

Herbivore damage and riparian shade constrain biomass distribution in American water willow (*Justicia americana*)

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ABSTRACT

Emergent macrophytes can create important linkages between aquatic and terrestrial ecosystems. American water willow (*Justicia americana*) is an ecological engineer that provides structure and takes up nutrients in aquatic habitats but is subject to herbivory by terrestrial animals. Here, potential constraints that terrestrial herbivory, riparian shading, porewater nutrient stoichiometry, and co-occurrence with freshwater mussels may have on standing crops of aboveground and belowground water willow biomass were investigated across nine study sites in the Kiamichi River catchment, Oklahoma, USA. Stem damage – used to indirectly assess herbivore effects – and riparian shading were both associated with significant reductions in aboveground biomass. However, these variables were also somewhat correlated with each other, suggesting a possible interaction between shade and herbivory. Belowground biomass was more variable between sites than aboveground biomass, but the environmental variables that were sampled failed to explain this variation consistently. Because shadier water willow patches tend to have nutrient-richer tissues, we suggest that the correlation between riparian shade and herbivore damage may result from selective feeding by terrestrial herbivores at shadier sites. However, further experimental work (e.g., using grazing exclosures) is needed to assess this possibility due to the limitations of using stem damage counts as an indirect representation of herbivory. Despite these limitations, the present study complements a growing body of evidence that shows emergent macrophytes are seemingly more important as a resource for herbivores than historically recognized. Emergent macrophytes may be especially important when consumed by terrestrial herbivores that then transfer aquatic-derived resources into the terrestrial habitat.

Data availability: The data used to generate this manuscript are available from the corresponding author upon reasonable request.

1. Introduction

The importance of aquatic macrophytes to food webs and ecosystem function, while largely neglected historically, has now become more broadly recognized (Bakker et al., 2016b; Lodge, 1991; Newman, 1991). The habitat preference that macrophytes exhibit for shallow waters near the aquatic-terrestrial interface makes them uniquely suited to facilitate linkages between aquatic and terrestrial ecosystems. Because they experience varying levels of submergence as water levels rise and fall, emergent macrophytes can interact strongly with terrestrial ecosystems, while submersed and floating macrophytes are more restricted to the aquatic habitat. Many emergent macrophytes are vulnerable to

herbivory by terrestrial animals ranging in size from insects to large mammals (Bakker et al., 2016a; Newman, 1991). Yet the nutrients that emergent species use to grow and function are almost exclusively acquired in the aquatic ecosystem. Because of this linkage across the aquatic-terrestrial interface, it is important to understand the factors that govern their growth and propagation under natural conditions.

When terrestrial herbivores consume aquatic primary production, they transfer nutrients from aquatic ecosystems—where dissolved nutrients tend to concentrate due to the downhill flow of water – to nearby terrestrial systems that are often comparatively poorer in nutrients (Schindler and Smits, 2017; Shurin et al., 2006). Although emergent macrophytes experience slightly lower herbivory rates (36–48 %) than

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submersed macrophytes (48–60 %; Bakker et al., 2016b), their shoots may still be consumed by a wide range of animal species including waterfowl (van den Wyngaert et al., 2003), insects (Medeiros dos Santos and de Assis Esteves, 2002), and mammals (Ceacero et al., 2014). Intense feeding on macrophytes by terrestrial herbivores may be critical in dictating ecosystem function across the aquatic-terrestrial transition. Furthermore, the aquatic-derived carbon (C) and nutrients, such as nitrogen (N) and phosphorus (P), that terrestrial animals consume are transported into and beyond the riparian zone via assimilation, mortality, and waste excretion or egestion (Bastow et al., 2002; Bump et al., 2009). The deposition of aquatic nutrients can then form an ecological subsidy (*sensu* Polis et al., 1997) that is assimilated into terrestrial ecosystems, consequently increasing primary productivity and altering consumer communities (Ben-David et al., 1998; Polis and Hurd, 1996). Emergent macrophytes are distributed across aquatic-terrestrial interfaces on every continent except Antarctica (Chambers et al., 2008), indicating that they may play a widespread role – in conjunction with herbivores – in subsidizing surrounding terrestrial habitats with aquatic nutrients.

Understanding the potential of emergent macrophytes and associated herbivores to generate an ecological subsidy starts with an understanding of the four major qualities that define animal-mediated resource subsidies: quantity, quality, timing, and duration (Subalusky and Post, 2019). The most direct way to determine the quantity of emergent macrophyte resources that are available to terrestrial herbivores at a given point of time is to quantify standing biomass. In reality, primary productivity is a more accurate representation of resource quantity, as it provides a time-integrated metric of a plant's growth that accounts for the removal of plant biomass via senescence and herbivory—yet, primary productivity is notoriously difficult to measure in aquatic ecosystems (Lieth and Whittaker, 1975). Fortunately, primary productivity and biomass tend to be positively correlated, even in highly-grazed ecosystems (McNaughton et al., 1989). Resource quality is often quantified using nutrient ratios (e.g., C:N:P stoichiometry) or concentrations (e.g., % N or % P) (Sterner and Elser, 2002). Aquatic vegetation tends to be more nutrient-rich, and thus higher quality, than terrestrial vegetation due to the reduced need for C-rich structural compounds (Elser et al., 2000). The timing and duration of resource availability are critical because temperate macrophytes exhibit strong seasonality by growing out in the spring, peaking in the mid to late summer, and then senescing in the fall and winter (Villa et al., 2018).

