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Habitat modification by the stream macrophyte *Justicia americana* and its effects on biota

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Abstract We conducted an in-stream experiment to determine if and by what mechanisms the emergent macrophyte, *Justicia americana*, enhances streambed stability and influences associated benthic organisms. Treatments included removal of aboveground stems, removal of stems and rhizomes, and a control. Stone stability and embeddedness were higher within intact patches of *Justicia* compared with areas where stems and rhizomes were removed. Presence of belowground structures binding stones and higher embeddedness were responsible for differences in stone stability among treatments. Sediment deposition was highly variable among treatments; however, silt and clay deposition was highest in the control when *Justicia* stems reached maximum biomass. Response of neighboring benthic organisms to *Justicia* treatments varied with organism mobility and trophic level. Sedentary unionid mussels were more abundant in the control than in the stem and rhizome-removal treatment, whereas abundance of mobile snails (*Elimia ucheensis*) and sessile plants (*Podostemon ceratophyllum* and mosses) did not differ among treatments. *Justicia* appears to modify the stream environment by: (1) increasing stability of streambed sediments, and (2) reducing current velocity, thereby enhancing deposition of fine sediments and organic matter.

Keywords Habitat modification · Stream macrophyte · Substrate stability · *Justicia americana* · Disturbance

Introduction

Positive interactions (i.e., facilitation, mutualism, or commensalism) among two or more species include all non-consumptive interactions benefiting at least one of the associated species but not impacting the other (Bertness and Callaway 1994). Such interactions are hypothesized to be more evident in communities subject to high physical stress, where primary inhabitants (species with a large physical presence) may modify the local environment and thus act as environmental buffers for neighboring organisms (sensu Bertness and Callaway 1994; Brooker and Callaghan 1998). Such primary inhabitants have been termed “allogenic ecosystem engineers” (Jones et al. 1994), “foundation species” (Dayton 1972), and “habitat modifiers” (Bruno and Bertness 2001). Habitat modifiers differ from keystone species (sensu Paine 1969; Power et al. 1996) because their large effect on species interactions and resource availability occurs from constituting a large proportion of community biomass (large physical presence) rather than from an active association (e.g., feeding, bioturbation). Although several studies have documented the importance of habitat modifiers in marine (Bruno 2000; Peterson and Heck 2001; Stachowicz 2001) and terrestrial plant ecosystems (Greenlee and Callaway 1996; Tewksbury and Lloyd 2001), the role of habitat modifiers in lotic ecosystems is largely unknown (but see Naiman et al. 1988; O’Conner 1993; Stanzner et al. 1999).

Positive interactions (direct and indirect) increasingly have been recognized as important mechanisms in structuring stream communities (Power 1990; Creed 1994; Soluk and Richardson 1997). However, most positive interactions documented within stream communities involve trophic interactions that ameliorate competition or enhance food resources (e.g., Feminella and Resh 1991; Flecker 1996). Despite a general consensus that impacts of physical disturbance, such as flood events or droughts, are a central structuring force in stream communities (Resh et al. 1988; Reice 1994; Lake 2000), little work has been done to determine if and when habitat

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modifiers facilitate other species by reducing impacts of hydrologic disturbance in streams.

Floods re-shape channels, scour streambed material, and may cause catastrophic reductions in benthic organisms (i.e., Feminella and Resh 1990; Giller et al. 1991; Fritz and Dodds, *in press*). Persistence of organisms within unstable, flood-prone streams has been attributed to traits that enhance their resilience and/or resistance to disturbance (Greulich and Bornette 1999; Lytle 2002). The use of spatial or temporal refugia can increase survival and provide a recolonization source for areas more severely affected by disturbance (Sedell et al. 1990; Lancaster and Belyea 1997). Stable substrate patches are widely recognized refugia from scouring spates. Reductions in density of benthic organisms during spates often are higher in areas of unstable substrata than areas of stable substrata (Biggs et al. 1997; Hax and Golladay 1998; Suren and Duncan 1999; Matthaei et al. 2000; but see Bond and Downes 2000).

Stream macrophytes have been shown to modify habitats through promoting sedimentation, reducing current velocity, retaining organic matter and shading streambeds (Watson 1987; Sand-Jensen 1998; Koetsier and McArthur 2000; Dodds and Biggs 2002), but less is known about their role in stabilizing streambeds and therefore providing flood refugia for neighboring organisms. In a previous study of five Alabama streams, we found stones (≥ 40 mm dimension perpendicular to flow) associated with beds of the emergent macrophyte *Justicia americana* L. (Vahl.) (hereafter called *Justicia*) were more stable than stones outside macrophyte beds (Fritz and Feminella 2003). Positive associations between stone stability and: (1) degree of embeddedness, and (2) abundance of binding rhizomes and presence of attached roots suggested that *Justicia* physically modified local streambed habitat. Alternatively, substrate stability may have coincided or controlled the distribution of *Justicia*. The objectives of our study were to determine: (1) if and through what mechanism *Justicia* modified streambed sediment deposition, and stone stability and embedded-

ness, and (2) the effects of punitive habitat modification (i.e., enhanced stability and embeddedness) on the distribution of associated benthic organisms. We designed a field experiment to test the hypothesis that *Justicia* enhances stone stability and, in so doing, facilitates persistence of benthic organisms during stone-moving spates.

