

Review

Ecology of the macrophyte *Podostemum ceratophyllum* Michx. (Hornleaf riverweed), a widespread foundation species of eastern North American rivers

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ABSTRACT

Podostemum ceratophyllum, commonly called Hornleaf Riverweed, occurs in mid-order montane and piedmont rivers of eastern North America, where the plant grows submerged and attached to rocks and stable substrates in swift, aerated water. Multiple studies, mostly conducted in the southern portions of the plant's range, have shown that *Podostemum* can variously influence benthic communities in flowing waters. However, a synthetic review of the biology and ecology of the plant is needed to inform conservation, particularly because *P. ceratophyllum* is reported to be in decline in much of its range, for mostly unknown reasons. We have thus summarized the literature showing that *Podostemum* provides substantial habitat for invertebrates and fish, may be consumed by invertebrates, turtles, and other vertebrates, removes and sequesters dissolved elements (i.e., nitrogen, phosphorus, calcium, zinc, etc.) from the water column, and contributes organic matter to the detrital pool. *Podostemum* may be tolerant to some forms of pollution but appears vulnerable to sedimentation, epiphytic over-growth, and hydrologic changes that result in desiccation, and possibly increased herbivory pressure. Much remains unknown about *Podostemum*, including aspects of morphological variation, seed dispersal, and tolerance to changes in temperature and water chemistry. Nonetheless, *Podostemum* may be considered a foundation species, whose loss from eastern North American rivers is likely to affect higher trophic levels and ecosystem processes.

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1. Introduction

Macrophyte ecology is an active area of aquatic research and research has shown that plants influence aquatic community structure and species composition (Argentina et al., 2010b; Camp et al., 2014), nutrient cycling (Keitel et al., 2016), benthic foodwebs (Lodge, 1991) and ecosystem level processing, and the retention of elements within the system (Vila-Costa et al., 2016). However, there still exist large deficiencies in our understanding of how riverine macrophytes are influenced by land use and subsequent changes in water quality (Argentina et al., 2010a; Manolaki and Papastergiadou, 2013; Bakker et al., 2016). To maintain the ecological integrity of river systems, it is important to be able to identify stressors to riverine macrophytes and predict species persistence for a given environmental change. Here we review the available literature concerning what we believe to be the most ecologically influential macrophytes in mid-order montane and piedmont rivers of eastern North America. *Podostemum ceratophyllum* Michx., commonly called Hornleaf Riverweed, is a flowering plant (angiosperm) that grows submerged and attached to stable benthic substrate (Fig. 1a). The plant is most common in rivers with an open canopy and a cobble or bedrock substrate, but it can also be found in smaller tributaries in locations with abundant light and perennial flow (e.g., waterfalls and cascades). *Podostemum ceratophyllum*, henceforth referred to as *Podostemum* (except where inclusion of the specific epithet provides needed clarity) can cover vast areas of the streambed and provides habitat, and potentially food, for a diverse group of aquatic organisms. *Podostemum* may also influence nutrient and carbon dynamics in the swift-flowing rivers where it occurs (Fig. 2).

Dayton (1972) used the term “foundation species” to describe an organism that strongly influences community structure and function. Later Ellison et al. (2005) employed the foundation species concept to illustrate how the loss of certain tree species altered the local environment and important ecosystem processes like decomposition, nutrient flux, carbon sequestration and energy flow. Similarly, we propose that *Podostemum* can be considered a foundation species based on the plant’s extensive geographic range and substantial influence on ecosystem processes and benthic community structure (Nelson and Scott, 1962; Everitt and Burkholder, 1991; Grubaugh and Wallace, 1995; Hutchens et al., 2004). *Podostemum* is morphologically and ecologically similar to riverine bryophytes, which also grow attached to stable substrates, provide substantial habitat for macroinvertebrates and epiphytic biofilms, and increase retention of organic matter and stream metabolism (Stream Bryophyte Group, 1999; Wood et al., 2016). However, we hypothesize that *Podostemum* has a stronger influence on ecosystem processes than bryophytes because it grows more quickly and in a broader range of light conditions, and sustains higher grazing pressure (Parker et al., 2007).

Podostemum is also of interest because the plant appears to be declining across much of its native range. Local extinction or substantial decline of *Podostemum* has been documented in several northern rivers including the Cochecho River near Dover, New Hampshire, the West River near Jamaica, Vermont (Philbrick and Crow, 1983), tributaries of the Roanoke River in Virginia (Connelly et al., 1999), several rivers in Pennsylvania (Munch, 1993) and possibly throughout much of the eastern Piedmont. The species is listed as *Endangered*, *Historical*, a *Species of Concern* or *Threatened* in many northern States (USDA, 2014). Decline and extirpation have

been attributed to sedimentation, dewatering, inundation by water impoundment, and unspecified pollutants from industry, mining operations and urban runoff (Adams et al., 1973; Munch, 1993; Connelly et al., 1999). However, neither the underlying factors nor the ecological significance of changes in *Podostemum* abundance have been extensively investigated.

This review provides a synopsis of the biology and ecology of *Podostemum* and identifies research needed to understand the causes and consequences of changes in abundance of the plant across its native range. We review reports describing *Podostemum* occurrence, important life history traits, and its role as a foundation species in eastern North American rivers (Table 1). We then hypothesize how *Podostemum* will likely respond to future environmental change, and how changes in *Podostemum* occurrence will likely affect river ecosystems.