There are many environmental factors that constrain macrophyte biomass, including herbivory itself. In some cases, herbivory is strong enough to limit standing crops of macrophyte biomass (Wood et al., 2017, 2012). Conversely, damage to aboveground shoots by herbivores may stimulate compensatory growth, or interact with nutrient availability to increase plant standing crops (Gruner et al., 2008; McNaughton, 1983). Riparian vegetation can also reduce emergent macrophyte biomass in forested systems by reducing light penetration and thus photosynthesis (Sender, 2016; Wilcock et al., 2002). In nutrient-limited ecosystems, natural variation in the stoichiometry and availability of N and P may drive patterns in biomass allocation. Experimental additions of N and P have been shown to impact biomass allocation in clonally reproducing plants, and may cause biomass allocation to shift towards belowground structures or to aboveground structures depending on the species and environmental conditions (Dong and de Kroon, 1994; Nicholls, 2011; Xie et al., 2004). Furthermore, some submersed macrophytes and marine seagrasses are thought to benefit from mutualistic relationships with burrowing invertebrates dwelling in nearby sediments, especially bivalves (Aquilino et al., 2009; Crane et al., 2020; Peterson and Heck, 2001). In these cases, invertebrates are thought to promote macrophyte productivity via nutrient recycling (Aquilino et al., 2009; Peterson and Heck, 2001), but there is not always a clear link between invertebrate density and ambient nutrient concentrations (Crane et al., 2020). The connection between burrowing invertebrates and macrophyte growth thus deserves

further exploration.

American water willow (*Justicia americana*; hereafter water willow) is a broadly distributed emergent macrophyte found across eastern North American streams (Penfound, 1940). Water willow biomass is consumed regularly in the late summer by feral hogs, cattle, and white-tailed deer, which are thought to transfer nutrients they obtain from water willow into the terrestrial environment through their feces (Lopez et al., 2020, 2022a). Water willow is also an ecological engineer – it forms thick networks of roots, rhizomes, and stolons that trap sediment, creating elevated gravel bars at the margins of aquatic ecosystems (Fritz et al., 2004b; Fritz and Feminella, 2003). These belowground biomass networks facilitate vegetative clonal reproduction and nutrient uptake from subsurface porewater. The networks provide habitat and sediment stability for North American freshwater mussels (Bivalvia: Unionoida); the mussels, in turn, provide bioavailable nutrients to the macrophytes via excretion (Atkinson et al., 2014; Fritz et al., 2004b; Lopez et al., 2020). Mussel presence is also associated with elevated levels of essential mineral nutrients such as calcium and their burrowing behavior alters ion fluxes across the sediment-water interface (Lopez, 2022; Matisoff et al., 1985). Water willow produces vertical stems and aboveground leaves and flowers, the biomass and density of which are thought to be limited by riparian shading (Fritz et al., 2004a; Lopez et al., 2022a). The aboveground structures account for ~92 % of the plant's net primary productivity, but only 33% of the standing biomass at a given time (Fritz et al., 2004a; Twilley et al., 1985). This imbalance is caused by herbivory and turnover of the aboveground structures that occurs throughout growing season in April–September, and in the fall when all of the aboveground structures senesce (Lopez et al., 2020; Twilley et al., 1985). In late summer, nutrient-rich macrophytes may help meet elevated nutrient demand for terrestrial herbivores (Ceacero et al., 2014; Fraser et al., 1984; Jones and Hanson, 1985). Water willow's widespread distribution, importance as an ecological engineer, and its inputs to the green and brown food webs justify further investigation of the factors regulating biomass distributions and standing crops in the species. The present investigation is focused on sampling the factors that constrain the quantity of emergent macrophyte biomass available in the late summer because this is a period of overlap between high macrophyte availability and high nutritional demand for terrestrial herbivores.

In the present study, relationships were tested between the environmental variables in extenso and the above- and belowground standing crops of water willow biomass. A comparative field study was conducted to test the following predictions: (P1) Stem damage, a proxy for herbivory, is associated with decreased aboveground standing stocks. (P2) Riparian shading limits both above- and belowground water willow biomass by limiting photosynthesis. (P3) In an N-limited ecosystem, increases in the N:P ratio of gravel bar porewater may increase standing crops of belowground biomass for propagation, or aboveground structures as the need for biomass allocation to nutrient acquisition structures is alleviated. (P4) Freshwater mussel presence is associated with increased standing stocks in aboveground and belowground biomass, in response to biogeochemical effects that burrowing invertebrates create via excretion, mortality, and burrowing behavior.