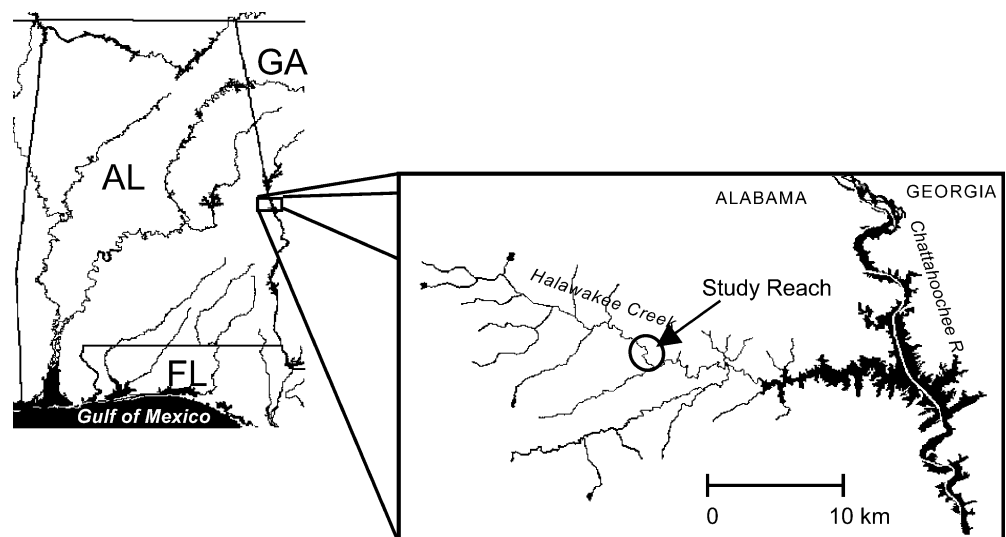
Materials and methods

Study location and organisms

The study was conducted at Halawakee Creek, a third-order tributary of the Chattahoochee River within the Piedmont physiologic province of Alabama (latitude 35°42'N, longitude 85°16'W, Fig. 1). The geology of the study reach was a fine-grained biotite-oligoclase gneiss (Auburn Gneiss; Osborne et al. 1989). The adjacent land use was silviculture (primarily *Pinus taeda* L.) and low-density residential with some livestock agriculture in the upper reaches. Deciduous riparian trees (e.g., *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., *Acer* spp., and *Quercus* spp.) shaded ~60% of the wetted channel, which was ~14 m wide at summer baseflow. Besides *Justicia*, herbaceous vegetation within the active stream channel included *Leersia oryzoides* (L.) (cutgrass), *Triadenum walteri* (Gmel.) Gl. (marsh St. John's wort), and *Saururus cernuus* L. (lizard's tail). Stream water was circumneutral to slightly alkaline (pH 7.1–7.8) and moderately low in dissolved ions (specific conductance 41–65 $\mu\text{s cm}^{-1}$ 25°C).

The geographic range of *Justicia* in North America extends from Georgia to Texas and north to Quebec and Kansas (Penfound 1940; Radford et al. 1968). *Justicia* is found in unshaded stream habitats, such as in shallow riffles, along shores, and on gravel bars (Penfound 1940; Godfrey and Wooten 1981). *Justicia* is a clonal plant, capable of vegetative reproduction from fragments of vertical stems or rhizomes (Penfound 1940; Lewis, 1980) and adapted to natural flow fluctuations because of a deeply rooted, rhizomatous growth form. Rhizomes and roots are perennial structures, whereas the aboveground stems and leaves senesce prior to winter flooding. Flexible, erect stems with well-developed, fibro-vascular and aerenchymatous systems (Penfound 1940) are resilient to spring floods that occur after the onset of the growing season (late March–April). The combination of these morphological and growth characteristics enables *Justicia* to propagate and persist in stream systems where scouring floods are common (Haslam 1978) and potentially provide a refuge for associated benthic organisms. In this

Fig. 1 The study reach within Halawakee Creek, east-central Alabama (AL), USA. GA Georgia, FL Florida



context, there are two mechanisms through which *Justicia* may enhance streambed stability: (1) rhizomes and roots anchoring and binding substrate, and (2) emergent stems reducing flow and enhancing embeddedness by the deposition and filling of crevices between stones with fine sediments.

The benthic organisms chosen for study included a mobile algae-grazing snail, *Elimia ucheensis* (Lea) (Pleuroceridae), sedentary filter-feeding mussels [*Elliptio complanata* (Lightfoot) and *Quincuncina infucata* (Conrad), (Unionidae)], and two sessile epilithic plants, mosses (*Fontinalis* prob. *novae-angliae* Sull. and *Fissidens* prob. *fontanus* Steud.) and *Podostemon ceratophyllum* Michx. In addition to their susceptibility to scouring floods, all of these organisms are considered to play key roles in stream ecosystem function in eastern North America. These benthic organisms have been shown to play important functional roles in streams of the southeastern United States (e.g., Nelson and Scott 1962; Newbold et al. 1983; Stream Bryophyte Group 1999; Vaughn and Hakenkamp 2001).