2. Distribution and biology of *Podostemum ceratophyllum*

2.1. Biogeography

The family Podostemaceae Rich. ex C. Agardh is the largest family of strictly aquatic flowering plants in the world (Philbrick and Novelo, 1995; Philbrick and Novelo, 2004). These plants possess distinctive morphological adaptations including specialized root structures and long, thin durable leaves well-adapted to their swift-water habitat (van Steenis, 1981). North, Central, and South America contain about 60% of the species in the family, with the remaining species distributed throughout Africa, Madagascar, and Southeast Asia (Philbrick and Alejandro, 1995). Recent investigations have concluded that the genus *Podostemum* is restricted to the New World (Philbrick and Novelo, 2004), with the greatest species diversity occurring in South America, mainly in Brazil. South American Podostemaceae taxonomy remains uncertain (Philbrick et al., 2010) and ecological studies on these species are sparse. Mexico is reported to have four genera (*Marathrum*, *Oserya*, *Podostemum*, *Tristicha*) with higher diversity in the Pacific coast slopes compared with Atlantic slopes (Novelo and Philbrick, 1997; Tippery et al., 2011). Altogether, the Americas are thought to contain about 135 species of Podostemaceae with only a single species, *Podostemum ceratophyllum*, known from the continental U.S.A. and Canada (Graham and Wood, 1975; Philbrick et al., 2010; Tippery et al., 2011).

Podostemum ceratophyllum’s native range is confined to montane and piedmont regions of the eastern United States and Canada, ranging from Georgia to Ontario, with scattered populations westward as far as Arkansas, Oklahoma, Minnesota and North Dakota, and disjunct populations in Honduras and the Dominican Republic (Philbrick and Crow, 1983; Philbrick and Novelo, 2004). Reduced genetic variation (based on nucleotide markers and isozymes) in populations north of North Carolina indicates range expansion northward following the last glacial-maximum from refugia several hundred km south of the glacial boundary (Philbrick and Crow 1992; Fehrmann et al. 2012).

2.2. Morphology

Two of the earliest papers about *Podostemum* detailed the structure of the plant’s vegetative and reproductive organs (Warming, 1881, 1882). *Podostemum* follows the Root-Shoot model with the presence of distinct roots, stems (shoots) and leaves (Rutishauser

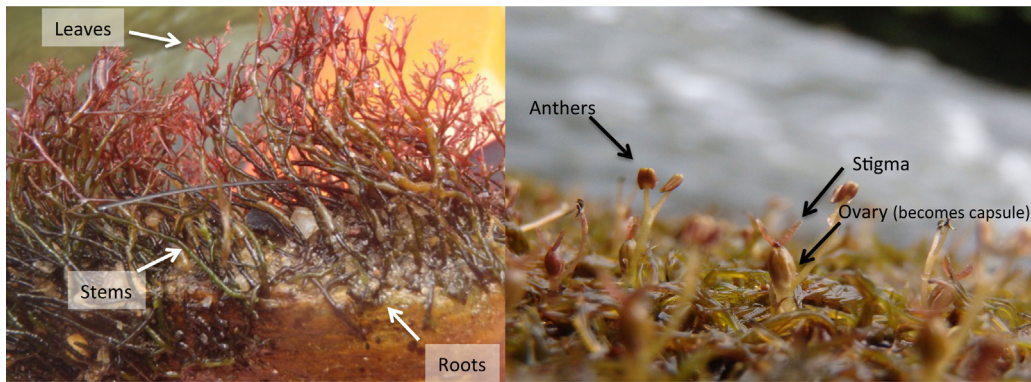


Fig. 1. (a) *Podostemum ceratophyllum* grows submerged, attached directly to rocks in fast flowing eastern rivers. Stems and leaves can be green, black and red and the leaves are deeply dichotomously lobbed. Roots are also green, black and red and attach the plant to the rock with structures called haptera. (b) Flowers emerge as water levels expose the plant above the water's surface. Flowers are small with reduced petals and prominent anthers above the stigma and ovary. Photo by J. Wood. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

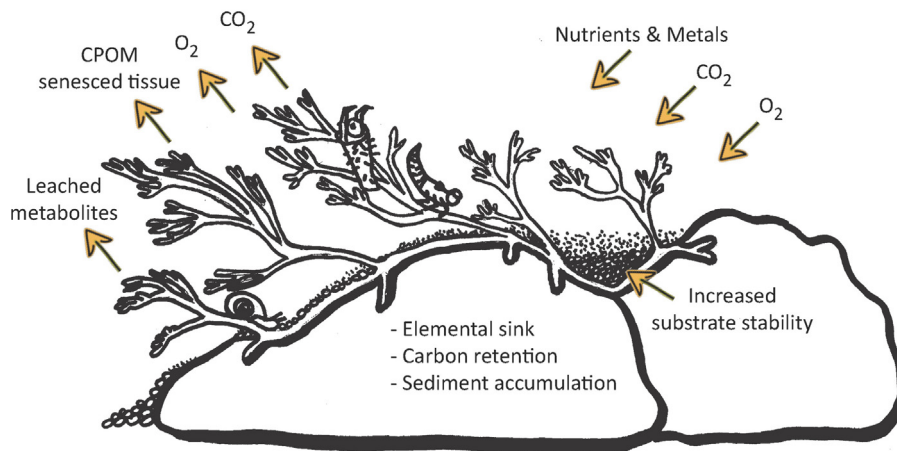


Fig. 2. A diagram illustrating *Podostemum ceratophyllum*'s interactions with the benthic environment. *Podostemum* provides structure and increases habitat complexity over bare rock, which attracts riverine biota. *Podostemum* influences elemental cycling through: retention of detrital material in plant colonies; assimilation of elements from the water column into plant tissue; and leaching of metabolites into the water column. *Podostemum* also increases substrate stability by binding gravels and cobbles together.

et al., 2003). The stems may be heavily cutinized (hardened), appearing dark green to black, often in stark contrast to its leaves, which can be a vibrant green. Cutinization can result from damage to the stem (Hammond, 1937), and heavily cutinized stems may correlate with abrasion from suspended sediments in swift current. New growth is often a luxuriant green in spring and summer, while in the winter leaves often are completely senesced or take on a deep reddish color (Hammond, 1937). The red coloration is caused by an increase in the light-absorbing pigment anthocyanin, which reduces tissue damage from UV light but may have other functions. Production of anthocyanin is a common stress response in plants and has also been linked to nutrient imbalance (Marschner, 1986). Supportive of this conclusion, Munch (1993) only found *Podostemum* exhibiting the red coloration in surface water that had a total nitrate-N to total phosphorous ratio of more than 18:1.

