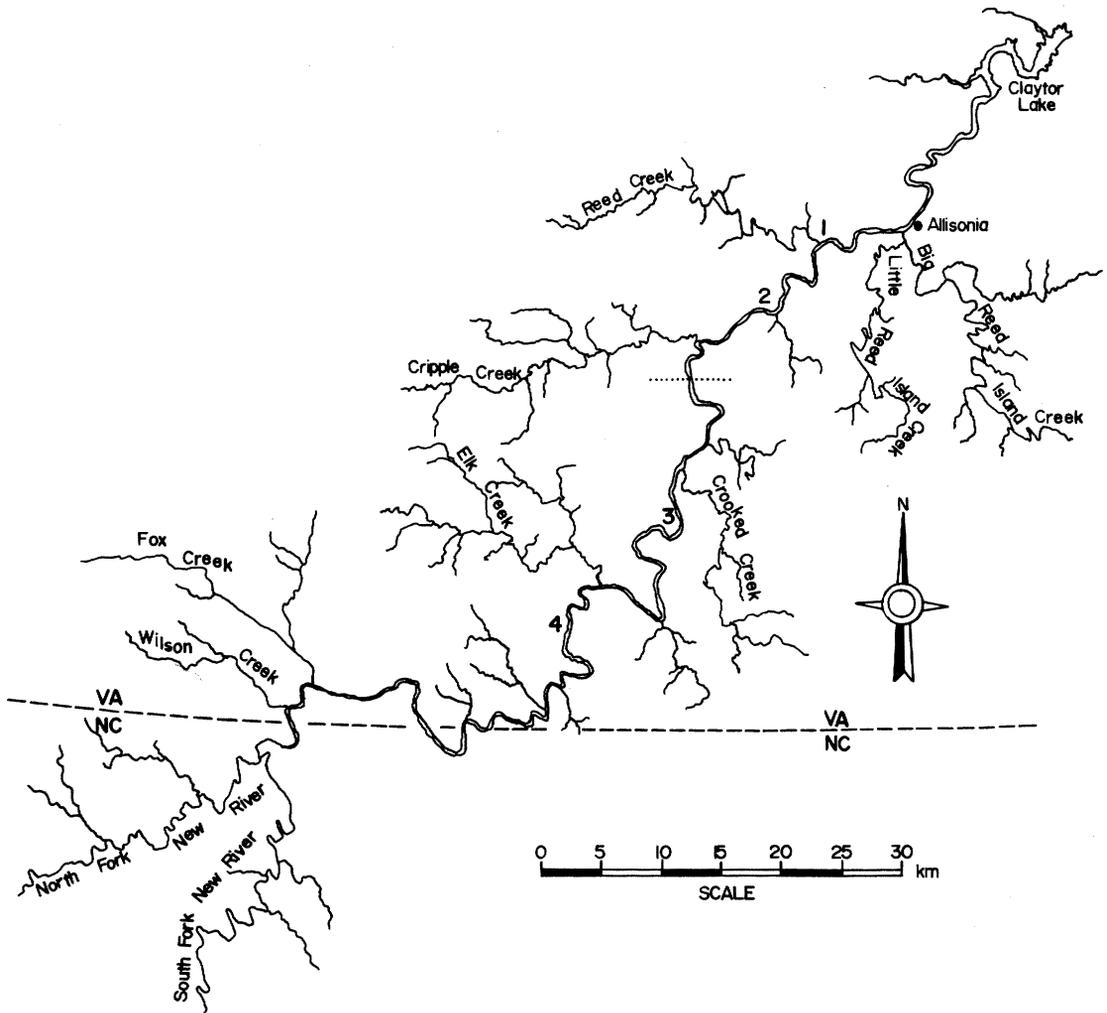


Fig. 1. Map of the New River showing sampling sites and the change from the softwater to hardwater (dotted line in center of figure) regions.

lomite, which divide the river into distinct softwater (upstream) and relatively hardwater (downstream) reaches. The softwater and hardwater reaches represent 66% and 34% of the study area, respectively. 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, forming a sixth-order stream, downstream 135 km to Allisonia, Virginia, at the head of Claytor Lake (Fig. 1).