Experimental design

We conducted a field experiment to test the hypothesis that *Justicia* modifies streambed stability, and to determine the relative importance of above- and belowground macrophyte structures in contributing to stability. We used a randomized block design to separate effects of the two potential mechanisms with the following three treatments: (1) removal of aboveground *Justicia* structures by cutting emergent stems at the streambed surface (=stem removal), (2) removal of stems and rhizomes by clipping to eliminate *Justicia* yet maintain the integrity of the stream bottom (=stem and rhizome removal), and (3) a control (no removal of *Justicia* structures). Care was taken not to disrupt the streambed integrity by stabilizing nearby surface stones by hand while clipping stems and rhizomes and only rhizomes visible at the streambed surface were removed. Six experimental blocks (macrophyte beds) each >3 m wide (perpendicular to flow) and ≥7 m long were established in August 2000. Treatments within a block were arranged as three contiguous 1-m-wide×7-m-long sections (Fig. 2). The six possible treatment combinations (ordered from near bank side to center of channel across the blocks) were randomly assigned to blocks. *Justicia* stem density (measured in three randomly selected 0.125-m² circular

plots) did not differ among sections prior to manipulating the beds (ANOVA, $F=2.50$, $df=7,10$, $P=0.092$). A comparison of rhizome and root biomass from excavations (by shovel) in nearby *Justicia* beds indicated that the belowground removal treatment removed >70% of rhizome biomass and >63% of root biomass (K. M. Fritz, unpublished data). We maintained the stem removal treatment by clipping resprouting vertical stems at least once in every 2 weeks during the growing season (May–September).

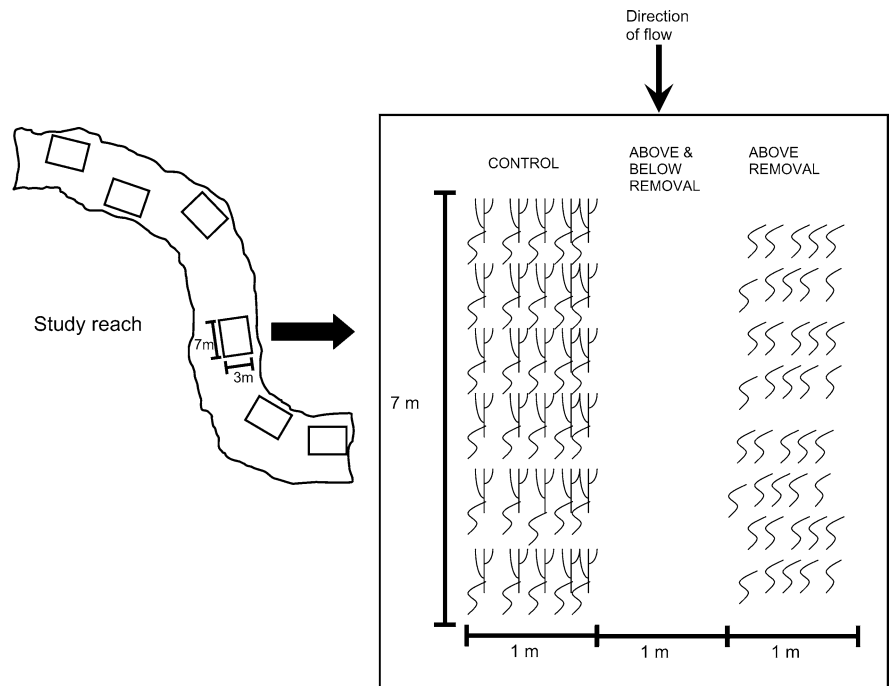
We measured streambed properties and abundance of *Elimia* and epilithic plants 3 times during the experiment: (1) prior to manipulating the *Justicia* beds (August 2000), (2) at the start of the *Justicia* growing season (April 2001, >7 months after bed manipulation), and (3) at the end of the growing season (August 2001, 1 year after bed manipulation).

Measurement of streambed properties

Substrate stability was measured as the force required to shift stones from the streambed (Sousa 1979; Downes et al. 1997). Force was measured with a spring balance attached to a pair of curved grappling hooks. Spring balances (Homs tubular scales) were pre-calibrated for the mass of the grappling hook (measurable ranges of 0.05–5, 0.1–10, and 0.25–25 kg, for small, medium, and large stones, respectively). In use, the grappling hook tips were placed in contact with the upstream edge of a selected stone. One of the three spring balances was then attached between the hooks and pulled parallel (downstream) in the direction of flow. The mass required to shift the stone 5 cm was recorded and then used to calculate critical force (F_C) (sensu Downes et al. 1997). This method provides a more realistic, in situ estimate of the force needed to move stones during a spate than either one based on equations developed in artificial flumes that predict the number or size of stones that move during a spate of a given magnitude or frequency, or monitoring movement of marked stones (see Downes et al. 1997, 1998; Matthaei et al. 1999; see Fritz and Feminella 2003 for more information on this method).

Stones selected for measurement (hereafter called focal stones) within the treatments were selected with random coordinates. Prior to manipulation of the *Justicia* beds (August 2000) five focal stones were measured per treatment and used as subsamples. Thereafter, ten focal stones (subsamples) were measured per treatment (i.e.,

Fig. 2 Arrangement of the three *Justicia* treatments within a block (3 m×7 m) used in the field experiment designed to quantify the streambed modification by aboveground and belowground *Justicia* structures. Branched+S-shaped symbol represents aboveground +belowground structures and S-shaped symbol represents belowground structures



April and August 2001, $n=6$ per time period). After locating focal stones with an underwater viewscope (Aquascope II), but prior to measuring F_C , we measured water depth and estimated the degree of stone wedging. Stones were assigned values of 0, 1, 2, and 3, corresponding to 0, 1–33, 34–66, and 67–100% of focal stone surface area touching adjacent stones, respectively. If a stone could not be moved within measurable limits of scales another stone was randomly selected and used as a replacement (<6% of total stones measured during the study). After stones were moved, we quantified stone embeddedness by assigning stones to one of five categories (i.e., 0, 1–25, 25–50, 50–75, or 75–100% of stone surface area embedded by smaller particles, usually sand). Embeddedness was scored visually by the contrasting coloration of the stone surface exposed to current to that surface surrounded by sediments. Unembedded stone surfaces were usually darker than embedded surfaces due to manganese oxide deposits and organic staining, common in Piedmont streams (G. Lockaby, personal communication). Additional factors measured included stone size (length, height, and width), current velocity (Marsh-McBirney Flowmate), numbers of rhizomes binding focal stones, and presence of roots attached to stones.

