Understanding the relative roles of disturbance and species interactions in shaping Mississippi River island plant communities

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Abstract: In order to better understand the factors governing community assembly on riverine islands, we conducted a greenhouse experiment that examined the effects of species interactions in combination with flooding that mimicked hydrologic gradients found on Mississippi River islands. Specifically, we examined the effects of inter and intra-specific competition and three disturbance treatments (drained, drought, and flood) on the growth performance of three island-ubiquitous herbaceous plant species (Amaranthus palmeri, Cyperus strigosus, and Xanthium strumarium). We predicted a decrease in interspecific competitive effects in disturbance treatments. Specifically, we expected A. palmeri to be most affected by flooding treatment based on its facultative upland status suggesting that it should be a poor tolerator of flooded conditions. X. strumarium and C. strigosus both facultative wetland species in their status, should tolerate flooding, but we predict that C. strigosus should have greater stress tolerance due to its perennial life history. Because we find these species coexisting at the same elevation zones on riverine islands, we also predicted stronger intraspecific competition effects. Our results indicate that disturbance indeed affected competitive interactions, but the effects were species-specific. X. strumarium showed stronger competitive effects when grown with conspecifics while C. strigosus experienced greater competition with heterospecifics under drought treatments. Based on its wetland indicator status and life history characteristics, we expected A. palmeri to exhibit a facilitative effect, which is typically an upland species, but instead it was impacted most by interspecific competition. Our study indicates that factors other than competition, facilitation, and flood tolerance (e.g., priority effects) may be controlling island plant community dynamics, further studies are required.


Introduction

The assembly of communities following disturbance and subsequent colonization depends on propagule pressure, abiotic filters (suitability), and biotic interactions (both positive and negative), all of which may be altered by disturbance. Disturbance may increase opportunity for invasion because of decreased competitors, increased space and more available resources (fluctuating resource hypothesis, Davis et al. 2000). Contrarily, disturbance may be a stress filter where high disturbance frequency or intensity filters out the regional species pool and select the few that are either resistant or able to colonize (niche-selection filtering and tolerance, Chase 2007, Muller-Landau 2010). Such dynamics suggest some species may be good colonizers and others good competitors or tolerators, but the empirical evidence of such trade-offs suffers from a lack of quantification (Lenssen et al. 2004). In addition to competition and tolerance, Brooker et al. (2008) summarized work suggesting that facilitation increases the range of stress-intolerant competitive species into harsher physical conditions, such as frequently or intensely disturbed areas. Disturbances are thus responsible for affecting species’ interactions and community assembly (Wedin and Tilman 1993, Suding and Goldberg 2001, Lenssen et al. 2004).

To better understand how communities assemble, it is important to understand how disturbance affects species’ interactions. Many studies have focused on how disturbance directly weakens competition effects (Wilson and Tilman 1993, Turkington et al. 1993), while others examined competition along gradients such as wave exposure (Wilson and Keddy 1986), salt marsh flooding (Pennings and Callaway 1992), and nutrient availability (Chesson and Huntly 1997). Niche theory suggests species’ coexistence when intraspecific competition is greater than interspecific competition, or when some other factor weakens interspecific competition (Goldberg and Barton 1992, Tilman and Pacala 1993). Goldberg (1996), for example, proposed that intense competition at the least disturbed end of the disturbance gradient excludes species with low competitive ability (competitive response), and weaker competitors find refugia at the most disturbed end of the gradient. Another proposed mechanism suggests that certain species increase in competitive ability along the
disturbance gradient relative to other species (Tilman 1988, Suding and Goldberg 2001); a competitive change. This competitive change scenario does not need constant disturbance for a species to persist (Crawley 1990); however, ‘weaker’ competitors rely strongly upon regular disturbance for some competitive release (Huston 1979). A natural study conducted on Mississippi River islands showed that diversity was highest with intermediate flooding disturbance, and niche constraints (tolerance to disturbance in the form of flooding and competitive interactions with other species) likely controlled community composition at the ends of the gradient: a general release of such constraints occurred at intermediate elevations (Moore et al. in review).