2. Materials and methods

2.1. Study system

The Kiamichi River in southeast Oklahoma is a ~4700 km² tributary of the Red River that flows from the Ouachita Highlands to the Gulf Coastal Plain geographic regions of the south-central USA. This mid-sized river is relatively undisturbed by anthropogenic impacts other than cow pasture (USDA National Agricultural Statistics Service, 2017). Recent studies in the Kiamichi catchment have documented ecological relationships between water willow density, nutrient content, and the surrounding biotic and abiotic conditions (Atkinson et al., 2014; Lopez

et al., 2020, 2022a; Lopez, 2022). Here, water willow standing crops and biomass distributions are compared at nine sites, eight of which were on an ~118 km long segment of the mainstem Kiamichi River and one on a major tributary, North Jackfork Creek (Fig. A.1). Jackfork Creek is impounded by Lake Sardis, a ~58 km² reservoir. Five sites were above the impoundment (including the North Jackfork Creek site), and four sites were below the impoundment (Fig. A.1).

2.2. Environmental variable sampling

2.2.1. Gravel bar sampling

Environmental data for each study site were collected as part of a related study outlined in Lopez et al. (2022a). Each site consisted of a single gravel bar covered by a water willow bed. Water willow beds were nearly monocultural, with few other plant species growing within them. The proportion of clipped (damaged) stems was quantified during a survey of water willow stem density using 0.25 m² quadrats and averaged at the site level (see Section 2.3). At each site, light availability was quantified as percent shade at the center of the water willow bed by the same individual using a spherical densiometer (Spherical Crown Densiometer Convex Model A, Forestry Suppliers, Jackson, MS, USA). Porewater was sampled using a metal porewater sampler, which was driven into the gravel bar subsurface at both the upstream and downstream ends of each water willow bed. The upstream and downstream porewater samples were stored frozen until analysis due to the remote nature of the field sites, and then the average nutrient concentration between the two samples was used as a site-level composite nutrient composition value. Porewater nutrient composition was assessed using colorimetric methods by quantifying NH₄-N via the phenol hypochlorite method and soluble reactive phosphorus (SRP) concentrations via the molybdate blue method (United States Environmental Protection Agency, 1993, 1978), and converting these to molar N:P ratios.

2.2.2. Mussel bed sampling

Semi-quantitative freshwater mussel surveys were conducted over a five-year period preceding the water willow sampling that was the focus of the present investigation. Five years is thought to be within the acceptable sampling interval for mussels because they are long-lived (4 to >200 years) and sampling of their habitat can be destructive (Haag and Rypel, 2011; Lopez et al., 2022b). Surveys on the mainstem Kiamichi were conducted in August 2015, 2016, and 2018 following methods described in Hopper et al. (2018). Depending on the size of a given mussel bed, 15–20 haphazardly placed 0.25 m² quadrats were sampled across a representative spatial distribution of the mussel bed at the site (Vaughn et al., 1997). The survey at the Jackfork Creek site was conducted in July of 2020 following the same procedure, but with five quadrats due to the small size of this tributary and its associated mussel assemblage. Mussels were counted and identified to species level prior to being placed back in the stream. Mussel densities were then averaged at the site level.

2.3. Water willow biomass sampling

Water willow biomass was sampled by harvesting all the above- and belowground biomass from the quadrats placed during a water willow stem density survey (Lopez et al., 2022a). Sampling took place once at each site from 10 July to 14 August 2019 because during this late summer period the Kiamichi River undergoes low flows where water willow beds can be sampled safely and are accessible to terrestrial herbivores (Atkinson and Vaughn, 2015). Water willow biomass varies on a monthly time scale (Twilley et al., 1985). Thus, the intent of this approximately one-month sampling duration was to capture a snapshot of spatial variation in nutrient availability at the time when macrophytes are most likely to form an aquatic-terrestrial linkage, while minimizing temporal variation.

Sampling design was similar to the design of the mussel surveys

where 0.25 m² plots were established across a representative spatial distribution of the water willow bed under study (Atkinson et al., 2014). A minimum of one plot was sampled per ~15 m in a zig-zagging fashion along the length of the water willow bed, parallel to stream flow. Sites ranged from 13.3 to 113.4 m in length, resulting in a total of 2–10 plots at each site (Table 1). Aboveground biomass was harvested by cutting the stems of all water willow within each quadrat at their bases. Leaves and stems were harvested together. Then, belowground biomass was harvested by excavating the plot to a depth of 10–15 cm and removing all roots, rhizomes, and stolons present. Stolons on the sediment surface were classified as belowground biomass, as they are used for vegetative propagation and typically have adventitious roots (Penfound, 1940). All tissues were then dried at 70 °C for 72 h (Thelco 130D Laboratory Oven, Precision Scientific, Winchester, VA, USA) and weighed to a precision of ± 0.1 g (Scout Pro SP401 Portable Balance, Ohaus Corporation, Parsippany, NJ, USA).

