Factors affecting biomass allocation in the riverine macrophyte *Justicia americana*

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Abstract

The relative effects of hydrologic disturbance, abundance of root parasites, and ambient physicochemical conditions on total biomass, biomass allocation, and architecture of the emergent macrophyte *Justicia americana* (L.) Vahl. (Acanthanceae) were investigated in six south-central Alabama streams, USA. *Justicia* total biomass was negatively related to shading by riparian vegetation, which accounted for 45 and 31% of the total variation at the beginning and end of the growing season, respectively. Contrary to our predictions, total *Justicia* biomass was unrelated to disturbance by flooding as indicated by the likelihood of streambed movement by bankfull discharge, nor was biomass allocation to below-ground structures positively related to likelihood of substrate movement. Stem density at the end of the growing season was negatively related to abundance of nematode-parasites, but total *Justicia* biomass was unrelated to parasite abundance. This macrophyte appears to persist in the dynamic environment of eastern North American streams by firm anchorage of below-ground structures and high capacity for regeneration following storm flows.
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1. Introduction

Physical disturbance, especially during floods, is considered a predominant force regulating biotic productivity and diversity in streams (Resh et al., 1988). Most investigations of organism persistence within streams have centered on short-lived and/or mobile taxa,

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such as macroinvertebrates and fish (e.g., Meffe and Minckley, 1987). Biotic resilience to flood disturbance has been attributed to rapid development and vagility (e.g., Gray, 1981), whereas biotic resistance has been associated with stable substrate or areas with low shear stress during floods (e.g., Lancaster and Hildrew, 1993). In contrast, few investigations have explored resistance to floods by long-lived sessile organisms, particularly macrophytes.

Classification schemes have been used to predict relationships between habitat characteristics (e.g., nutrient availability and disturbance intensity) and life history traits (e.g., Grime, 1979; Bornette et al., 1994). Allocation of more biomass to anchoring structures is a potential strategy that may enhance perennial macrophyte resistance to scouring spates. Alternatively, under more benign hydrologic conditions competition for light may become a key factor, thus promoting increased allocation to above-ground biomass. However, other factors related to stress (sensu Grime, 1979), such as shade or current velocity, also may more strongly govern allocation patterns.

The relationship between water depth and emergent macrophyte biomass allocation is well-known, especially in lakes and wetlands, where allocation patterns associated with depth directly relate to light limitation (Clevering and Hundscheid, 1998; Vretare et al., 2001). In addition to water depth, light limitation is compounded in forested streams by riparian shading (Everitt and Burkholder, 1991), especially when plants are restricted (by current velocity) to stream margins where riparian influences are greatest.

In addition to physical and chemical conditions, macrophyte biomass and distribution also may be limited by biotic interactions such as competition, herbivory, and parasitism. Compared to herbivory and competition, less is known about the role of parasitism on aquatic macrophyte growth, allocation patterns, and architecture. Nematodes are a well-known group of plant parasites in terrestrial environments and have received some attention as pests of aquatic crop plants (Prot et al., 1994) and biocontrol agents of invasive macrophytes (Gerber et al., 1987). However, the ecological consequences of parasitic nematodes on native macrophytes are virtually unknown (but see Prejs, 1986).

Emergent riverine macrophytes are typically restricted to silted, slow-flowing stream reaches (Halsam, 1978). One notable exception is *Justicia americana* (L.) Vahl. (hereafter called *Justicia*) where it grows in shallow riffle margins and gravel bars in streams of eastern North America (Penfound, 1940). *Justicia* is a clonal dicotyledon with perennial rhizomes, stolons, and adventitious roots that firmly bind to the streambed. The above-ground leaves and stems are produced annually. The erect stems have well-developed fibro-vascular and aerenchymous systems and can reach >1 m in height (Penfound, 1940). Allocation of energy to sexual reproduction in *Justicia* represents only a minor portion (0.04%) of biomass when flowering (Twilley et al., 1985).