A randomized complete block design was used to compare F_C , stone size, embeddedness, amount wedged, water depth, current velocity, number of intersecting rhizomes, and presence/absence of roots among the *Justicia* treatments. Tukey's multiple comparison tests were done to identify specific differences among treatments when significant differences were detected with ANOVA. Because results of three-factor (treatment, time period, and block) analyses for several dependent variables indicated interactions between treatment and time periods (i.e., no differences during pre-manipulation, but differences among treatments after manipulation), sampling periods were analyzed separately. These and all subsequent analyses were done following confirmation of statistical assumptions. Normality was confirmed using the Shapiro-Wilk test, whereas residuals were plotted to assess inequality of variance (Zar 1984). Data were log-transformed when they did not meet statistical assumptions. The significance level was set at $\alpha=0.05$.

Sediment deposition among the three *Justicia* treatments (whole plots) was measured at two subplot locations, upstream and downstream (1 m from the upstream and downstream ends of the 7-m-long treatment sections), within each treatment. Deposited sediment was collected using 50-mL polyethylene centrifuge tubes over 2- to 7-week periods (depending upon discharge conditions) from September 2001 to July 2002 (nine intervals). Centrifuge tubes were held flush with the streambed surface with PVC cylinders (3 cm diameter, 11 cm height) installed vertically into the streambed. Upon return to the laboratory, the tube contents were placed in ceramic crucibles and dried at 105°C for 24 h, cooled in desiccators, and then weighed. Organic matter [as ash-free dry mass (AFDM)]

was measured by weighing samples before and after combusting the samples at 550°C in a muffle furnace for 2.5 h and then cooling them in a desiccator. The ashed samples were then sieved into gravel (<28 to 2 mm diameter), sand (<2 to 0.063 mm), and silt-clay (<0.063 mm) size fractions and then weighed. Differences in percent particulate organic matter, sand, and silt-clay deposited were tested using a randomized complete block design, with a split-plot, repeated-measures ANOVA.

We monitored the stage height of Halawakee Creek and movement of marked stones (mean maximum diameter 68.4 mm) over the study period to identify the timing, frequency, and intensity of floods. Stones from Halawakee Creek were uniquely marked for each treatment and experimental block. Within each treatment section six stones were positioned 20 cm downstream from the upstream deposition tube in a line perpendicular to flow. Distances of stone movement were measured at 1- to 2-week intervals.

Sampling of associated biota

Abundance of *E. ucheensis* (≥ 2.0 mm opercular diameter) and percent cover of epilithic plants were quantified during the three time periods when streambed properties were measured. Before measuring F_C , all attached snails (located with a viewscope) were removed from focal stones and counted. After F_C was measured, any attached snails remaining were collected and percent cover of epilithic plants was assigned to category values of 0, 1, 2, 3, and 4 corresponding to 0, 1–25, 26–50, 50–75, and 76–100% of focal stone surface area covered by epilithic plants. Differences in abundance of *Elimia* and epilithic plants among treatments were compared by season using ANOVA.

We quantified unionid mussels once during the study (spring, before the *Justicia* growing season) because of limited visibility within intact stands of *Justicia* in summer and high water and turbidity in winter. Unionids were counted with a viewscope using a 10-min timed search of each treatment section. Mussel density was highly variable and was not normally distributed; therefore statistical comparisons were done using a non-parametric Kruskal-Wallis test.

Table 1 Comparison of environmental conditions prior to manipulation of *Justicia*. Means (± 1 SE) and ANOVA results for critical force (F_C) needed to move stones, stone size (mm, α -axis length or the longest dimension), stone embeddedness, stone wedging,

number of intersecting rhizomes, presence of attached roots on focal stones, water depth (m), current velocity ($\text{m}^3 \text{s}^{-1}$), number of *Elimia*/stone, and percent cover by epilithic moss and *Podostemon ceratophyllum*. For all measures, full model $df=7,10$

Dependent variable	Control	Stem removal	Stem and rhizome removal	MS	F	P
F_C^a	38.72 (10.198)	37.07 (13.774)	36.40 (10.417)	0.2762	0.37	0.8988
Stone size ^a	93.13 (17.452)	103.20(10.714)	75.43 (4.653)	0.1073	1.04	0.4636
Embeddedness	2.40 (0.146)	1.90 (0.349)	1.73 (0.251)	0.6308	1.96	0.1618
Wedged	0.27 (0.067)	0.30 (0.144)	0.40 (0.137)	0.0708	0.81	0.5996
Rhizomes ^a	0.73 (0.133)	0.47 (0.123)	0.33 (0.161)	0.0759	1.69	0.2177
Roots	0.73 (0.067)	0.60 (0.115)	0.47 (0.084)	0.0495	0.81	0.6003
Depth ^a	0.04 (0.003)	0.05 (0.004)	0.05 (0.011)	0.0915	0.81	0.5992
Current velocity ^a	0.06 (0.014)	0.07 (0.025)	0.08 (0.019)	0.5828	1.08	0.4404
<i>Elimia</i> ^a	1.87 (0.489)	1.87 (1.125)	1.83 (0.454)	0.3718	2.10	0.1384
Epilithic plant	0.73 (0.161)	0.97 (0.167)	0.53 (0.133)	0.1851	1.31	0.3358