The roots of *Podostemum* attach to stable substrates (rock, wood, and other debris) with distinct root hairs called haptera (Rutishauser et al., 2003). While the root hairs were once thought to exude a sticky substance that attached the plant to rocks, a study of Old World species of Podostemaceae proposed that attachment is facilitated by a film of cyanobacteria (Jäger-Zürn and Grubert, 2000). The nature of this relationship is not understood, and has not been investigated in *P. ceratophyllum*.



Fig. 3. Examples of the morphological variation, from extended, narrow leaves to short, broader leaves, common in *Podostemum ceratophyllum*. These stems were collected on the same day and in close proximity to each other. Small squares in the background are 1 mm × 1 mm. Photo by J. Wood.

Aside from the basic root-stem-leave structure, *Podostemum* is highly variable in appearance (Fig. 3). Four varieties have been described based on this variation (van Royen, 1951) but these varieties have been condensed into one species with highly plastic morphology (Philbrick and Novelo, 2004). *Podostemum* can have long leaves (4–20 cm) in the form once recognized as *P. ceratophyllum* var. *ceratophyllum*, or shorter leaves that are densely

Table 1
Papers on the ecology of *Podostemum ceratophyllum* Michx. or that contain ecologically relevant information on the ecology the plant.

Topic	Foci	Author	Study Location
Macroinvertebrates	secondary production and community composition	Nelson and Scott (1962)	GA, Middle Oconee River
	habitat preference and density of black flies (<i>Simulium decorum</i> Walker)	Hudson and Hays (1975)	AL, Alabama Agricultural Experimental Station at Auburn University, Farm Pond no 1. artificial channel
	habitat preference of riverine snails (<i>Oxytrema</i> (=Goniobasis) suturalis Haldeman)	Kreiger and Burbanck (1976)	GA, Yellow River
	secondary production and community composition	Grubaugh and Wallace (1995)	GA, Middle Oconee River
	secondary production and impact of plant removal treatment	Hutchens et al. (2004)	NC, Little Tennessee River
	habitat of the caddisfly (<i>Brachycentrus etowahensis</i> Wallace)	Duncan PhD Dissertation (2008)	GA, Upper Etowah River
	dietary preference and habitat of Hydropsychid caddisflies	Tinsley BS Thesis (2012)	KY, Upper Green River
Macrophyte community dynamics and regrowth	interspecific competition between benthic autotrophs	Everitt and Burkholder (1991)	NC, Main stem and Cedar Fork of the Little River
	regrowth from root fragments	Philbrick et al. (2015)	CT, Pootatuck River
Fishes	habitat use by Riverweed Darter (<i>Etheostoma podostemone</i> Jordan & Jenkins)	Connelly et al. (1999)	VA, North and South Fork of Roanoke River
	habitat preference of riverine fish and influence of <i>Podostemum</i>	Argentina et al. (2010b)	GA & TN, Conasauga River
	habitat preference of the Snail Darter (<i>Percina tanasi</i> Etnier)	Ashton and Lazer (2010)	TN, French Broad and Hiwassee Rivers
Flow	flow alteration and plant recovery	Pahl MS thesis (2009)	GA, Middle Oconee River, Honeycutt Creek
Herbivory	consumption by River Cooter (<i>Pseudemys concinna</i> (LeConte))	Fahey (1987) in Aresco and Dobie (2000)	AL, Tallapoosa River
	consumption by Canada geese, crayfish, & amphipods	Parker et al. (2007)	GA, Chattahoochee River and in the laboratory
	consumption by triploid Grass Carp (<i>Ctenopharyngodon idella</i> (Valenciennes))	Weberg et al. (2015)	VA, Upper New River
Habitat	influence of land use, light, and substrate size	Argentina et al. (2010a)	GA & TN, Conasauga River
	influence of channel morphology and substrate size	Duncan et al. (2011)	GA, Upper Etowah River
Decomposition rate	<i>P. ceratophyllum</i> breakdown rate	Hill and Webster (1982) Rodgers et al. (1983)	NC & VA New River TN, Watauga & VA, New Rivers
Productivity	<i>P. ceratophyllum</i> production	Hill and Webster (1984)	NC & VA New Rivers
Elemental	plant elemental composition	Adams et al. (1973)	DE, Susquehanna
	copper and lead bioaccumulation	Heisey and Damman (1982)	CT, Natchaug, Willimantic and Shetucket Rivers
Biogeography	species distribution	Philbrick and Crow (1983)	Eastern US, Arkansas, Honduras, Dominican Republic
	isozyme variation	Philbrick and Crow (1992)	Eastern US
	interspecific nucleotide diversity	Fehrmann et al. (2012)	Eastern US, Arkansas and Honduras
Other	cyanobacterial symbiotic relationship	Jager-Zurn and Grubert (2000)	herbarium samples (Old World species only)
	carbon Isotope fractionation	Ziegler and Hertel (2007)	herbarium samples

clustered at the end of the stem, giving the plant a distinctly bristly appearance (in the form once recognized as *P. ceratophyllum* var. *circumvallatum*). Hammond (1937) notes that these different forms can grow side by side but that plants in a given colony are generally uniform in size and structure. We hypothesize that specific aspects of the habitat such as flow velocity, herbivory, or both may exert a large influence on growth form.