Preliminary examination of *Justicia* roots in Halawakee Creek, AL revealed large numbers of the gall-forming nematode, *Meloidogyne* sp. (Nematoda: Meloidogynidae), a widespread genus commonly known as root-knot nematodes. This observation prompted us to examine the relationship between *Justicia* and *Meloidogyne*. Female *Meloidogyne* are distinctive because of their sessile lifestyle and saccate body rather than the typical vermiform shape. Presence of female nematodes causes the formation of enlarged multinucleate cells (i.e., giant cells) in plant roots, which subsequently form galls (Bird and Bird, 2001). Root-knot nematodes impact plants by removing vascular tissue and inhibiting uptake of water and essential nutrients (Bird and Bird, 2001).

The objective of our study was to examine the roles of hydrologic disturbance, parasitism by the nematode *Meloidogyne*, current velocity, water depth, and water chemistry on the biomass, biomass allocation, and stem density of the macrophyte *Justicia*. We predicted that disturbance by spates and parasite load (=*Meloidogyne* density) would be negatively related to total biomass, and disturbance by spates also would be negatively related to allocation to above-ground biomass (=positively related to below-ground biomass). We also predicted that stem density would be limited by greater shear stress associated with higher current velocities and that stem-specific biomass (=greater stem lengths) would be positively related to water depth.

2. Materials and methods

2.1. Study sites and experimental design

The study sites were in six 3rd- to 4th-order piedmont streams containing extensive beds of *Justicia*. Streams were tributaries within the three major Alabama drainages: Coosa River (Terrapin, Shoal, Hatchet, and Talladega creeks), Tallapoosa River (Choctafaula Creek), and the Chattahoochee River (Halawakee Creek). Within each stream three *Justicia* beds (30–700 m^2) were selected ($n = 18$ total beds) with a large proportion of bed area occurring within the wetted stream channel during summer baseflow. Beds were usually ≥ 1 km apart and all occurred within stream reaches containing intact riparian zones of mixed-deciduous forest (e.g., mostly *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., *Acer* spp., and *Quercus* spp.).

2.2. Field sampling

Justicia was sampled twice, at the beginning (April–May, prior to vertical stem emergence) and end (July–August, prior to senescence) of the 2001 growing season. All 18 sites were sampled within 10 days for each of the two periods. Plants were sampled by taking three randomly placed 0.1 m^2 quadrat subsamples; nine quadrats were taken per bed from Choctafaula Creek beds during spring.

Water depth, current velocity (Marsh–McBirney Flowmate$^®$), and percent canopy closure of riparian vegetation (spherical densiometer) were measured prior to collecting *Justicia*. Above-ground tissues (leaves and vertical stems) within 0.1 m^2 quadrats were counted and cut even with the streambed, and below-ground rhizomes and roots were then excavated. Loss of tissues during sampling was minimized by using a 120 μm-mesh net along the downstream end of each quadrat. *Justicia* samples were stored in resealable plastic bags, placed on ice, and then returned to the laboratory.

Reach-level physical measurements were taken at each site to estimate the streambed disturbance likely to occur during a bankfull flood event. Critical tractive force at bankfull discharge (τ_{bf}) on the streambed was quantified (Newbury, 1984):

$$\tau_{\mathrm{bf}} = D_{\mathrm{bf}} S \rho$$

where D_{bf} is the average depth at bankfull (m), S the average slope of reach, and ρ the mass density of water ($1000\,kg\,m^{-3}$). Bankfull depth and slope were estimated for each reach as an average of three measures. Reach-level τ_{bf} was then divided by the median substrate size (ϕ^{50}) of each study reach to derive an estimate of streambed instability (instability index, sensu Cobb and Flannagan, 1990). With this index, instability values increased as the likelihood of substrate movement during a bankfull flood increased.

Ambient physicochemical parameters of the study sites also were measured during each sampling period. Specific conductance, pH, and instantaneous water temperature were measured in the field. Grab water samples were collected in acid-washed polyethylene bottles and filtered (0.45-μm filters) after the summer *Justicia* sampling (baseflow conditions) for dissolved nutrients (NH_4–N, NO_3–N, and K). Phosphorus (PO_4–P) concentration was uniformly low (<0.5 ppm) for all study sites.