^aLog-transformed

Results

Streambed properties

Physical conditions of the streambed did not differ among treatments during the pre-manipulation period (Table 1). There were at least three spates prior to the spring measurement period, including a bankfull flood in March (~141 m³ s⁻¹) about 7 months after we manipulated the *Justicia* beds (Fig. 3). This flood moved 96% of marked stones placed on the streambed surface (2–80 m downstream) within the treatment sections, compared with ≤11% of marked stones by prior events of lower magnitude.

Size of focal stones, current velocity, and stone wedging did not vary among treatments in either spring or summer (Fig. 4a, Table 2). Differences in rhizomes binding focal stones among treatments during spring indicated that our manipulation successfully reduced rhizomes in the stem-rhizome removal treatment (Fig. 4b, Table 2). However, the number of binding rhizomes in the stem removal treatment declined during summer (Fig. 4b, Table 2). Presence of attached roots followed similar patterns seen in rhizomes (Table 2). In the spring, >50% of focal stones in the stem removal and control treatments were attached to roots compared with only 12% of stones in the stem-rhizome removal treatment. During summer, presence of roots attached to stones in the control sections (~95% on average) was higher than stem removal (53%) or stem-rhizome removal (8%) treatments ($P < 0.05$, Tukey's post-hoc test).

Stone embeddedness was lower in the stem-rhizome removal treatment than in the control or stem-removal treatments (Figs. 4c, Table 2). Differences in F_C among treatments during spring and summer followed the same patterns as rhizomes, in that the force needed to shift stones in control sections was higher than in the stem-rhizome removal treatment (Fig. 4d, Table 2). F_C to shift stones in the stem removal treatment did not differ from

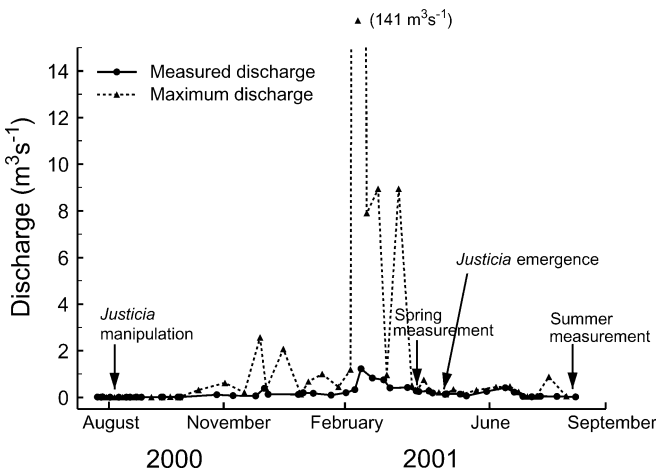


Fig. 3 Hydrograph indicating measured and maximum discharge during the experiment. Periods when streambed properties were measured are indicated by arrows

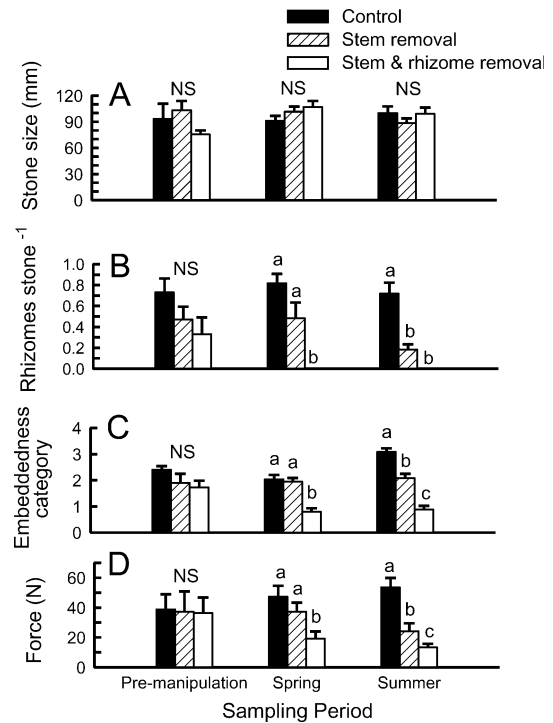


Fig. 4 Pre-manipulation (August 2000), spring (April 2001), and summer (August 2001) measurements of **a** stone size (α -axis, mm), **b** number of rhizomes per focal stone, **c** embeddedness category (see Materials and methods for details), and **d** critical force (N) among the control, stem removal, and stem-rhizome removal treatments ($\bar{X} \pm 1$ SE, $n = 6$). Bars with different letters indicate significant differences (Tukey's post-hoc test, $\alpha = 0.05$) within a sampling period. NS No significant differences among *Justicia* treatments

the control sections in spring, but was less than controls in summer (Fig. 4d, Table 2). Water depth differed among treatments in both seasons (Table 2). Water depth in the stem removal treatment did not differ between control and stem-rhizome removal treatments in spring; however, the latter two treatments differed from each other ($P < 0.05$, Tukey's post-hoc test). During the summer both stem and stem-rhizome removal treatments had greater water depths than the control ($P < 0.05$, Tukey's post-hoc test).