2.3. Reproduction

Flower buds open as water levels decline and the plant is exposed above the water surface (Philbrick, 1984). Flowers emerge from an enclosed spathellae, and mature flowers (Fig. 1b) have obvious anthers subtended by an enlarged ovary with two stigma (Philbrick, 1984). Pollination is most likely facilitated by wind or insects, but not water, and pre-anthesis cleistogamy (pollination

before the flower opens) has also been reported (Philbrick, 1984). After pollination maturation of the seed capsule is reported to take 2–3 weeks (Philbrick, 1984) and seed capsules may appear mature while still developing (Philbrick and Novelo, 1995). The seeds are small and the seed coat produces a sticky mucilaginous coating when wetted, allowing seeds to stick to suitable substratum. While pollination and seed dispersal mechanisms have not been intensively investigated (Philbrick, 1984), gene flow between populations appears erratic (Fehrmann et al., 2012) and seed dispersal is presumably facilitated by migrating wildlife (birds & large mammals), while long distance dispersal is probably limited to avian vectors (Philbrick and Crow, 1992).

Philbrick and Novelo (1994) propose that Podostemads use the type 1 seed germination strategy, first proposed by Thompson and Grime (1979), where seeds germinate soon after being released from the capsule. Indeed, the seeds lack an endosperm, show no

need for cold stratification or dormancy, and seem unlikely to persist for years before germination (Philbrick, 1984). Additionally, asexual reproduction is facilitated by root fragmentation, where detached root segments can reattach to rocks over time (Philbrick et al., 2015). For additional details about morphology, development and reproduction refer to (Graham and Wood, 1975; Philbrick, 1984; Philbrick and Alejandro Novelo, 1997; Rutishauser, 1997; Rutishauser et al., 2003; Philbrick and Novelo, 2004).

2.4. Physiology

Information about oxygen and carbon dioxide uptake rate and almost all other physiological responses of Podostemaceae is limited. Unlike most other aquatic plants which can utilize bicarbonate in addition to dissolved carbon dioxide, *Podostemum* may only be able to absorb dissolved carbon dioxide from the water column (Pannier, 1960; Hill and Webster, 1984) – a trait shared with bryophytes. Thus, a study on the New River attributed reduced ^{14}C uptake at soft-water sites to reduced availability of free CO_2 compared to hard-water sites (Hill and Webster, 1984). While the respiration rate of *Podostemum* has not been investigated, the neo- and paleotropical taxon (*Tristicha trifaria* (Bory ex Willd.) Spreng.) is reported to have an ability to absorb oxygen at an extremely high rate ($14 \text{ mg O}_2 \text{ g dry wt}^{-1} \text{ h}^{-1}$) in oxygen-saturated water (Pannier, 1960).

3. *Podostemum* as a foundation species

3.1. High biomass and productivity

Several studies have indicated that *Podostemum* is highly productive and capable of obtaining large standing stock biomass, although variation among locations, seasons and years may be substantial. Hill and Webster (1983) estimated that *Podostemum* contributed 1154 T ash free dry weight (AFDM) yr^{-1} to their New River, Virginia study area, approximately 80% of the total macrophyte contribution. *Podostemum* production was 10 times that of periphyton on an aerial basis and the ratio of production to biomass (P/B) was as high as 4 (most aquatic macrophytes are closer to 2; Hill and Webster 1984). The authors interpreted this high production relative to biomass as indicative of substantial biomass loss to scouring (Hill and Webster, 1984), although the potential influence of herbivory was not measured. Not surprisingly, measures of productivity have varied substantially, likely reflecting the influences of flow, water chemistry and location within the channel. For example, estimated productivity spanned 3 orders of magnitude ($0.05 \text{ g C m}^{-2} \text{ d}^{-1}$ to $1.08 \text{ g C m}^{-2} \text{ d}^{-1}$) on the New River and Watauga River (Tennessee) (Hill and Webster, 1984).

Biomass measurements have also varied widely, likely reflecting multiple influences. Rodgers et al. (1983) reported a seasonal maximum biomass between 22 and 98 g AFDW m^{-2} on the New River and Watauga River, in contrast to substantially higher mean monthly standing stocks (between 386 and 587 g AFDW m^{-2} , to a maximum of just over 1000 g AFDW m^{-2} in November) on the Middle Oconee River, Georgia, (Grubaugh and Wallace 1995). Biomass measurements at the same Middle Oconee River site during a prolonged drought were an order of magnitude lower (Pahl, 2009).

3.2. Influences on benthic biota

For almost 100 years, ecologists have known that macroinvertebrates utilize the habitat produced by *Podostemum* (Hammond, 1937) and more recent studies have shown strong correlations between *Podostemum* and abundances of some riverine biota (Hutchens et al., 2004; Argentina et al., 2010b). A study in the Little Tennessee River, North Carolina, found *Podostemum* enhanced the

surface area of macroinvertebrate habitat on bedrock by at least 3–4 times, and that removal of *Podostemum* reduced macroinvertebrate biomass by over 90% and abundance by almost 88% (Hutchens et al., 2004). A wide diversity of macroinvertebrates are associated with *Podostemum*. Rocks colonized by *Podostemum* in the Middle Oconee River contained at least thirty-four genera of aquatic insects (plus an additional 13 taxa only identified to family level or the order Hemiptera) representing all major aquatic insect orders, as well as Cnidaria, Tubellaria, Mollusca, Annelida, Hydracarina, Cladocera, and Copepoda (Nelson and Scott, 1962; Grubaugh and Wallace, 1995).