2.3. Laboratory processing

Freshly collected *Justicia* structures were sorted into three categories: above-ground structures (leaves + vertical stems), rhizomes, and roots, and all dead material were removed. Rhizomes and roots were considered dead if they appeared skeletonized (i.e., only lignified fibro-vascular bundles present). Abundances of *Meloidogyne* nematodes were estimated by counting visible galls on *Justicia* roots. Gall counts were made by spreading root material of a *Justicia* quadrat subsample evenly across a grided pan (partially filled with tap water), and then counting galls on roots within four randomly selected sections (12.5% of total sample). Presence of parasitic nematodes within galls was confirmed by dissecting 5–10 galls from roots collected in at least one site per stream. *Meloidogyne* gall abundance for each site was estimated by averaging across the three quadrat subsamples, the number of galls per *Justicia* root mass. All *Justicia* structures were dried for at least 48 h at 85 °C, weighed, ashed (550 °C for 2 h), and then reweighed to determine ash-free dry mass (AFDM).

2.4. Data analysis

We used multiple regression (PROC REG with MAXR selection procedure, SAS Release 8.2) to test our predictions regarding the separate relationships of substrate instability, parasitic nematodes, and ambient physicochemical conditions on *Justicia* biomass (as total AFDM), below-ground biomass allocation (proportion rhizome + root biomass), and above-ground architecture (as stem density and biomass per stem). Data were log-transformed where parametric assumptions of normality or heteroscadascity were not met (Shapio–Wilk Test for normality and residual plots for equality of variance). Best-fit models were selected based on improvements of R^2 and Mallow's *Cp* criterion. Mallow's *Cp* is a measure of the quality of fit for a model (function of the error sum of squares of the reduced model) and tends to be less dependent than R^2 on the number of terms in the model (Myers, 1986). Under the best model, *Cp* is approximately equal to the number of terms in the model (intercept and beta coefficients). Significance level was set at $\alpha = 0.05$ for all analyses.

Table 1
Locality and characteristics of the *Justicia americana* study beds along six south-central Alabama streams

Stream	Bed	Location		*Justicia* bed area (m^2)	Bankfull width (m)	Tractive force (kg m^{-2})	Number of *Meloidogyne* m^{-2}	
		Latitude	Longitude				Spring	Summer
Choctafaula	1	32°30′29.3″N	85°34′43.4″W	102	19.8	16.3	10240	32844
	2	32°30′11.2″N	85°34′46.0″W	27	13.4	40.8	20244	24669
	3	32°30′6.6″N	85°34′45.3″W	91	14.2	30.6	17195	16644
Halawakee	1	32°42′29.5″N	85°16′23.3″W	123	24.5	20.3	7581	33914
	2	32°41′48.3″N	85°15′59.6″W	44	18.6	22.4	3838	17843
	3	32°41′39.5″N	85°15′53.1″W	161	27.4	38.5	9255	29620
Hatchett	1	33°11′21.2″N	86°2′42.4″W	102	41.5	13.5	1999	5394
	2	33°7′56.0″N	86°3′18.0″W	170	26.5	21.7	1188	8213
	3	32°5′13.0″N	86°4′32.3″W	271	24.2	22.0	1336	1073
Shoal	1	33°45′8.6″N	85°34′17.8″W	37	11.3	7.0	61	4303
	2	33°45′30.6″N	85°35′43.2″W	53	14.4	4.3	12902	15306
	3	33°43′28.2″N	85°36′1.7″W	149	17.4	12.8	5928	8042
Talladega	1	33°19′49.1″N	85°59′22.1″W	197	16.4	12.1	2904	9465
	2	33°20′11.8″N	85°59′20.2″W	145	18.3	33.0	1633	1776
	3	33°22′35.8″N	85°1′35.6″W	708	22.9	44.3	4286	6144
Terrapin	1	33°51′41.4″N	85°31′33.2″W	69	17.2	25.5	7521	13772
	2	33°54′22.6″N	85°32′5.3″W	199	26.2	13.1	1335	4970
	3	33°59′3.0″N	85°36′5.8″W	184	41.9	23.9	84	87

3. Results

Several study site characteristics are summarized in Table 1. Tractive force (used to calculate the instability index) ranged from 4.3 to 44.3 kg m^{-2}, whereas nematode densities varied from 61.4 to >33,000 m^{-2} over the course of the study.