Four sites were located within the overall study area, two each in the soft and hardwater reaches of the New River (Fig. 1). Site 1, located near the downstream end of the study area, is characterized by hardwater, sand and bedrock

substrate, a 175-m-wide channel, and an average depth of 1.5 m. Most *Podostemum* growth at this site occurred 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 channel width, and water depth less than 0.5 m. This site is dominated by a large bedrock riffle. Site 3, located in the softwater reach, was 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. Channel width at this site was 100 m. Average channel width and water depth for the New River study area are 167 m and about 0.5 m, respectively.

METHODS—Harvests of *P. ceratophyllum* biomass at the four sites were undertaken at monthly intervals from May through early November 1980. Sampling sites were selected randomly from areas in which the plants occurred. The plant samples were collected by scraping the plant from the rock substrate contained by a 0.10 m² box sampler. Replicate samples ($n = 5$) from each site were returned to the laboratory, air dried (22 C, 5 days), weighed, and subsampled. Subsamples were weighed, ashed (525 C, 30 min), and reweighed to determine ash free dry weight (AFDW).

Carbon-14 uptake by *P. ceratophyllum* was measured at the four sites during the 1980 growing season. Uptake of ¹⁴C was measured during replicate ($n = 5$) 90 minute incubations in recirculating (battery powered submersible pumps, 300 ml min⁻¹), 1.9-l polystyrene chambers (Hornick, Webster and Benfield, 1981). Rock substrates with healthy *P. ceratophyllum* were placed in the chambers, filled with river water, sealed, and placed on the river bed at approximately the depth from which they were removed (about 0.25–0.5 m). Incubations were initiated by injecting 5 μ Ci NaH¹⁴CO₃ into each chamber. Following each incubation, but before opening the chambers, 1-ml samples of the water within the chambers were removed with a syringe and transferred to scintillation cocktail to test for inorganic carbon depletion. The chambers were then opened and *P. ceratophyllum* was removed, placed in plastic bags, and packed on ice until returned to the laboratory. In the laboratory, samples were either frozen or processed immediately. Sample processing included removal of three equal subsamples of *P. ceratophyllum* from each rock substrate. One subsample was placed in an aluminum drying pan, air dried, weighed, and ashed to determine AFDW. The two remaining subsamples were placed in shell vials and fumed with concentrated HCl for 1 hour to remove any residual inorganic ¹⁴C (Wetzel, 1965). After fuming, samples were frozen then wet oxidized with

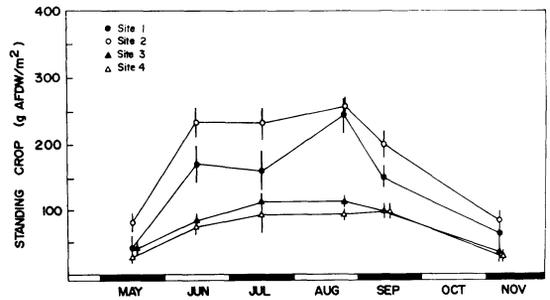


Fig. 2. Standing crop of *Podostemum ceratophyllum* in the New River during 1980. Vertical bars indicate \pm SE.

cold potassium dichromate (Shimshi, 1969), and evolved ¹⁴CO₂ was trapped in 0.25 N NaOH and transferred to the scintillation cocktail for counting. 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%. Productivity of the samples was calculated using the formula of Volenweider (1974).

A diurnal productivity curve for *P. ceratophyllum* was determined using a series of 90-min incubations, as above, from before sunrise to after sunset on 12 August 1980, at Site 2.

Temperature, pH, and alkalinity (titration with 0.2 N H₂SO₄, methyl purple endpoint, pH 4.5) of the river water were determined for each site on each sampling date to estimate dissolved inorganic carbon (DIC). Photosynthetically active radiation (PAR 390–710 nm) was measured on site on eight dates during the study period as a check against the PAR data collected on the VPI & SU campus 50 km north of Site 1.