2.4. Data analysis

All analyses were conducted in R v4.1.2 (R Core Team, 2021). We compared the magnitude of aboveground and belowground biomass allocation at the riverscape level (all plots at all sites) using a Wilcoxon signed rank exact test. We compared the absolute variability between aboveground and belowground allocation at the riverscape level using a Levene test. We also compared variability relative to the mean for riverscape-level aboveground and belowground biomass using coefficients of variation (CV) for the two biomass pools. Ordinary least squares (OLS) linear regressions were performed to test whether each of the site-level means of the environmental variables (percent clipped stems, percent shade, porewater N:P ratio, and mussel density) explained significant variation in the standing crops of both aboveground and belowground biomass. Prior to the regression analyses, a pairwise Pearson correlation matrix was used to test for collinearity between environmental predictor variables. We tested for normality and equal variance of residuals using Shapiro-Wilk and studentized Breusch-Pagan tests respectively. All residuals were normally distributed, but not all models had equal variance in the residuals, so we replaced this OLS regression with weighted least squares regressions when this was the case. Only the relationship between herbivore damage and aboveground biomass required the use of weighted regression. Regression weights were assigned by regressing the absolute residuals versus the OLS fitted values, then taking the inverse of the resultant squared fitted values, thus down weighting the high-variance observations. Percent shade was natural log + 1 transformed because there was a large gap in the distribution of the dataset between low-shade and high-shade sites.

3. Results

Mean (± SD) values for areal biomass allocation to aboveground and belowground tissues by water willow across all plots at all sites are presented in Fig. 1. On average, water willow allocated 56 % more biomass to belowground tissues than aboveground tissues ($V = 56$, $P < 0.001$). Absolute variation in areal biomass was also significantly greater in belowground than in aboveground tissues ($W_{1,94} = 26.6$, $P < 0.001$), as was relative variation (belowground CV = 74 %, aboveground CV 57 %). No predictor variables were correlated at $r > 0.70$ ($P > 0.05$ for all pairwise Pearson correlations), so all variables were modeled using independent univariate regressions. However, stem damage and riparian shading were somewhat correlated at $r = 0.61$ ($P = 0.078$).

Both stem damage and riparian shading were significantly and individually related to site-level variation in aboveground biomass (Table 2), which varied by 77 % across sites (range = 42.4–186.16 g m⁻²). The proportion of stems showing herbivore damage ranged from 0.15 % to 57 % across sites. Univariate regression models showed that stem damage was associated with a linear decrease in aboveground biomass

Table 1

Sampling dates and number of plots sampled for water willow biomass across nine sites in the Kiamichi River catchment. Dates sampled are for all abiotic variables, and water willow biomass. *Mussel surveys were conducted as part of previous publications and do not correspond directly to dates of water willow sampling.

Site	Date (2019)*	Bed length (m)	No. of plots	Clipped stems (% [± SD])	Shade (%)	Porewater N:P	Mussel density (ind. m ⁻²)
K1	23 Jul.	65	6	44 [12]	37	12	0
K2	25 Jul.	113.4	10	0.2 [0.3]	1.3	103	11
K3	26 Jul.	21.7	5	3.5 [2.3]	1.8	30	0
K4	26 Jul.	30.7	5	46 [11]	9.1	172	10
K5	14 Aug.	69.1	5	22 [21]	4.9	11	38
K6	14 Aug.	42.2	5	57 [20]	8.3	26	0
K7	2 Aug.	48.8	6	25 [14]	0.0	13	24
K8	5 Aug.	29	4	11 [10]	6.0	103	0
JF	10 Jul.	13.3	2	50 [4.4]	42	18	3

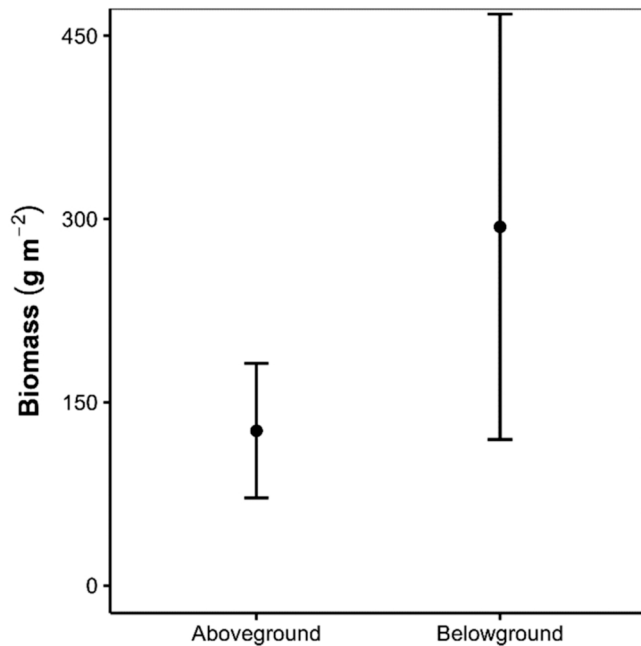


Fig. 1. Plot-level mean (± SE) biomass (expressed as dry weight) in aboveground and belowground tissues in American water willow (*Justicia americana*) across all nine study sites.