Podostemum may particularly enhance habitat availability for filter-feeding insects by providing points of attachment with access to swiftly-flowing water. The silk nets of hydropsychid caddisfly larvae are commonly observed in *Podostemum* mats (*pers. obs.* J.W.), and the plant is reported to support significantly higher abundances of hydropsychids (Tinsley, 2012) than bare rock. Similarly, densities of the filter-feeding Etowah caddisfly, *Brachycentrus etowahensis* Wallace, have been positively correlated with *Podostemum* (Willats, 1998; Duncan, 2008). The plant also appears to be a preferred habitat for filtering black fly larvae (*Simulium*), with measured densities of 4.2–4.5 individuals per square cm of *Podostemum* stem, among the highest densities recorded for the 54 plant taxa examined in a mesocosm study (Hudson and Hays, 1975). Furthermore, Hutchens et al. (2004) report that filterers were the best represented macroinvertebrate functional feeding group (FFG) in *Podostemum* by biomass.

Podostemum may also attract other FFGs because the plant traps organic matter and provides a substrate for epiphytic overgrowth of diatoms and other algae (Fig. 4). Thus, insects that feed by scraping periphyton (scrapers) or by collecting fine detrital particles (collector-gatherers) can be the most abundant FFGs associated with *Podostemum* (Hutchens et al., 2004; Grubaugh and Wallace, 1995). Similarly, snails, which are among the most endemic and threatened riverine invertebrates in eastern rivers (Johnson et al., 2013), are frequently observed grazing on *Podostemum*. In a study on the Yellow River, Georgia, Krieger and Burbanck (1976) found that *Podostemum* created the optimum habitat for the freshwater snail *Pleurocera catenaria* (Say) and other investigators have concluded that the presence of *Podostemum* and stable benthic substrates were the most important factors in predicting pleurocerid (especially *Elimia* spp.) snail distribution (Mulholland and Lenat, 1992; citing Krieger and Burbanck's 1976 study).

Associations between fish and *Podostemum* have been noted (Freeman and Freeman, 1994; Connelly et al., 1999; Skelton and Albanese, 2006; Argentina et al., 2010b; Ashton and Layzer, 2010) but a general lack of experimental research prohibits definitive conclusions. Short-term experimental manipulations of *Podostemum* in the Conasauga River, Georgia, by Argentina et al. (2010b) showed declines or increases in local benthic fish densities where *Podostemum* was reduced or augmented, respectively. The increased habitat complexity provided by *Podostemum* may benefit fishes by increasing densities of insect prey and by providing shelter from larger predators. However, species associations with *Podostemum* at landscape-scales can be difficult to untangle from other basin wide stressors that negatively influence species (Argentina et al., 2010a).

Podostemum may influence aquatic flora other than epiphytic algae, although we know of only a single study of competition with other submerged macrophytes. Everitt and Burkholder (1991) conclude that *Podostemum* uses a strategy of niche preemption to maintain habitat and prevent invasion by other species such as the red alga *Lemanea australise* Atkinson. In cool temperature months *Lemanea* and *Podostemum* are co-dominant, however, *Podostemum* grows most readily in the spring and summer months wherever light permits. *Podostemum* then dominates during the warm sea-

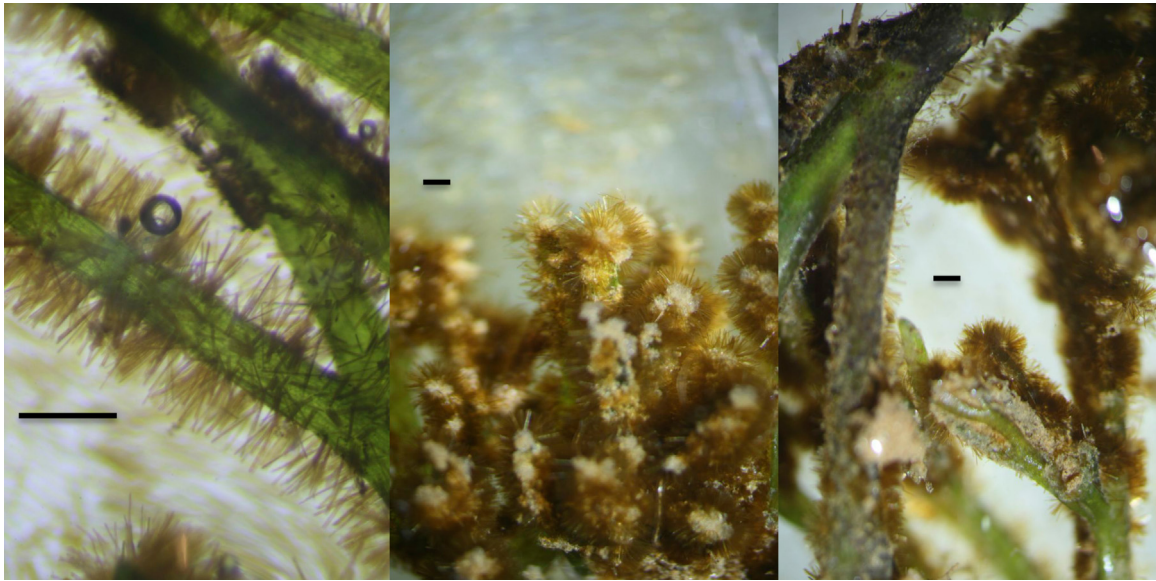


Fig. 4. Magnified images of *Podostemum ceratophyllum* stems with diatom (*Synedra ulna* c.f.) overgrowth. *Synedra ulna* cell length approximately 0.3 mm, scale bar approximately 5 mm in each picture. Fine sediments have accumulated between diatom cells and have encapsulated *Podostemum*'s stems and leaves in a nearly complete overcoating. Photos taken by J. Wood on November 11, 2013 from samples collected on a bedrock shoal on the Middle Oconee River, at Ben Burton Park, Athens, GA.

son but loses ground to other species in the fall and winter (Everitt and Burkholder, 1991).