Variation in sediment deposition was greater among *Justicia* beds (blocks) and across time than among *Justicia* treatments (whole plot) or locations (subplot; Table 3). When time periods were analyzed separately, percentage AFDM of sediment in June was higher in the control than the stem removal and stem-rhizome removal treatments, whereas percentage of sediment as silt-clay was higher in June and July in the control, compared to the other treatments. *Justicia* aboveground biomass was higher during the summer than in earlier sampling intervals. Current velocity above sediment tubes differed among treatments only during June ($F_{2,15} = 3.65$, $P = 0.05$) and July ($F_{2,15} = 6.41$, $P = 0.01$) sampling periods; on those occasions velocity was less in the control treatment than in both removal treatments ($P < 0.05$, Tukey's post-hoc test).

Table 2 ANOVA results for spring and summer measurements among *Justicia* treatments. See Table 1 for explanation of dependent variables

Dependent variable	Source of variation	Spring				Summer			
		df	MS	F	P	df	MS	F	P
F_C^a	Full model	7	1.10	3.24	0.045	7	1.10	6.43	0.005
	Treatment	2	1.93	9.11	0.006	2	3.10	18.02	0.0005
	Bed	5	0.19	0.90	0.518	5	0.31	1.79	0.202
	Residual	10	0.21			10	0.17		
Stone size ^a	Full model	7	0.03	2.46	0.096	7	0.06	1.64	0.231
	Treatment	2	0.03	2.25	0.130	2	0.08	0.53	0.603
	Bed	5	0.04	2.99	0.096	5	0.02	2.08	0.152
	Residual	10	0.01			10	0.04		
Embeddedness	Full model	7	0.97	4.81	0.013	7	2.20	12.61	0.0003
	Treatment	2	2.85	14.12	0.001	2	7.28	41.84	<0.0001
	Bed	5	0.22	1.08	0.427	5	0.16	0.93	0.504
	Residual	10	0.20			10	0.17		
Wedging	Full model	7	0.05	2.48	0.094	7	0.04	1.62	0.234
	Treatment	2	0.02	0.72	0.510	2	0.07	2.65	0.119
	Bed	5	0.07	3.18	0.056	5	0.03	1.22	0.370
	Residual	10	0.02			10	0.03		
Rhizomes ^a	Full model	7	0.16	4.05	0.023	7	0.13	8.95	0.001
	Treatment	2	0.53	13.20	0.002	2	0.44	29.83	<0.0001
	Bed	5	0.02	0.38	0.850	5	0.01	0.59	0.706
	Residual	10	0.04			10	0.01		
Roots	Full model	7	0.15	4.23	0.020	7	0.35	15.62	0.0001
	Treatment	2	0.36	9.95	0.004	2	1.13	49.98	<0.0001
	Bed	5	0.07	1.94	0.173	5	0.04	1.87	0.186
	Residual	10	0.04			10	0.02		
Depth ^a	Full model	7	0.24	8.78	0.001	7	0.43	4.69	0.014
	Treatment	2	0.14	5.04	0.031	2	0.99	10.90	0.003
	Bed	5	0.28	10.28	0.001	5	0.20	2.21	0.134
	Residual	10	0.03			10	0.09		
Current velocity ^a	Full model	7	0.11	0.97	0.502	7	0.96	3.24	0.046
	Treatment	2	0.20	1.86	0.205	2	0.79	2.65	0.119
	Bed	5	0.07	0.61	0.696	5	1.03	3.47	0.044
	Residual	10	0.11			10	0.30		
<i>Elimia</i> ^a	Full model	7	0.06	2.19	0.126	7	0.32	2.69	0.076
	Treatment	2	0.01	0.20	0.818	2	0.80	6.85	0.013
	Bed	5	0.09	2.98	0.066	5	0.12	1.02	0.455
	Residual	10	0.03			10	0.12		
Epilithic plants ^a	Full model	7	0.22	4.63	0.015	7	0.51	2.39	0.103
	Treatment	2	0.15	3.18	0.086	2	0.65	3.04	0.093
	Bed	5	0.24	5.22	0.013	5	0.45	2.12	0.146
	Residual	10	0.05			10	0.21		

^aLog-transformed

Effects of *Justicia* on benthic biota

In general, abundance of *Elimia* and epilithic plant cover did not vary among *Justicia* treatments (Fig. 5, Tables 1 and 2). Two-factor ANOVAs (date and treatment) of spring and summer data revealed that mean abundance per stone increased between spring and summer for *Elimia* ($F_{1,25}=79.61$, $P<0.0001$) and for epilithic plants ($F_{1,25}=35.27$, $P<0.0001$). However, both of these organisms apparently increased to a greater extent in the stem removal and stem-rhizome removal treatments than in

control sections (Fig. 5) because of a significant interaction between *Justicia* treatment and date for both *Elimia* ($F_{2,25}=6.62$, $P=0.005$) and epilithic plants ($F_{2,25}=3.80$, $P=0.036$).