Table 2

Regression models explaining variation in standing crop of aboveground and belowground water willow standing biomass. Models correspond to those presented in Fig. 1.

Response	Terms	Estimate	SE	F _{1,7}	P	R ²
AG biomass	(Intercept)	180.92	12.07	9.44	0.018	0.57
	% Clipped	-1.93	0.63			
	(Intercept)	188.67	26.71	7.31	0.030	0.51
	log(% Shade + 1)	-31.79	11.76			
	(Intercept)	120.94	27.52	0.09	0.775	0.01
BG biomass	Porewater N:P	0.11	0.36			
	(Intercept)	112.95	23.07	0.97	0.356	0.12
	Mussel density	1.44	1.46			
	(Intercept)	402.79	96.07	1.92	0.209	0.22
	% Clipped	-3.79	2.74			
	(Intercept)	403.89	110.52	1.35	0.283	0.16
	log(% Shade + 1)	-56.58	48.66			
	(Intercept)	211.44	75.65	2.37	0.168	0.25
	Porewater N:P	1.52	0.98			
	(Intercept)	265.76	75.87	0.37	0.562	0.05
Mussel density	2.92	4.80				

(Fig. 2a). Percent shade ranged from 0 % to 42 % across sites, and riparian shading was logarithmically associated with a decrease in aboveground biomass (Fig. 2b). Porewater N:P ratio and mussel density did not show significant univariate relationships to aboveground biomass (Fig. 2c–d).

Belowground biomass varied widely, by 91 % across sites (range = 47.9–565.3 g m⁻²). Stem damage, riparian shading, and porewater N:P ratio all explained small amounts of variation in site-level belowground biomass in independent univariate regression models (Table 2); however, none of these variables were significantly related to belowground biomass (Fig. 2e–g). Mussel density was not related to belowground biomass (Fig. 2 h).

4. Discussion

Belowground biomass in American water willow varied significantly more than aboveground biomass did across the nine study sites. Variation in aboveground standing crops was constrained by herbivore-induced stem damage and riparian shading; however, variation in belowground crops was not constrained well by the environmental parameters that were sampled. As predicted, stem damage was associated with a decline in water willow biomass in aboveground tissues and did not affect belowground biomass (P1). Riparian shading was also associated with a decline in aboveground biomass that was consistent with our predictions but did not impact belowground biomass as we expected (P2). Counter to our initial predictions, porewater N:P ratio did not explain significant variation in aboveground or belowground biomass (P3), nor did mussel density (P4).

4.1. Herbivory and light as limiting factors of aboveground biomass

The univariate regression model that best explained variation in aboveground biomass was the percentage of stems that were clipped, consistent with damage caused by ungulate herbivores. In a 2019 camera trap survey of terrestrial vertebrate herbivory on water willow, white-tailed deer (*Odocoileus virginianus*) and feral hogs (*Sus scrofa*) were found to be the most frequent consumers of emergent macrophyte biomass in the Kiamichi River (Lopez et al., 2020). Other mammalian herbivores, such as beavers, muskrats, and moose are known to selectively consume certain emergent and submersed macrophyte species, thus reducing macrophyte biomass and altering plant community structure (Bergman and Bump, 2015; Bhattacharjee et al., 2007; Danell, 1977; Law et al., 2014; Parker et al., 2007; Smirnov and Tretyakov, 1998). While the aforementioned species are semi-aquatic, as opposed to fully terrestrial like white-tailed deer and hogs, it is not unreasonable to surmise that mammalian herbivores play a role in limiting water willow biomass in the late summer when the Kiamichi River has low water levels that leave its emergent macrophyte assemblages exposed to the terrestrial environment. The present study employed an indirect estimate of herbivory by quantifying stem damage – a method used in prior investigations of emergent macrophyte herbivory (Medeiros dos Santos and de Assis Esteves, 2002; Petruzzella et al., 2015). However,