3.1. Factors affecting total biomass of Justicia

The best-fit linear regression model for total biomass of *Justicia* included three environmental variables in spring ($F = 6.26$, $P = 0.006$; ∼57% of the total variation) and summer ($F = 4.36$, $P = 0.023$; 48% of the total variation, Table 2). Riparian shading was inversely correlated with total *Justicia* biomass in spring and summer (45 and 31% of the total variation, respectively). Specific conductance explained an additional five and 12% of the total variation in total *Justicia* biomass in the spring and summer, respectively. Substrate instability and abundance of *Meloidogyne* nematodes were minor contributors to the total observed variation seen in total biomass of *Justicia* (Table 2).

3.2. Factors affecting biomass allocation

The best-fit linear regression model for biomass allocation to below-ground structures in spring ($F = 8.46$, $P = 0.002$) included three environmental variables, which accounted for

Table 2
Best-fit multiple regression models for *Justicia americana* characteristics

Dependent variable	Season	Independent variable	b (SE)	Cumulative R^2	Cp
Total biomass	Spring	Shade	−0.016 (0.0052)	0.4533	
		Conductivity[a]	0.268 (0.1733)	0.5039	
		Substrate instability[a]	0.176 (0.1170)	0.5728	1.431
	Summer	Shade	−0.005 (0.0037)	0.3099	
		Conductivity[a]	0.218 (0.1185)	0.4266	
		Nematoda[a]	−0.050 (0.0405)	0.4832	1.214
Below-ground allocation	Spring	Current velocity[a]	0.086 (0.0278)	0.4682	
		Conductivity[a]	0.037 (0.0181)	0.5648	
		Depth	−0.326 (0.0184)	0.6444	2.335
	Summer	Depth	−0.724 (0.2181)	0.2296	
		Conductivity[a]	−0.059 (0.0180)	0.3565	
		Shade	−0.002 (0.0006)	0.5458	
		Current velocity[a]	0.029 (0.0168)	0.6298	2.650
Stem density	Spring	Shade	−0.117 (0.0653)	0.1667	−0.565
	Summer	Nematoda[a]	−1.974 (0.6471)	0.2912	
		Conductivity[a]	3.739 (1.7541)	0.3930	
		Substrate instability[a]	−1.913 (1.1952)	0.4869	1.279
Biomass per stem	Spring	Depth	1.597 (0.5267)	0.3354	
		Conductivity[a]	−0.095 (0.0534)	0.4518	1.592
	Summer	NO_3–N	0.313 (0.0817)	0.5841	
		Depth	4.220 (2.6728)	0.6433	−0.615

Shown are mean regression coefficients (b) with associated estimated standard errors in parentheses, cumulative R^2, and Mallow's Cp for best-fit equation. $n = 18$.

[a] Log-transformed.

∼64% of the total variation (Table 2). Proportion of below-ground biomass was positively correlated with current velocity, the most important measured factor (>46% of the total variation). Proportion of biomass allocated to below-ground structures in summer was best explained by 4 physicochemical measures ($F = 5.53$, $P = 0.008$; ∼63% of the total variation, Table 2). Contrary to our prediction, substrate instability was not positively related to below-ground allocation in either season (Fig. 1).

3.3. Factors affecting Justicia architecture

None of the measured environmental variables were significantly related to *Justicia* stem density in the spring ($F = 3.20$, $P = 0.0926$, Table 2). Abundance of *Meloidogyne* nematode galls was negatively related to stem density in summer (Table 2), when they were most abundant (Table 1), accounting for most of the explained variation ($F = 4.43$, $P = 0.022$). Neither current velocity nor light availability was related to stem density.