RESULTS—Standing crop of *P. ceratophyllum* increased from mid-May until late August before starting to decline (Fig. 2). Maximum standing crops and productivity of *P. ceratophyllum* are given in Table 1. Productivity of

TABLE 1. Standing crop and productivity of *Podostemum ceratophyllum* in the New River (\pm SE). Vertical bars after productivity values indicate no significant differences ($P > 0.05$) between sites

Site (Date)	Maximum productivity		
	Standing crop		¹⁴ C uptake
	(g AFDW m ⁻²)	(g C m ⁻² d ⁻¹)	(g C m ⁻² d ⁻¹)
1 (27 Aug)	244.8 \pm 30.7	1.08 \pm 0.12	2.77 \pm 0.44
2 (27 Aug)	193.8 \pm 18.7	0.86 \pm 0.08	2.10 \pm 0.45
3 (26 Aug)	128.5 \pm 14.9	0.58 \pm 0.06	0.34 \pm 0.04
4 (26 Aug)	101.3 \pm 6.9	0.45 \pm 0.03	0.28 \pm 0.03

TABLE 2. Abiotic variables effecting *Podostemum ceratophyllum* productivity in the New River (June–September 1980)

Variable	Mean ± SE	Range	n
pH			
Softwater	7.5 ± 0.2	7.0–8.0	11
Hardwater	7.7 ± 0.4	7.2–8.2	13
ALKALINITY (mg CaCO₃/l)			
Softwater	7.5 ± 0.8	6.0–8.0	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
PAR (μEin/m²/s)			
	1830.2 ± 334.5	1078.1–2222.5	24

P. ceratophyllum based on ¹⁴C uptake was fairly constant from mid-June to early September, but dropped off markedly by early November (Fig. 3). Productivity during August at the four sites is given in Table 1.

Productivity of *P. ceratophyllum* through the course of a day followed typical diurnal productivity patterns closely associated with PAR (Fig. 4), however, there was an absence of an afternoon depression often reported for other aquatic macrophyte species (Wetzel, 1975). Maximum productivity in this study actually occurred in the afternoon. Production followed PAR closely but lagged in response by about 4 hours.

Extrapolation of ¹⁴C uptake data to daily values, adjusted for daylength and the diurnal productivity curve, were compared to measured standing crop on four dates between 15 June and 12 September 1980. Ratios of productivity to standing crop biomass (P/B) from the harvest studies ranged from 2.38:1 to 7.88:1 in the hardwater reach and from 0.46:1 to 1.14:1 in the softwater reach. The low values in the softwater samples suggest that some chamber effect, perhaps DIC limitation, caused low estimates of carbon assimilation. Highest P/B were measured in the September samples and reflect the active photosynthesis of healthy tissue and the sloughing of senescent tissue, causing net biomass loss in spite of high productivity. Differences between ¹⁴C productivity and biomass productivity estimates make comparison of studies using these methods difficult. The higher productivity estimated by ¹⁴C uptake suggests that this method does not measure net primary productivity, but measures

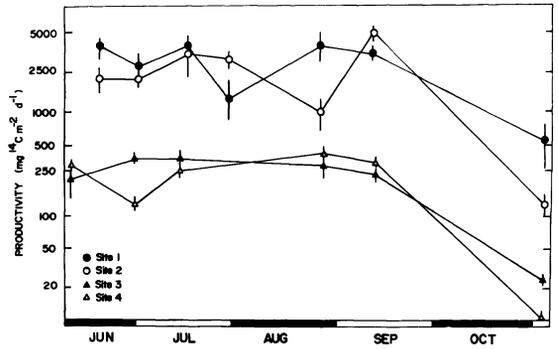


Fig. 3. Production (as ¹⁴C uptake) by *Podostemum ceratophyllum* in the New River during 1980. Vertical bars indicate ±SE.

rates closer to gross primary productivity. However, productivity based on biomass change appears to underestimate net primary productivity by losses of plant tissue to consumption by grazers and by fragmentation and sloughing.