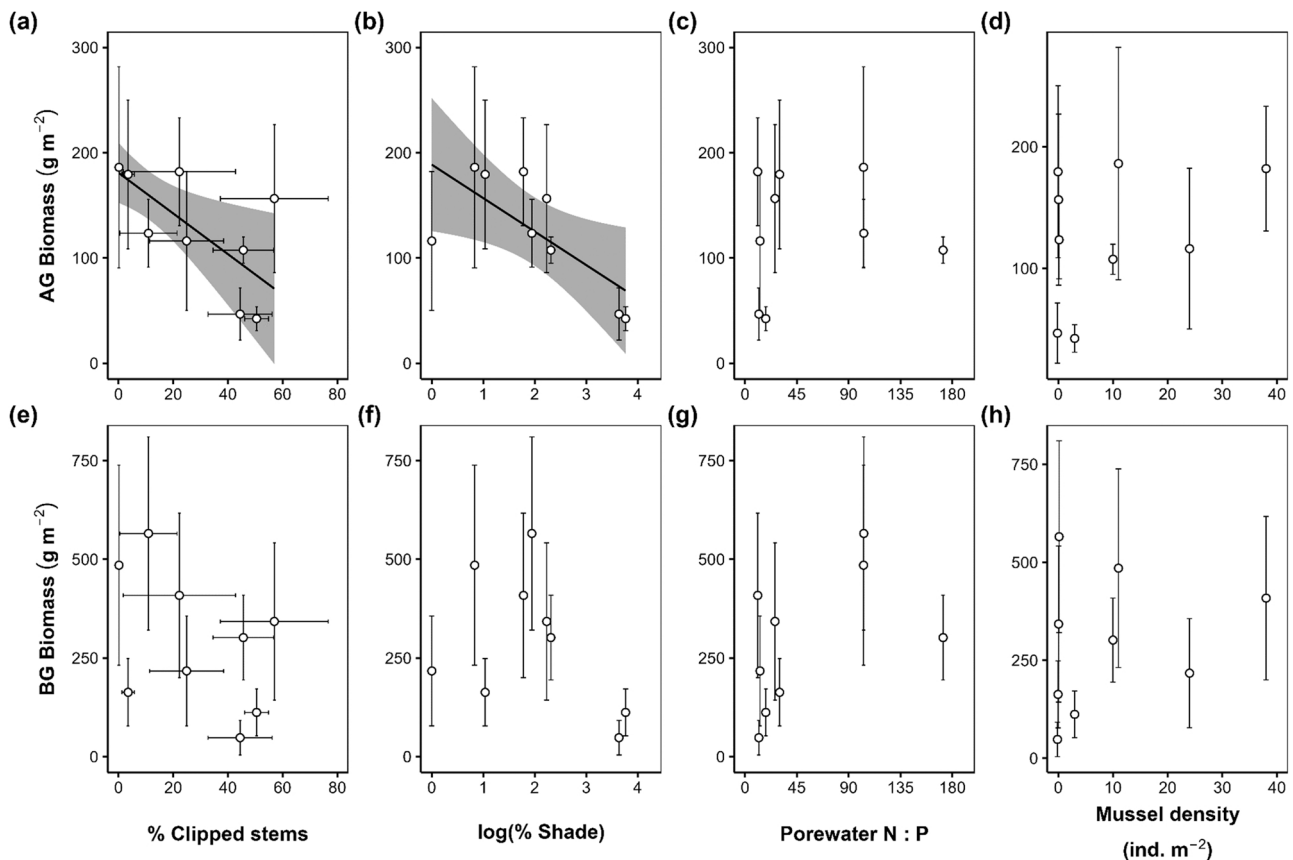


Fig. 2. Constraints of stem damage (% clipped), riparian shading (% shade), porewater N:P ratio ($\text{NH}_4^+ \text{-N:SRP}$), and freshwater mussel density (ind m^{-2}) on aboveground (AG) and belowground (BG) areal biomass (expressed as dry weight) in American water willow (*Justicia americana*). (a) Stem damage, a proxy for herbivory, and (b) riparian shading (natural log + 1 transformed) were related to significant decreases in aboveground biomass. (c) Porewater N:P and (d) mussel density were unrelated to aboveground biomass. Areal belowground biomass was not significantly related to (e) stem damage, (f) riparian shading, (g) porewater N:P, or (h) mussel density. Solid lines with dark gray ribbons (95% CI) represent statistically significant regression slopes at $P < 0.05$.

this observational method is limited; while stem clipping is consistent with herbivory, we cannot rule out other causes of stem breakage, such as trampling or other non-consumptive losses (Law et al., 2014). Beyond the question of how tightly linked stem damage is to true herbivory, proportional estimates do not allow estimation of the quantity of biomass that has been removed. Other studies have employed grazing exclosures to quantify the effects of herbivores on macrophyte assemblage structure and function (Bergman and Bump, 2015; Parker et al., 2007). A quantitative grazing exclosure experiment is the logical next step in disentangling the role of herbivores from other environmental factors in constraining water willow biomass.