Most Unionidae occurring within the study reach were *Elliptio complanata* (>95% of total mussels). A single specimen of *Quincuncina infucata* was found within a control treatment section. Mussel density was higher within control sections compared with the stem-rhizome removal treatment; however, neither of these treatments

Table 3 Results of repeated measures split-plot ANOVA for sediment among *Justicia* treatments (whole plots) and location (subplots). *AFDM* Ash-free dry mass

Sediment variable	Source of variation	df	MS	F	P	
Percentage of sediment as AFDM	Between subject					
	Treatment	2	1.73×10^{-2}	0.92	0.426	
	Bed (treatment)	12	1.89×10^{-2}	5.70	0.033	
	Location	1	9.09×10^{-3}	2.74	0.159	
	Treatment×location	2	1.62×10^{-3}	0.49	0.641	
	Residual	5	3.32×10^{-3}			
	Within subject					
	Time	8	2.69×10^{-2}	18.40	<0.0001	
	Time×treatment	16	2.69×10^{-3}	0.79	0.057	
	Time×bed (treatment)	96	1.57×10^{-3}	1.07	0.412	
	Time×location	8	1.33×10^{-3}	0.91	0.518	
	Time×treatment×location	16	2.28×10^{-3}	1.56	0.126	
	Residual	40	1.46×10^{-3}			
	Percentage of sediment as sand	Between subject				
		Treatment	2	5.82×10^{-2}	0.49	0.622
		Bed (treatment)	12	1.18×10^{-2}	8.80	0.013
Location		1	2.30×10^{-2}	7.20	0.009	
Treatment×location		2	1.62×10^{-2}	1.21	0.372	
Residual		5	1.34×10^{-2}			
Within subject						
Time		8	3.28×10^{-2}	13.66	<0.0001	
Time×treatment		16	1.55×10^{-2}	0.68	0.825	
Time×bed (treatment)		96	2.23×10^{-2}	0.95	0.590	
Time×location		8	2.40×10^{-2}	1.00	0.450	
Time×treatment×location		16	3.35×10^{-2}	1.40	0.193	
Residual		40	2.40×10^{-2}			
Percentage of sediment as silt and clay		Between subject				
		Treatment	2	7.11×10^{-2}	1.13	0.356
		Bed (treatment)	12	6.31×10^{-2}	3.05	0.113
	Location	1	1.26×10^{-1}	6.07	0.057	
	Treatment×location	2	1.32×10^{-2}	0.64	0.568	
	Residual	5	2.07×10^{-2}			
	Within subject					
	Time	8	2.11×10^{-1}	15.62	<0.0001	
	Time×treatment	16	1.33×10^{-2}	1.02	0.445	
	Time×bed (treatment)	96	1.31×10^{-2}	0.97	0.562	
	Time×location	8	1.62×10^{-2}	1.20	0.323	
	Time×treatment×location	16	2.61×10^{-2}	1.93	0.046	
	Residual	40	1.35×10^{-2}			

differed in density from the stem removal treatment (Fig. 6).

Discussion

Among lotic systems, much more is known of the function of macrophytes in lowland and impounded streams (James and Barko 1990; Poi de Neiff et al. 1994; Sand-Jensen 1997), where spates either lack the power to cause substantial streambed movement or have been removed from the hydrologic regime. In streams prone to bed-moving spates, macrophytes that stabilize substrate may play important roles as refugia for associated biota and by

increasing overall habitat heterogeneity. For instance, presence of the exotic grass *Cynodon dactylon* (bermuda-grass) was correlated with higher survival of native macrophytes following three flood events in a Sonoran Desert stream (Dudley and Grimm 1994). Similarly, habitat modified by *Justicia* may function as a spatial refuge from floods for associated benthic organisms in eastern North American streams.

The results of our experiment demonstrate stabilization of streambed sediments by the roots and rhizomes of *Justicia* against substrate-moving spates. Following the spates occurring during our study, it was evident that the streambed within the stem-rhizome removal treatment was scoured more deeply than within the control treatment (K.

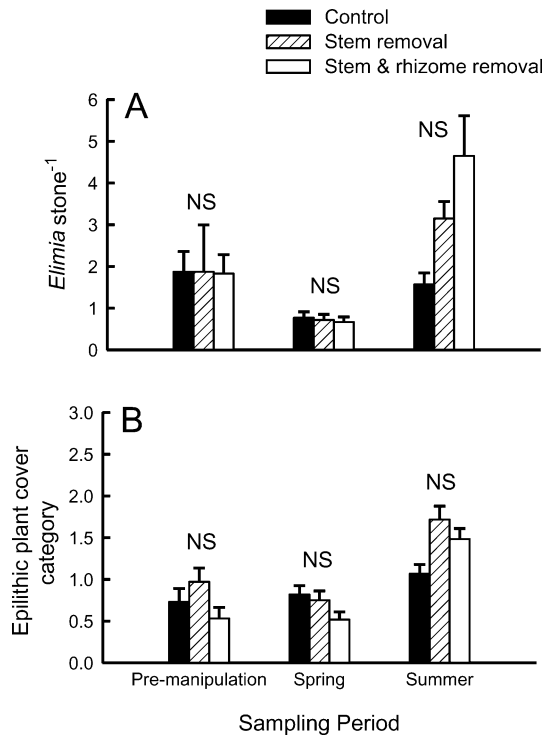


Fig. 5 Pre-manipulation (August 2000), spring (April 2001) and summer (August 2001) measurements of **a** *Elimia ucheensis* (Pleuroceridae: Gastropoda) abundance, and **b** percent cover of epilithic plants (mosses and *Podostemon ceratophyllum*) among the control, stem removal, and stem-rhizome removal treatments ($\bar{X} \pm 1$ SE, $n = 6$).