Research on the positive interactions of species has been stimulated by the ‘stress gradient hypothesis’ (SGH) (Bertness and Callaway 1994) that predicts the relative importance of facilitation and competition vary inversely across gradients. The basis for the SGH is that facilitative interactions should be rare in areas where the physical environment is relatively benign (Bertness and Callaway 1994). Empirical evidence of facilitative effects between plants has been shown in severe environments (e.g., deserts, arctic, and salt marshes: Brooker et al. 2006) and could potentially be important on riverine islands.

While species’ occurrences in periodically disturbed areas may be due to their weak competitiveness, their occurrence may also be due to an increased tolerance to disturbance-imposed stress (Grime 1977, Gaudet and Keddy 1995). In a study of experimental ponds, Chase (2007) found drought-affected communities were determined by niche-filtering processes; only those species adapted to the drought disturbance remained. In an effort to show tolerance as a mechanism of coexistence, Muller-Landau (2010) modeled a tolerance-fecundity tradeoff along stress gradients. The compilation of the above work suggests a dynamic mechanistic process where facilitation, competition, and tolerance interaction effects vary with different disturbance regimes and ecosystems.

One drawback to examining disturbance gradients is confounding variables such as salinity, water, and nutrient availability (Wilson and Keddy 1986, Chesson and Huntly 1997). Here, we use a greenhouse experiment to aid in our understanding of the mechanistic controls over community assembly along an island disturbance gradient. We measured effects of inter and intra-specific competition under three disturbance regimes for three common ruderal species found throughout the flooding gradient on all islands. We also employed a series of flood and drought treatments to mimic natural regimes found on the islands. We expected disturbance to decrease the growth of all species in the greenhouse, but not by similar amounts due to varying species tolerances. Specifically, we expected Amaranthus palmeri S. Watson to be most affected by the flooding treatment based on its facultative upland status; it should be less tolerant of flooded conditions than species with wetland status. Xanthium strumarium L. and Cyperus strigosus L. are both facultative wetland species in their status and should tolerate flooding, but we predict that C. strigosus should have greater stress tolerance due to its perennial life history (H1: disturbance tolerance C. strigosus X. strumarium A. palmeri). Based on the changes in interactions along the gradient, we expected a decreased interspecific competitive effect in disturbance treatments (H2) and an increased facilitation effect, as A. palmeri is more abundant than the other two species at low elevations despite its more upland status (H3). Because we find these species coexisting on the islands at similar elevation zones, we expected - based on classic competition theory – a stronger intraspecific competition effect than interspecific competition effect (H4).

Methods

Species selection and biology

We selected three species that were ubiquitously found on all five study islands (from previous experiments) and that encompassed the entire disturbance gradient in 2007 and 2008 (see Moore et al. in review, for details; Table 1). The three species rarely occurred together at the plot level on study islands. Examining pairwise comparisons, A. palmeri and C. strigosus occurred most often together and more often were together at higher elevations (50.5% in 2007 and 38.2% in 2008). A. palmeri and X. strumarium occurred less often together, but again were more often found together at higher elevations (31.1% in 2007 high and 36.5% in 2008 intermediate). X. strumarium and C. strigosus rarely occurred together in 2007; however, they were found together 24.4% of the time in plots at intermediate elevations following disturbance (i.e., 2008) (Table 2).

*A. palmeri* (Palmer’s amaranth) is an annual C₄ plant with a facultative upland (FAC-U) status and is widely distributed throughout the U.S. (USDA NRCS 2010). *A. palmeri* commonly invades disturbed habitats, waste places, railroads, streambanks, sandy areas, and agricultural fields.

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### Table 1. Natural distributions of experimental species found on Mississippi River islands in 2007 and 2008. *Denotes number of stems of each species found in each 1 m × 2 m experimental plot (N ≥ 36) for each species.