Riparian shading also explained significant variation in water willow aboveground biomass. This is consistent with prior evidence that water willow stem density in the Kiamichi is negatively related to shade (Lopez et al., 2022a), and with evidence from other stream ecosystems showing emergent macrophyte biomass is limited by light availability (Wilcock et al., 2002). This pattern is intuitive and simple to explain, as light places an upper limit on a plant's potential to produce biomass (Beadle and Long, 1985). However, light and other environmental factors (e.g., nutrients, disturbance) interact strongly with herbivore activity to determine distributions of plant biomass and primary productivity—especially in aquatic ecosystems (Polis, 1999). Such an interaction may be present in the current study, where herbivore-induced stem damage was positively correlated, albeit nonsignificantly, with riparian shading. Relative C content of water willow leaves in the Kiamichi is negatively associated with riparian shading (Lopez et al., 2022a). Thus, as shade increases, the nutrient content of water willow increases. This may drive a correlation between herbivore damage and shade if

terrestrial herbivores are selectively feeding at nutrient-richer patches of water willow. Terrestrial ungulates are known for their capacity to distinguish between resource patches of variable nutrient content (Jones and Hanson, 1985). This is another open line of investigation that could be addressed through a field experiment. An exclosure experiment similar to that referenced above could be designed factorially so that grazing effects in shaded and unshaded macrophyte beds could be compared, thus determining the interactive relationships between herbivory, riparian shading, and water willow biomass.

Although porewater N:P and freshwater mussel density did not explain variation in aboveground biomass, that does not necessarily indicate they are unrelated to water willow productivity. Positive plant growth effects can often be nullified by negative herbivory effects of similar magnitude (Gruner et al., 2008). This could explain the lack of a positive nutrient effect in water willow aboveground biomass. It is possible that changes in porewater stoichiometry or bivalve-generated ecosystem effects altered primary productivity in water willow, but that this productivity effect could not be observed in standing biomass due to high turnover rates (Twilley et al., 1985). Sites with high N:P ratios are less likely to be nutrient-limited, as the Kiamichi River is known to be N-limited for algal production, and mussel-derived nutrients can alleviate this nutrient limitation (Atkinson et al., 2013). One major limitation to the interpretation of porewater stoichiometry in the present study is the fact that only $\text{NH}_4^+ \text{-N}$ was quantified. While $\text{NH}_4^+ \text{-N}$ is the form of inorganic N that is excreted by mussels, mesocosm experiments have also shown increases in nitrate ($\text{NO}_3^- \text{-N}$) associated with increasing mussel biomass (Vaughn et al., 2004), possibly as a result of burrowing activity by mussels, which oxygenates sediments. Coarse,

oxic sediments are more likely to contain both nitrate and nitrite ($\text{NO}_2\text{-N}$), as well as $\text{NH}_4^+\text{-N}$ (Krause et al., 2009). The Kiamichi River has coarse substrates (Oklahoma Department of Wildlife Conservation, 2016), thus an important pool of bioavailable N may have been missed by sampling only for $\text{NH}_4^+\text{-N}$ in gravel bar porewater.

4.2. Variability in belowground biomass remains unexplained

None of the environmental variables we tested successfully explained the observed variability in water willow belowground biomass standing crops. While stem damage was not expected to be related to belowground biomass, it is somewhat surprising that riparian shade was not significantly related to belowground biomass. If light is truly limiting to water willow aboveground biomass production, we would also expect belowground biomass formation to be limited by light, as photosynthesis is the ultimate source of C for plants, regardless of the tissue type (Beadle and Long, 1985). This suggests that perhaps the apparent light limitation of aboveground biomass is an artifact of the observed correlation between herbivore damage and shade.

The lack of a response in belowground biomass to porewater nutrient composition and mussel density was similarly surprising. Positive responses of belowground biomass to nutrient additions have been shown in other wetland plants, and promote vegetative reproduction (Nicholls, 2011). A natural question is why no increase in belowground biomass allocation occurred in response to increasing N:P. Prior experimental work shows that mussels and associated changes in the nutrient environment can impact water willow growth (Lopez et al., 2020). Yet here no such relationships were detected. There was no correlation between mussel density and porewater stoichiometry, and $\text{NH}_4^+\text{-N}$ concentrations in Kiamichi gravel bar porewater vary far more than could be reasonably expected if this variation were a function of mussel excretion (Lopez et al., 2022a; Trentman et al., 2018). Further, the absence of nitrate/nitrite concentration data confounds our ability to assess potential nutrient effects on belowground biomass, just as with the assessment of aboveground biomass. Water willow density has previously been shown to depend on void surface area in bedrock shoals of the Cahaba River, AL, USA (Vaughn and Davis, 2015). While the Kiamichi River is predominantly a cobble-gravel system, it is possible that geomorphic processes control variability in water willow biomass production here as well. Wide variability in substrate geomorphology could explain much of the variation in belowground biomass stocks, as well as some of the unexplained variation in aboveground biomass.