3.3. Contributions to detrital and autotrophic foodwebs

Podostemum contributes to foodwebs directly and indirectly. *Podostemum* may indirectly enhance organic detritus retention by trapping particles entrained in the water column and accumulating fine sediments around the base of the plant. Stems and leaves directly contribute to detrital pathways (Nelson and Scott, 1962) and may senesce at biologically important times, i.e. late fall and early winter (Hill and Webster, 1982). Indeed, studies of seasonal changes in *Podostemum* biomass generally indicate that biomass is highest in early fall then declines as the plant senesces sensitive tissue (Rodgers et al., 1983; Grubaugh and Wallace, 1995) (but see Nelson and Scott, 1962). Seasonal changes in biomass may also be related to minimum water temperature, light availability, or other biotic and abiotic factors.

The leaves and stems of *Podostemum* decompose relatively quickly and contribute to the detrital pool. Rodgers et al. (1983) report a breakdown rate (K) between 0.05 and 0.08 $\text{g g}^{-1} \text{d}^{-1}$ (5–8% per day, depending on water temperate), and a 95% loss interval of 60 days in the New and Watauga rivers. Hill and Webster (1982) found a similar breakdown rate of 0.04 $\text{g g}^{-1} \text{d}^{-1}$, with a 95% loss interval of 81 days on the New River. These breakdown rates are an order of magnitude (or more) greater than the rate for allochthonous material, where $K < 0.02$ (Petersen and Cummins, 1974; Rodgers et al., 1983; Kominoski et al., 2007), indicating that carbon stored in *Podostemum* tissues is more rapidly recycled through the ecosystem compared to terrestrially-derived leaf litter.

The importance of *Podostemum*'s direct contribution to the food web is uncertain. Herbivory by Canada geese (*Branta canadensis* (Linnaeus)) and White Tubercled crayfish (*Procambarus spiculifer* (LeConte)) has been reported (Parker et al., 2007), and Weberg et al. (2015) raised the possibility of consumption by introduced triploid Grass Carp (*Ctenopharyngodon idella* (Valenciennes)) in the New River. We and others have observed aquatic turtles (e.g., *Pseudemys* spp; Fahey (1987) in Aresco and Dobie (2000)), White-tail deer (*Odocoileus virginianus* (Zimmermann)) and Beaver (*Castor canadensis* Kuhl) grazing on *Podostemum* (pers. obs. M.F.). However,

quantitative studies of herbivory rates or the relative contribution of *Podostemum* to aquatic primary consumers are lacking.

The nutritional value of *Podostemum* is not well known. At present, only two published studies are known to have reported the elemental composition of *Podostemum* tissue. A study conducted in Pennsylvania rivers by Adams and coauthors (1973) reported concentrations of P, K, Ca, Fe, Mg, B, Cu, Mn, Al, Zn, and Na, while Heisey and Damman (1982) investigated copper and lead accumulation in aquatic plants including *Podostemum* downstream of industrial outfall into the Shetucket and Natchaug Rivers, CT. Adams and coauthors (1973) report that *Podostemum* was 0.25% P by dry mass, while K, Ca, and Mg were 1.63, 1.38 and 0.24% respectively. Unpublished data (J.W.) indicate that on average *Podostemum* is 2.7% nitrogen and 36.4% carbon, with a molar carbon:nitrogen ratio of 16.2:1 (Unpublished J.W.), similar to other submerged freshwater plants (Bakker et al., 2016). While only limited inferences can be made from these studies, *Podostemum* may be a source of ecologically important elements for grazing organisms, especially nitrogen, phosphorus, calcium, and trace metals.

4. Environmental stressors

4.1. Sedimentation and flow alteration

Fast-flowing water, stable benthic substrate and sufficient light are the major factors consistently correlated with the occurrence of *Podostemum* (Everitt and Burkholder, 1991; Connelly et al., 1999; Argentina et al., 2010a; Duncan et al., 2011). *Podostemum* commonly occurs on coarse sediments of sandstone, shale, or granite (but rarely limestone (Meijer, 1976)), as well as other submerged substrates including wood, tires, plastics, aluminum, ceramics and other debris (per. obs. J.W.). Excessive sedimentation either through increased sediment load in the river or reduced sediment transport capacity, has been cited as a reason for *Podostemum* decline. For example, Connelly et al. (1999) cite sedimentation and streambed instability as possible reasons for declines in *Podostemum* abundance in the Roanoke River, Virginia. Similarly, Grubaugh and Wallace (1995) attribute an increase in *Podostemum* biomass on shoals in the Middle Oconee River to declining agriculture, and presumably sedimentation, in the watershed.

Hydrologic alteration can reduce *Podostemum* cover by decreasing wetted instream habitat and influencing flow velocity. Substantial dieback of *Podostemum* has been documented during a severe drought in the southeast U.S. that resulted in extended exposure of *Podostemum* above the waterline (Pahl, 2009), and flow manipulations downstream from a reservoir are reported to have resulted in the extirpation of a population of *Podostemum* in the West River at Jamaica, VT (Countryman, 1978). Although *Podostemum* has subsequently been found at other locations in the West River (Zika and Thompson, Zika and Thompson, 1986) (pers. obs. J.W.), flow regulation may influence population dynamics for many kilometers downstream of the source of regulation. Periodic exposure to drying and substantial reductions in water velocity may be mechanisms by which flow regulation reduces *Podostemum* cover and biomass. Supportive of this idea, Everitt and Burkholder (1991) report that *Podostemum* in their study could not tolerate even short periods of desiccation. Furthermore, slack water behind impoundments may permanently extirpate populations. For example, two populations of *Podostemum* in New Brunswick, Canada are reported to have been inundated to a depth that prevented persistence (Philbrick and Crow, 1983). Collectively, these studies support a conceptual model that includes flow as an important ecological variable, with diminution in water level and flow velocity potentially reducing *Podostemum* occurrence and biomass.