Average values for pH, alkalinity, DIC, temperature, and PAR are given in Table 2. No differences between softwater and hardwater reaches were found for pH, temperature, or PAR. Significant differences (*t*-test, *P* < 0.05) were found for DIC and alkalinity between the softwater and hardwater reaches, with values in the hardwater reach 4–5 times greater than in the softwater reach.

Production of *P. ceratophyllum* was tested for significant correlation with the abiotic variables. At the hardwater sites (1 and 2) productivity was significantly correlated (*t*-test,

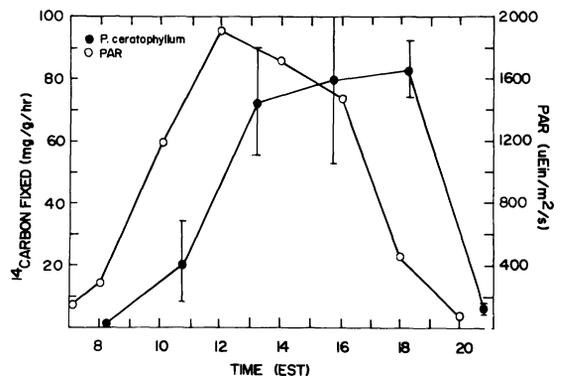


Fig. 4. Diurnal production of *Podostemum ceratophyllum*, and photosynthetically active radiation (PAR) on 28 August 1980 (measured at Site 2) (each point plotted as the mid-point of 90 minute incubations). Vertical bars indicate ±SE.

$P < 0.05$) with alkalinity. Correlations in the softwater reach were significant for PAR. Linear regression of productivity along a DIC gradient showed only a poor response ($r^2 = 0.33$) of *P. ceratophyllum* to increasing DIC availability.

DISCUSSION—Data on *P. ceratophyllum* productivity are found only for studies from the Appalachian region (Nelson and Scott, 1962; Rodgers et al., 1983). Based on differences in standing crops between May and August, productivity of *P. ceratophyllum* in our study ($0.45 \pm 0.03 - 1.8 \pm 0.12 \text{ g C m}^{-2} \text{ d}^{-1}$) was 1.9 to 4.6 times greater than estimates of *P. ceratophyllum* productivity ($0.235 \text{ g C m}^{-2} \text{ d}^{-1}$) for the Middle Oconee River, Georgia (Nelson and Scott, 1962). Rodgers et al. (1983) reported changes in *P. ceratophyllum* standing crops for the Watauga River, Tennessee and for the New River, Virginia, at a site 128 km downstream from our study area. Using their data for standing crops in June and September (a period of about 91 days) *P. ceratophyllum* productivity is estimated as $0.40 \text{ g C m}^{-2} \text{ d}^{-1}$ for the Watauga River and $0.05 \text{ g C m}^{-2} \text{ d}^{-1}$ for the New River. These values are 1.1 to 21.6 times lower than the productivity values we are reporting for our study. The extremely low *Podostemum* productivity reported by Rodgers et al. (1983) for the New River is probably due to increased scouring caused by daily pulses of discharge from an upstream hydroelectric dam.

Podostemum productivity is comparable to productivity by other submerged aquatic macrophytes in streams and lakes. Owens and Edwards (1961, 1962) reported productivity of $0.04\text{--}2.30 \text{ g C m}^{-2} \text{ d}^{-1}$ for *Ranunculus fluitans*, *Callitriche* sp., *Potamogeton lucens*, and *P. densus*. Adams and McCracken (1974) reported *Myriophyllum spicatum* productivity as $1.77 \text{ g C m}^{-2} \text{ d}^{-1}$; Fisher and Carpenter (1976) reported productivity at $0.36 \text{ g C m}^{-2} \text{ d}^{-1}$ for *Potamogeton crispus*; and Hannan and Dorris (1970) reported a productivity of $1.24 \text{ g C m}^{-2} \text{ d}^{-1}$ for a stream community composed of 15 species of submerged macrophytes.