4.3. Conclusions

The present study has characterized associations of herbivore damage, light, nutrients, and burrowing bivalves with biomass standing crops and allocation in American water willow (*J. americana*). The findings herein highlight important caveats that must be considered when interpreting standing stock biomass data, and contrast directly with a survey of water willow stem density conducted across the same sites and a related mesocosm experiment testing factors promoting water willow growth (Lopez et al., 2022a, 2020). We hypothesize that removal of aboveground water willow tissue by herbivores such as white-tailed deer, feral hogs, and livestock was the primary limitation on aboveground biomass standing crops. While riparian shading was also negatively related to aboveground biomass, this may be a byproduct of increased tissue nutrient concentrations that make shaded patches of water willow more palatable to herbivores. Field experiments using

grazing enclosures like those employed in terrestrial grassland or lake ecology would help quantify primary productivity and clarify the role that herbivores may play in limiting emergent macrophyte biomass. Unfortunately, herbivore enclosures are difficult or impossible to employ in flowing systems as they become damaged or are washed away by hydraulic forces or clogged with debris following flow events, confounding the measurement of the parameters of interest. Overcoming this hurdle would be an important breakthrough in understanding how emergent macrophytes connect stream ecosystems to the surrounding terrestrial environment.

Quantifying fundamental environmental relationships helps determine the conditions under which the ecological link between aquatic and terrestrial systems that is formed by emergent macrophytes may thrive. Macrophytes and their herbivores are globally distributed, indicating that the potential of emergent species to mediate aquatic-to-terrestrial resource subsidies may be greatly underappreciated (Bakker et al., 2016b; Chambers et al., 2008). Combining the use of direct observational methods such as camera trap surveys with experimental approaches such as enclosure construction will allow the exploration of such subsidies. Further, the use of stable isotopes and modern technology such as radio tracking and remote sensing to determine the quantity and spatial distribution of aquatic-derived resources that may be transferred into the terrestrial environment by herbivores will allow for a more objective quantification of the importance of macrophyte-derived aquatic-to-terrestrial subsidies (Ellis-Soto et al., 2021). However, before more cutting-edge and quantitative approaches such as these can be employed, it is essential to assess the basic ecological relationships that underpin ecosystem function at the aquatic-terrestrial interface.

CRedit authorship contribution statement

Jonathan W. Lopez: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (lead); visualization (lead); writing—original draft (lead); writing—review and editing (equal). **Caryn C. Vaughn:** funding acquisition (lead); investigation (supporting); methodology (supporting); resources (lead); writing—review and editing (equal).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data availability

Data will be made publicly available prior to publication.

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Appendix

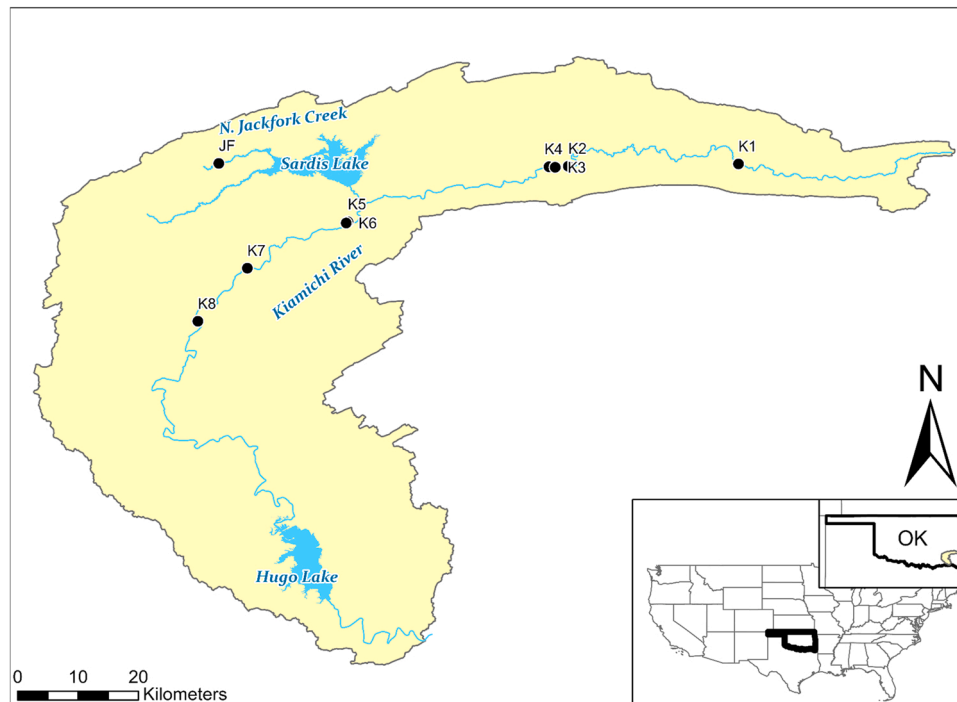


Fig A1. Map showing the Kiamichi River watershed and the nine study sites in the present investigation. Inset shows watershed location within the USA state of Oklahoma.

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