4.2. Influences of temperature and water chemistry

The influence of water temperature and dissolved gas concentration on *Podostemum* have not been evaluated but may be important given predictions of increasing water temperature with climate change (Ficke et al., 2007) and watershed urbanization (Wenger et al., 2009). Munch (1993) reports finding *Podostemum* in rivers in PA between 0 and 30 °C, but some southern populations likely experience water temperatures routinely exceeding 30 °C during summer months. Restricted CO₂ availability, such as in slow moving water or with dense epiphytic algal overgrowth (Fig. 4) may also reduce *Podostemum* growth rate and accrual of biomass. Furthermore, Hill and Webster (1984) hypothesize that differences in water hardness are responsible for a two-fold difference in biomass between study sites on the New River, NC (see Section 2.3. Physiology). Investigations of variation in stable carbon ratios could elucidate differences in CO₂ availability among habitats. Ziegler and Hertel (2007) argue that observed variation of $\delta^{13}\text{C}$ in *Podostemum* leaf tissue reflects variation in boundary layer “diffusional resistance” because the plant appears to preferentially utilize the ¹²C isotope of CO₂ compared to the heavier ¹³C isotope.

4.3. Tolerance to environmental pollutants

Meijer (1976) reports that *Podostemum* is generally found in clear streams with good aeration and sufficient light, and speculates that *Podostemum* might be useful as an indicator of clean water. However, Philbrick and Crow (1983) note that several populations have been found in polluted water, including in the Mousam River in Kennebunk Maine, where the river is polluted by domestic sewage. Similarly, a study of nutrient levels in Mexican rivers containing Podostemaceae documented occurrences of *Podostemum ricciiforme* (Liebm.) P. Royen at sites ranging from ultraoligotrophic to hypertrophic (Quiroz et al., 1997), showing that certain species of *Podostemum* can tolerate high nutrient levels or other forms of water pollution. Nonetheless, road salts (Jackson and Jobbagy, 2005; Kaushal et al., 2005), deicers (Fay and Shi, 2012) and other aspect of urbanization (Walsh et al., 2005; Chin, 2006) may constitute significant stressors to *Podostemum*.

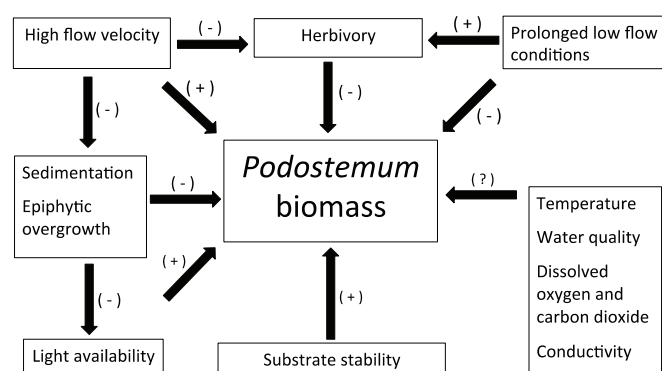


Fig. 5. Hypothesized relationships between *Podostemum ceratophyllum* and the dominant environmental variables of the habitat. Arrows indicate the directional nature of the relationship; positive associations are shown as (+) and negative associations are shown as (-).

4.4. Response to climate and land use change

A warming climate may facilitate the spread of *Podostemum* northward, continuing historical range expansion patterns (Philbrick and Crow, 1992; Fehrmann et al., 2012). Climate change may also exacerbate stresses already experienced by the plant, such as increased flow alteration, increased water temperature and increased sedimentation resulting from intense precipitation events. Accurately predicting the future distribution of *Podostemum* is complicated by the complexity of interacting stressors and the differing scales of controls on species migration (Pearson and Dawson, 2003).

Investigations into how *Podostemum* responds to changes in land use are needed in light of the rapid landscape changes occurring in many parts of this species' range. Isotopic nitrogen signature ($\delta^{15}\text{N}$) has been used to investigate the impacts of urbanization and land use on microbial biofilms (Kaushal et al., 2006), fish (Northington and Hershey, 2006) and riparian plants (Kohzu et al., 2008), and could be useful in assessing land use impacts on *Podostemum*, as well as measuring *Podostemum*'s role in food chains (Cabana and Rasmussen, 1996). Urban runoff can also contain high concentrations of metals (Davis et al., 2001; Sörme and Lagerkvist, 2002; Rule et al., 2006) available for uptake by primary producers. If *Podostemum* bioaccumulates metals then herbivory would facilitate the transfer of water column pollutants into higher trophic levels, with possible ecological and human health concerns.

5. Synthesis: causes and consequences of changes in *Podostemum* abundance

Known and hypothesized influences on *Podostemum* biomass include several interacting factors: severity and duration of low-flow periods, water velocity, herbivory, sedimentation, light and nutrient availability, and substrate stability (Fig. 5). Previous studies have shown that prolonged reductions in discharge reduce plant biomass (Nelson and Scott, 1962; Pahl, 2009), thus we hypothesize that high-velocity habitats support higher *Podostemum* biomass by limiting herbivory by consumers unable to hold position in swift currents, and by reducing sedimentation and algal build-up that, in turn, reduce light availability. Discharge and water velocity may also influence water temperature, conductivity and dissolved gases (CO₂ and O₂) but the direct effects of these variables on *Podostemum* are not well known (Fig. 5).