The differential productivity of *P. ceratophyllum* in the soft and hardwater reaches of our study area appears to be in response to water hardness and available DIC. This is not uncommon among aquatic plants (Raven, 1976; Hutchinson, 1975; Adams et al., 1978) and is either attributable to higher concentrations of bicarbonate or greater availability of free CO_2 , because of the chemical equilibrium of the different carbon species. At the mean pH of 7.6, the percent of DIC as CO_2 and HCO_3^- is 9.8 and 90.2, respectively (Wetzel,

1975). Thus the difference in DIC, especially to a plant that uses only CO_2 in photosynthesis becomes critical. Since *P. ceratophyllum* uses only free CO_2 (Hill, 1981; Hill, Webster and Linkins, in press), the availability of DIC to the species is reduced from 2.0 to 0.20 mg l^{-1} and 9.5 to 0.93 mg l^{-1} of total inorganic carbon, respectively for the soft and hardwater reaches. Productivity is almost 3 times greater in the hardwater reach, comparable to the differences in DIC. Because of the limiting free CO_2 availability at the softwater sites correlation of *P. ceratophyllum* productivity to free CO_2 was not significant ($r = 0.397$).

Measurement of *P. ceratophyllum* productivity in the New River is complicated by two factors. First, the plant grows in swift-flowing riffles where losses of biomass due to fragmentation and scouring may be considerable. This is reflected by the high P/B ratios in the hardwater reach of the river. Second, the plant appears to use only free CO_2 (Hill, 1981; Hill et al., in press) in photosynthesis, and thus may be carbon limited in the chamber studies of productivity in the softwater reach, as indicated by P/B less than 1.

Estimation of productivity based on biomass changes over time has the inherent weakness of underestimating productivity because of loss of plant tissue due to sloughing, grazing, fragmentation, and/or scouring between sampling times. Underestimation of net productivity because of this error may be considerable if times between sampling are lengthy (Fisher and Carpenter, 1976). P/B ratios are generally near 2 for aquatic macrophytes (Nelson and Scott, 1962; Adams and McCracken, 1974), but were nearer to 4 for *P. ceratophyllum* in the hardwater reach, suggesting that losses of plant tissue from this species, due to scouring and fragmentation, may be considerable.

The inability of *P. ceratophyllum* to use HCO_3^- as an inorganic carbon source (Hill, 1981; Hill et al., in press) is unusual among submerged aquatic angiosperms, but not unexpected of plants growing in riffles (Gessner, 1959; Raven, 1970). While no previous reports of DIC use in *Podostemum* are available, another member of the Podostemaceae, *Apinagia*, has been shown to use only free CO_2 (Gessner, 1959). The inability to use HCO_3^- has been viewed as a competitive disadvantage in hardwater lakes (Moeller, 1978), however, this does not appear to be the case in swift-flowing, turbulent rivers which are well mixed and saturated with CO_2 . Aquatic mosses, the typical primary producers in swift-flowing waters, use only free CO_2 (Bain and Proctor, 1980).

Podostemum productivity was, on a per gram basis, lower than similar productivity estimates for periphyton (Hill and Webster, 1982, 1983) and reflects the greater metabolic and turnover rate of periphyton. On an areal basis, production of *P. ceratophyllum*, because of its growth out from the substrate, is as much as 10 times higher than periphyton productivity. Aquatic macrophyte and periphyton contributions to the New River organic matter budget are nearly equal (Hill and Webster, 1983).

It is generally assumed by stream ecologists that aquatic macrophytes play only a minor role in the middle reaches (4–6 orders) of streams, and overall are rarely significant to the entire stream ecosystem (Cummins, 1974; Vannote et al., 1980). Since aquatic macrophytes are not extensively grazed in most ecosystems (Westlake, 1965; Sculthorpe, 1967; Fisher and Carpenter, 1976; Rodgers et al., 1983) biomass accumulates throughout the growing season. Thus maximum aquatic macrophyte standing crop may be an adequate estimate of POM contributions from these plants to stream ecosystems. While the contribution of aquatic macrophytes to stream energy budgets may be small, it has been hypothesized that the timing of this POM input may make them an important link in the organic matter dynamics of stream ecosystems in which they occur (Hill and Webster, 1983). Such may be the case with *P. ceratophyllum* in the New River.

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