In support of our predictions, water depth was positively correlated with stem-specific biomass in spring (33% of total variation, Table 2). The higher biomass per stem at deeper
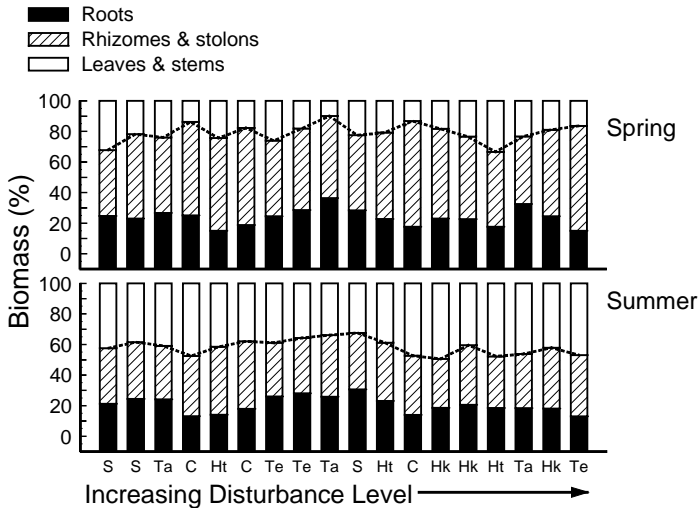
Fig. 1. Biomass partitioning (as percent of total biomass) in *Justicia americana* across study sites during the beginning (spring) and end (summer) of the growing season. Study sites are arranged in ascending disturbance level or instability index scores (see Section 2 for details). Dashed lines indicate separation of above- and below-ground categories. Each bar represents the mean of quadrat subsamples (three or nine) collected at each site. Stream abbreviations: C: Choctafaula, Hk: Halawakee, Ht: Hatchet, S: Shoal, Ta: Talladega, and Te: Terrapin.

locations primarily reflected an increased stem length with increased water depth. Streamwater NO_3–N concentration was positively correlated with biomass per stem during summer (∼59% of the total variation, Table 2).

4. Discussion

4.1. Total biomass

Our results indicate that across the six study sites variation in *Justicia* biomass during both spring and summer periods was primarily influenced by ambient physicochemical conditions (light availability and water conductivity) rather than by our estimates of disturbance or parasitism by nematodes. Disturbance from flooding has been shown to reduce macrophyte biomass (e.g., Bilby, 1977), however, we did not find evidence that *Justicia* biomass varied in manner consistent with estimates of disturbance level as indicated by substrate instability, among our sites. Based on finding two to six times higher total biomass and productivity of *Justicia* in reservoirs than streams, Boyd (1969) hypothesized that growth of stream populations were limited by more adverse riverine conditions than those conditions in relatively stable reservoirs. In our study, despite instability values differing by almost 13× among some sites (1.43–23.87), we expect that differences in disturbance intensity or frequency were minor compared with differences likely to be observed between reservoirs and streams. Moreover, light availability is also likely to be greater in reservoirs than

streams. Light availability has been shown to be an important factor in controlling growth and zonation patterns of macrophytes in streams (e.g., Everitt and Burkholder, 1991). For example, Howell (1975) noted that streambed coverage of *Justicia* in a Kentucky stream was $>2\times$ higher in east- or west-flowing reaches with longer daily exposure to direct sunlight than in north- or south-flowing reaches with shorter daily exposure to direct sunlight. Shading by riparian vegetation appears to be an important constraint on *Justicia* biomass within Alabama piedmont streams.

We are unaware of previous documentation indicating parasitism by *Meloidogyne* on *Justicia* (Gerber et al., 1987). Galls of the parasitic nematode *Meloidogyne* were present in *Justicia* roots from all study beds (see Table 1). Varying numbers of individuals may be present within a single gall (Bird and Bird, 2001, K. Fritz, pers. obs.), so our estimates of parasite abundance were conservative and may have underestimated parasite loads. Susceptibility of plants to infection by parasitic nematodes can be influenced by several physical and biological factors, such as water depth and above-ground herbivory (Ingham and Detling, 1984; Prot et al., 1994). Our results indicate that nematode parasite load is at least secondary to riparian shading in describing the variation in total *Justicia* biomass among our study sites. However, the *Justicia–Meloidogyne* association is likely complex and requires further study.