Understanding effects of more frequent and prolonged periods of low-flow may be essential to predicting persistence of *Podostemum* in areas experiencing declining rainfall or increased water diversions for human uses. We expect that *Podostemum* responds

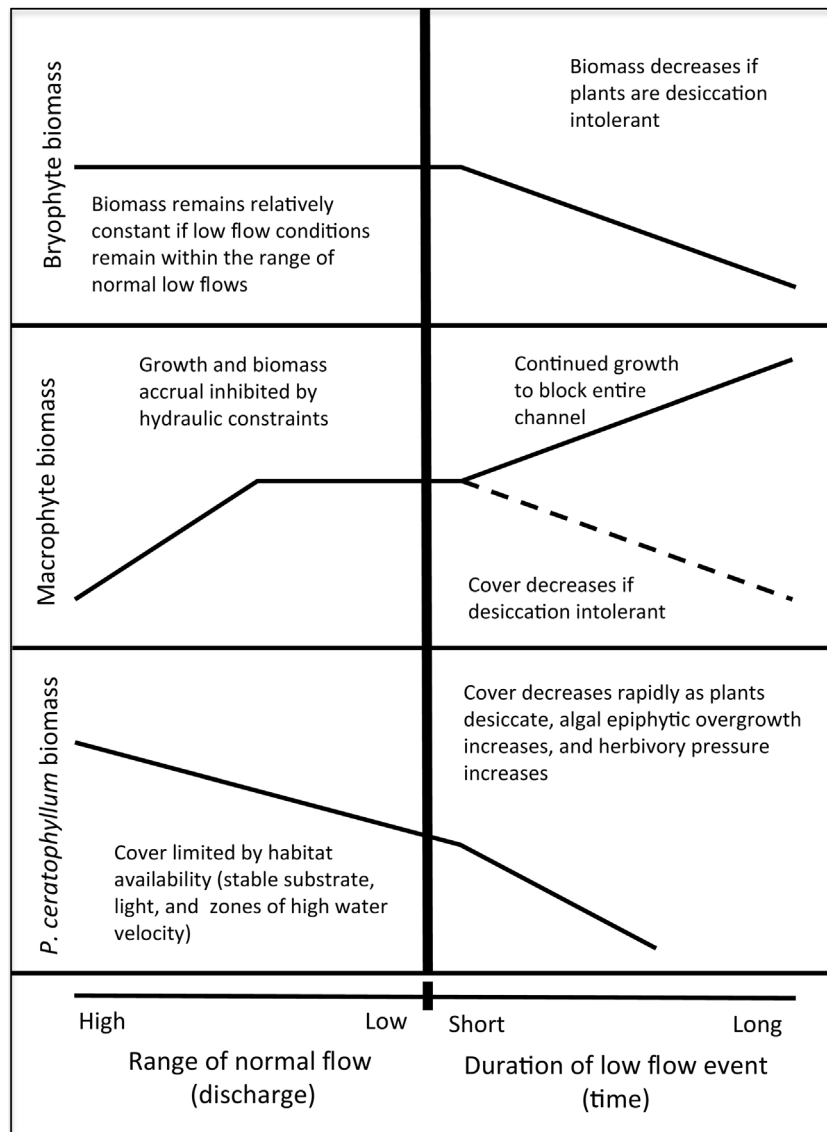


Fig. 6. Hypothesized relationships and comparisons between flow (discharge) and the duration of low flow events (time) for bryophyte, macrophyte, and *Podostemum ceratophyllum* Michx. biomass (modified from Suren and Riis, 2010).

differently to low-flow periods than other aquatic plants, and uniquely different from the macrophyte model proposed by Suren and Riis (2010). Specifically, we hypothesize that *Podostemum* biomass declines as rivers move into seasonal low flow periods, whereas rooted macrophytes exhibit a general increase in biomass with low flow conditions, and bryophytes maintain relatively stable biomass through the river's normal range of flow (Fig. 6). We also hypothesize that *Podostemum* biomass rapidly declines as the duration of low-flow conditions increases in response to increased herbivory, epiphytic overgrowth, and risk of drying, with the effect exacerbated by other water quality stressors.

One challenge for understanding *Podostemum* response to stressors is that field measurements may differ among local habitat types. Rivers in the eastern montane and piedmont regions are frequently characterized by alternating shoal (cascade, riffle, rapid) and pool habitats, and we hypothesize that these two habitats expose *Podostemum* to differing stressors as a result of differences in flow velocity and water depth. We speculate that biomass in pool habitats is strongly controlled by herbivory pressure, light availability and sedimentation rate, whereas shoal habitats provide

increased protection from herbivory and sedimentation but expose the plant to increased risk of drying during periods of low flow.

We conclude that evidence supports the notion that *Podostemum* acts as a foundation species in many eastern rivers, removing nutrients from the water column, accumulating substantial benthic biomass, and shuttling resources into the food chain, in addition to providing habitat for a diverse flora and fauna. Loss of the plant from rivers where it presently occurs could thus reduce: 1) invertebrate biomass and resources for aquatic and terrestrial insectivores; 2) retention of nutrients in the benthos, influencing carbon balance and nutrient spiraling length; 3) retention of organic matter and resources for aquatic detritivores; 4) stream bed stability and complexity, increasing the severity of flood scour on the benthos; and, 5) export of autochthonous organic matter and thus resources available downstream. However, much of what we know about the ecology of *Podostemum* derives from studies in the southern portion of the species range (Table 1) and regional differences in genetics may influence responses to stressors. Information on responses of the plant to environmental changes throughout its range is essential to understanding how to conserve or restore populations. Conservation efforts would also benefit from better documenta-

tion of *Podostemum* populations, a long recognized deficiency in our understanding of the plant (Muenscher and Maguire, 1931). As pressures on freshwater resources increase, conserving *Podostemum* appears crucial for preserving and improving the health and vitality of many eastern North American Rivers.

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