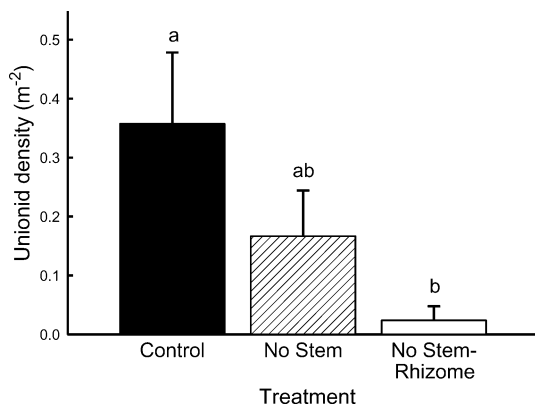


Fig. 6 Unionidae density among the control, stem removal, and stem-rhizome removal treatments during the spring period ($\bar{X} \pm 1$ SE, $n = 6$). Bars with different letters indicate significant differences (Kruskal-Wallis test, Tukey's post-hoc test, $\alpha=0.05$)

M. Fritz, personal observations). This resulted in the differences in water depth among treatments. During summer, higher F_C and stone embeddedness in control sections compared with the stem-removal treatment coincided with lower abundance of binding rhizomes and roots. Rhizome and root senescence, compounded by exposure to current, likely caused lower stone embeddedness and F_C in the stem-removal treatment than in control sections.

Fritz and Feminella (2003) found the streambed surface within *Justicia* beds to contain higher proportions of fine sediments (primarily sand) than areas outside *Justicia* beds. Previous investigations indicated macrophytes enhance deposition and retention of fine sediments by reducing current (e.g., Gregg and Rose 1982; Thornton et al. 1997), so we expected higher fine-sediment deposition within control sections than in stem-removal treatments. Deposited sediment measured in the present study was always >50% sand (by weight); however, we did not detect differences in sand deposition among treatments during any sampling interval. However, our measure of sediment deposition was limited because origin of the sediment was unknown. Additionally, the small spatial scale in which sediment was collected may not have been appropriate. The amount of organic matter and the percentage of sediment as silt and clay were significantly higher in control sections than the removal treatments during summer, a time when aboveground biomass was highest and discharge was at baseflow.

Variation of streambed properties across large scales (i.e., among reaches or streams) have been associated with stream channel characteristics, such as channel constraint, sinuosity, and gradient (Carling 1983; Fowler and Death 2000). However, variation in streambed properties at local scales (within reaches) also can be high (Downes et al. 1997). Our results indicate that habitat modification by *Justicia* is an important factor accounting for local variation in streambed properties. At larger scales, colonization, spread, and subsequent habitat modification by *Justicia* are likely limited by stream channel characteristics, as well as light availability and water chemistry (Howell 1975; Hill 1981).

Specific responses by biota to habitat modification by *Justicia* appeared to vary according to mobility and resource requirements. Organisms that were sedentary and did not directly or indirectly require sunlight (i.e., unionid mussels) were more abundant in areas with intact *Justicia* compared to areas where rhizomes were removed. In contrast, mobile grazers and autotrophic organisms showed no response (i.e., *Elimia* and epilithic plants). We were unable to assess the abundance of biota during and immediately following spates, so it is possible that individuals of mobile taxa (i.e., *Elimia*) inhabiting areas with *Justicia* prior to spates could quickly recolonize nearby, impacted stem-rhizome removal treatment areas following spates. Epilithic (stony) habitat within the stem-rhizome removal treatment in Halawakee Creek may have been more favorable for grazers following spates because of reduced densities of competitors, higher surface area of unembedded cobble, and a higher abundance of consumable periphyton. Sunlight is significantly reduced below the *Justicia* canopy and subsequently leads to lower periphyton biomass compared to areas where the emergent stems and leaves have been removed (Fritz and Feminella, submitted).

In addition to directly affecting stream habitat through shading and substrate stabilization, *Justicia* may indirectly increase habitat heterogeneity across the stream channel

(Koryak and Reilly 1984). In addition to providing substrate for attachment and feeding (e.g., Gastropoda, filter-feeding caddisflies), stems reduce current velocity through *Justicia* beds and redirect more flow through *Justicia*-free parts of the channel. These fast-flowing areas have coarser substrates that are free of sedimentation (Koryak and Reilly 1984; Fritz and Feminella 2003). Therefore, *Justicia* may not only be important in locally modifying streambed properties, but may affect reach-level physical habitat. The modifier roles of *Justicia* on streambed stability and seasonal streambed shading are not ephemeral, because the rhizomes of *Justicia* are perennial, allowing *Justicia* beds and their effects to persist for many years. The influence of *Justicia* on the habitat, like many macrophytes, expands by vegetative growth during more benign conditions and retracts following floods (Haslam 1978).

In summary, *J. americana* appears to be an important habitat modifier within Halawakee Creek, and possibly other eastern North American streams where it is abundant. Alteration of the physical environment by this emergent plant appears to have both positive and negative effects on benthic organisms, which may vary with organism mobility and resource requirements. *Justicia* does have an important role in controlling benthic primary production and the distribution of various benthic stream invertebrates. Identification of habitat modifiers and their function on the associated community provides a target for protecting whole communities as well as enhancing our understanding of community organization (Bruno and Bertness 2001).

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