<table>
<thead>
<tr>
<th>Island</th>
<th>Elevation Zone</th>
<th><em>A. palmeri</em></th>
<th><em>C. strigosus</em></th>
<th><em>X. strumarium</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Densford Bar</td>
<td>Low Intermediate</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Intermediate</td>
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<td>0</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>5</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Dean Island</td>
<td>Low Intermediate</td>
<td>15</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Intermediate</td>
<td>18</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>13</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Sunrise Towhead</td>
<td>Low Intermediate</td>
<td>17</td>
<td>11</td>
<td>1</td>
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<td>3</td>
</tr>
<tr>
<td></td>
<td>High</td>
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<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Keyos Point Bar</td>
<td>Low Intermediate</td>
<td>10</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Intermediate</td>
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<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wardlow Bar</td>
<td>Low Intermediate</td>
<td>10</td>
<td>0</td>
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</tr>
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<td>3</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Total by zone</td>
<td>Low Intermediate</td>
<td>54</td>
<td>16</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Intermediate</td>
<td>32</td>
<td>26</td>
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</tr>
<tr>
<td></td>
<td>High</td>
<td>23</td>
<td>15</td>
<td>10</td>
</tr>
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</table>
Seed germination for *A. palmeri* is typically high with maximum germination occurring within three days at 30°C (Steckel et al. 2004). Seed production ranges from 60,000 (Bensch et al. 2003) to 500,000 seeds m² (Sellers et al. 2003) depending on density and plant size, and birds are the primary mechanism of seed dispersal (Sellers et al. 2003). Field observations of *A. palmeri*'s rooting structure indicate a shallow taproot persists; however, in heavily disturbed areas such as our study islands this plant produces thick lateral roots for stabilization.

*C. strigosus* (false nutsedge) is a perennial, C₃ plant with a facultative wetland (FAC-W) status and wide geographical distribution. It is commonly found in or near pond shores, ditches, disturbed soils, and cropland near rivers (USDA NRCS 2010). Seed germination is rarely documented, this species persists primarily by vegetative growth; however, seed production can exceed 50,000 seeds m² and seeds attain 50% germination (Leck and Schütz 2005). Viability of seed for members of Cyperaceae is typically lost within three years (Leck and Schütz 2005). Rooting strategy is characterized by shallow rhizomes that form dense clusters from which runners can spread (Leck and Schütz 2005).

*X. strumarium* (common cocklebur) is an annual C₃ plant with a facultative wetland (FAC-W) status (USDA NRCS 2010). *X. strumarium* frequents waste places, roadides, and low ground; however, the primary natural habitat is along shorelines of rivers (Löve and Dansereau 1959). Seed germination for *X. strumarium* can be high (~ 78%); viability is greatly reduced after 18 months in natural conditions (Weaver and Lechowicz 1982). Seed production ranges from 500 to as high as 5400 burs plant⁻¹ in optimal garden conditions (Weaver and Lechowicz 1982). The primary modes of seed dispersal are water and animals. Seeds, while afloat, can remain viable for up to thirty days and can be carried vast distances in the fur of animals and on human clothing (Weaver and Lechowicz 1982). *X. strumarium* produces a long tap root with a dense network of finer roots (Reed and Hughes 1970).

We found no literature that examined the study species in a competitive hierarchy framework, but annual species are typically not competitors or tolerators; they are avoiders. The facultative upland status would suggest that *A. palmeri* would be most affected by flood and least affected by drought. Further postulating that if any species exhibited a facilitative relationship it would in fact be *A. palmeri*, as it was more abundant at low elevations than the other species possibly suggesting its range of tolerance was extended. All three species' occurrences (based on individual count data in plots) on the islands were greatest at intermediate elevations (3-6 m, Table 1; but also see Table 2).