Streamwater conductivity also may contribute to variation in total biomass. *Justicia* has a high affinity for Ca^+-, Mg^+-, and K^+-rich aquatic habitats (Adams et al., 1973; Twilley et al., 1985). In the New River, *Justicia* was limited to hardwater (limestone–dolomite) reaches where Ca^+ hardness $\geq 50 \, mg \, CaCO_3 \, l^{-1}$ and conductivity reached $150 \, \mu S \, cm^{-1}$, and absent in upstream, softwater (gneiss geology) reaches where conductivity was only $42 \, \mu S \, cm^{-1}$ (Hill, 1981). The range of conductivity among our study sites was $19–148 \, \mu S \, cm^{-1}$ (KMF, unpublished data), although 14 of our 18 sites had mean values $<60 \, \mu S \, cm^{-1}$. Low conductivity may thus explain why maximum total biomass estimates of our study beds were 25–79 times lower than the estimates of the New River population. However, because softwater tends to be lower in other limiting nutrients (e.g., N) and have lower pH (Dodds, 2002), there may be multiple chemical factors responsible for the lower biomass at our study sites compared to the New River population. Geological variation and associated differences in streamwater chemistry are likely to be important determinants of maximum biomass and productivity of *Justicia* across its range.

4.2. Biomass allocation and architecture

A trade-off exists in plants allocating biomass to above- and below-ground structures. On one hand, greater allocation of resources to above-ground leaves and stems increases carbon fixation and competitive ability; alternatively, higher allocation to above-ground structures may increase vulnerability to physical disturbance by increasing drag from above-ground structures (associated with higher current velocities) and reducing biomass of below-ground anchoring structures. For most riverine macrophytes, the reciprocal relationship between biomass and current velocity is not simple across the range of flow habitats found in streams. Photosynthetic rates tend to be positively related to current velocity over slower ranges (i.e., $0–0.2 \, m \, s^{-1}$), but is negatively correlated over wider current velocity ranges ($0.04–1 \, m \, s^{-1}$, Chambers et al., 1991). Our study showed that above-ground biomass allocation in *Justicia*

in the spring (prior to emergence from the water) was negatively related to current velocity. However, this relationship did not persist through the growing season because most of the above-ground biomass had emerged from the water by summer. It is possible that turbulent conditions inhibited growth of emerging stems (Halsam, 1978), but following emergence (in summer), current velocity had no affect on growth.

A commonly cited stress on emergent plants within lentic systems has been submergence, where decreased light and gas exchange lowers respiration and photosynthesis rates (e.g., Grace, 1989). Increasing allocation to above-ground structures with increasing water depth is a widespread strategy for emergent macrophytes, enabling rapid emergence to optimize metabolism (Vretare et al., 2001). The positive relationships observed between water depth and allocation patterns and architecture (biomass per stem) in our study suggested that *Justicia* may adjust stem length to optimize metabolism, and possibly increase fitness.

Our prediction that *Justicia* would allocate more biomass to anchoring structures in environments more likely to experience streambed-moving spates was not supported. These results conflict with those of Robertson and Mann (1984), who found greater allocation to below-ground structures of perennial forms of *Zostera marina* to disturbance by grinding ice in a subtidal zone, and Barrat-Segretain (2001), who reported that allocation in two perennial macrophytes (*Berula erecta* and *Myriophyllum spicatum*) was explained by a gradient of flood disturbance intensity rather than by differences in sediment organic carbon (i.e., productivity gradient). Plasticity and biomass of *Justicia* across our study sites were more strongly related to ambient physiochemical gradients in shade, current velocity, and water depth than to disturbance or productivity gradients. Therefore, environmental factors that govern allocation patterns in riverine macrophytes may be species-specific. Persistence of *Justicia* in flood-prone streams may be associated with strong fibro-vascular tissue, substrate stabilization by below-ground structures, and a high capacity for vegetative regeneration.

Acknowledgements

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