**Seed Collection.** Seeds of each species were collected in October 2008 from Dean Island in the lower Mississippi River at river mile 754 (1213 km) (35° 25' 54.9"N, 90° 0' 28.0"W). Seeds were collected from a minimum of five plants for each species that were located at least 20 m apart. All seeds were cold-stratified at 12°C for 2 months and then stored in a dark room for an additional 4 months to ensure seeds had adequate stratification and allowed time to set up the greenhouse for the experiment. For each species, seeds from all sources were mixed before sowing.
Experimental Design. We used a completely randomized greenhouse design to examine the effects of disturbance (Factor 1) and competition (Factor 2) on early seedling growth in different species. Species were analyzed separately, and for each species the experiment included a total of N = 36 pots (3 disturbance treatments [drained, flood, drought] x 2 competition treatments [inter and intraspecific] x 6 replicates). Densities were kept constant for treatments at six individuals pot⁻¹; either planted as a single species (intraspecific competition) or in mixture (two individuals of each species; interspecific competition). In addition, each species was planted alone (one individual pot⁻¹) under the three flooding regimes (see below; n=1). Competition treatment combinations were A6 = 6 A. palmeri plants/pot; C6 = 6 C. strigosus plants/pot; X6 = 6 X. strumarium plants/pot; Mixed = 2 plants/species/pot (n=6). Prior to treatments, 10 individuals [approximately 4 weeks old] of each species were randomly selected and weighed to give total beginning weights for comparison (A. palmeri = 0.1081 g ± 0.029; C. strigosus = 0.0472 g ± 0.011; X. strumarium = 1.18 g ± 0.291; where ± = 1S.D.) Individuals were randomly selected for placement in treatment plots.

Disturbance treatments (Drained [no disturbance], Drought, and Flood) were used to mimic growing season variability in water levels that plants experience on islands within the Mississippi River. For this study, stress was induced by the same resources (oxygen and water) needed by the ‘facilitator’ and the ‘facilitated’ species, if facilitation was occurring, so general paradigms of the SGH may not have held true (Callaway 2007). The first flood began on 24 May 2009 and floods lasted with varying duration until experiment termination on 18 Aug 2009, totaling seven floods (Fig. 1). Average greenhouse temperature for the experiment was 22.5°C. Water levels in flooding tub pots were kept at 5-10 cm above soil surfaces, drained tub pots were watered every other day, and drought tub pots differed based on irrometer (Watermark® Irrrometer Company Inc., Riverside, CA) readings (measured in kilopascals; kPa) due to species-specific water use. Irrrometer’s were randomly placed in two pots per treatment and moisture measurements were taken twenty-one times throughout the experiment. Irrometer readings of 0-10 kPa represent field capacity, 10-30 kPa represent adequate moisture in soils except sands, 30-60 kPa represents time to water, and 60-100 kPa indicates plants are experiencing drought. The average irrometer reading at the ending day of the drought treatment was 76 kPa; both other treatments were maintained between 0 and 30 kPa. Wilting was used to assess when to stop droughts, and X. strumarium was noticeably more wilted than other species each time the drought treatment was ended. At the end of twelve weeks, plants were extracted, separated into module parts, dried for 48 hrs at 80°C and weighed.

Statistical Analysis. We used general linear multiple analysis of variance (PROC GLM MANOVA, SAS 2003) with Type III Sums of Squares to determine the effects of disturbance treatments (flood, drought, and control), competitive effects (interspecific [mixed] = 2 plants of each 3 species/pot; intraspecific = 6 individuals of each species/pot), and their interactions on the dependent variables: root biomass, shoot biomass, root/shoot ratio, and total biomass. The dependent variables were then assessed for normality using Proc Univariate (normal) in SAS to determine if transformations were needed; none were. We then ran a general linear analysis of variance (PROC GLM, SAS 2003) (equivalent to a Two-Way ANOVA) to assess the effects of disturbance and competition on the dependent variables: root biomass, shoot biomass, root/shoot ratio, and total biomass for each species individually. Post-hoc comparisons were made using Tukey’s adjustment for multiple comparisons for each dependent variable.

As another dependent variable, we also quantified the competition intensity using the log Response Ratio (lnRR; Goldberg et al. 1999; also see Bartelheimer et al. 2010) with:

$$\ln RR = \ln (DW_{\text{control}} / DW_{\text{intespecific}})$$

where $DW_{\text{control}}$ are individual plants (one pot⁻¹) subject to each flooding treatment and $DW_{\text{intespecific}}$ are plants grown in pots of two individuals species’ pot⁻¹ examining interspecific competition or six individuals of one species pot⁻¹ examining intraspecific competition. One difference from Bartelheimer et al. (2010) is that we did not have multiple control pots, so our numerator (control) did not have variance. The lnRR was treated in the same statistical manner as the previous dependent variables.

Results

MANOVA results showed four significant main effects, specifically for A. palmeri and X. strumarium for the competition and treatment effects, respectively (Table 3). There were no significant interaction effects. Individual GLM ANOVA’s examined the main effects on plant growth parameters as assessed by root and shoot biomass, root/shoot ratio, total biomass, and lnRR.

Pairwise differences in disturbance effects on root biomass for X. strumarium (Drained vs. Drought P = 0.0001;
Table 3. GLM (Type III Sums of Squares) and GLM MANOVA results for growth response variables. Statistically significant F-values indicated by asterisks: * = P < 0.05, ** = P < 0.0001; indices indicate marginal significance. Abbreviations: comp = Competition treatment; trt = Disturbance treatment, and tub = used as blocking variable. lnRR = log Response Ratio.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num. of</th>
<th>Root Biomass (g)</th>
<th>Shoot Biomass (g)</th>
<th>Root/Shoot Ratio</th>
<th>Total Biomass (g)</th>
<th>lnRR</th>
<th>Pillai’s Trace</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F-value</td>
<td>F-value</td>
<td>F-value</td>
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</tr>
<tr>
<td>comp</td>
<td>1</td>
<td>A. palmeri</td>
<td>2.78</td>
<td>15.72*</td>
<td>0.04</td>
<td>7.04*</td>
<td>16.72*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C. strigosus</td>
<td>0.01</td>
<td>0.56</td>
<td>0.6</td>
<td>0.04</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td></td>
<td>X. strumarium</td>
<td>3.41</td>
<td>61.67***</td>
<td>2.62</td>
<td>15.94*</td>
<td>16.72*</td>
</tr>
<tr>
<td>trt</td>
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<td>A. palmeri</td>
<td>2.68</td>
<td>11.26</td>
<td>2.41</td>
<td>4.15*</td>
<td>26.45***</td>
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<td></td>
<td></td>
<td>C. strigosus</td>
<td>1.26</td>
<td>5.52*</td>
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<td>2.87</td>
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<tr>
<td></td>
<td></td>
<td>X. strumarium</td>
<td>12.03*</td>
<td>15.81***</td>
<td>9.73*</td>
<td>15.29***</td>
<td>53.51***</td>
</tr>
<tr>
<td>tub</td>
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<td>A. palmeri</td>
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<td>0.97</td>
<td>1.05</td>
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<td></td>
<td></td>
<td>C. strigosus</td>
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<td>0.16</td>
<td>0.77</td>
<td>0.55</td>
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<td></td>
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<td>X. strumarium</td>
<td>2.70*</td>
<td>1.3</td>
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<td>comp/tot</td>
<td>2</td>
<td>A. palmeri</td>
<td>1.81</td>
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<td>3.44*</td>
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<td>C. strigosus</td>
<td>0.33</td>
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<td>0.41</td>
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<td>X. strumarium</td>
<td>0.48</td>
<td>0.92</td>
<td>0.12</td>
<td>0.64</td>
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</tr>
</tbody>
</table>

Drained vs. Flood P = 0.0004; Drought vs. Flood P = 0.6373) were significant. Contrarily, A. palmeri and C. strigosus showed no significant differences in response to disturbance or competition treatments (Fig. 2). X. strumarium showed significantly greater root biomass in the drained treatment and grew least in the drought treatment (Fig. 2).

Like root biomass, there were differential responses among competition and disturbance treatments for shoot biomass (Table 3). X. strumarium showed greater overall shoot biomass compared to A. palmeri and C. strigosus regardless of competition or disturbance treatment (Fig. 3). X. strumarium showed significantly greater shoot biomass in drained and drought conditions compared to flood conditions (Fig. 3). Contrarily, C. strigosus accrued more biomass in flooded conditions, significantly greater than in drained or drought (Fig 3). Only X. strumarium and A. palmeri showed a significant competition effect. X. strumarium exhibited greater biomass when grown with conspecifics compared to heterospecifics (Fig 3). A. palmeri, on the other hand, grew better in the presence of heterospecifics (Fig 3).

There was only one significant effect, disturbance, on root/shoot ratio. X. strumarium showed a significantly higher root/shoot ratio when in drained conditions compared to drought or flood (Fig. 4). There was no significant competition effect on root/shoot ratio for any of the species.

Total biomass results were similar to shoot biomass results due to overwhelming shoot biomass compared to root biomass (Table 3; Fig. 5). The only difference was the significant effect of disturbance on A. palmeri, which had significantly greater biomass in drained conditions compared to drought, though the trends were the same (Figs. 3, 5).

Species identity and type of competition significantly influenced lnRR (Table 3). There was a significant effect of disturbance and competition on A. palmeri and X. strumarium (Fig. 6). A. palmeri exhibited a significantly greater interspecific competition effect (larger positive values) than intraspecific competition effect; the difference was noticeably more for the drained treatment than the drought or flood
A. palmeri were affected by disturbance as expected, both performing less under drought and flood disturbance. *X. strumarium* can tolerate flooding at all stages of growth and when grown under anaerobic conditions. *X. strumarium* has been shown to develop larger air spaces in the cortex when grown under aerobic conditions (Kaul 1968); they may also produce adventitious roots from the submerged portion of the stem that float and often become infested with oxygen-producing green algae which aids in aeration (Ambasht 1977) (Plate 1, this study). In a study in the southwestern U.S., *A. palmeri* was found to decrease in abundance as depth to water table increased (Wolden et al. 1995). Our data corroborate the intolerance of *A. palmeri* to drought.

Both annual species were more affected by disturbance; i.e., they were less tolerant than the perennial *C. strigosus*. The flooding treatment was the only factor that affected *C. strigosus* and it performed better. Evolution of tolerance would be expected for longer-lived species (Hegazy and Moser 1991, Heschel and Riginos 2005, Lambers et al. 2008).

Based on changes in interactions along gradients, we expected increased facilitation effects under disturbance. Based on the FAC-U status of *A. palmeri*, we hypothesized it would be the only species (if any) to show a facilitation response. Contrary to prediction, *A. palmeri* apparently was more negatively impacted by competition (specifically interspecific) in drained (control) conditions than *C. strigosus* or *X. strumarium* (least affected). However, *A. palmeri* grew better when with other individuals, especially conspecifics, than when grown independently in flooded conditions. *X. strumarium* had a similar response, growing significantly more when with conspecifics or hertospecifics in flood treatments than when growing alone. Some caution is required in this interpretation, as we did not replicate the single-grown pots, but the interaction deserves further scrutiny. Empirical studies have demonstrated that facilitation increases with environmental harshness (*sensu* stress-gradient hypothesis; Bertness and Callaway 1994, Callaway 1995).

Based on interaction switches along gradients, we expected decreased interspecific competitive effects in dis-

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**Figure 5.** Mean individual total biomass (g) for interspecific and intraspecific competition in different flooding treatments for *A. palmeri*, *C. strigosus*, and *X. strumarium*. Error bars represent ±1 SE. * Denotes significant differences between competition treatments within species P < 0.05. Capital letters indicate significant disturbance effects within species P < 0.05.

**Plate 1.** Adventitious root growth exhibited by *X. strumarium* in flooded treatments.

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**Discussion**

We expected disturbance to decrease the growth of all species, but not by similar amounts due to varying species tolerances. Biologically, the FAC-W species *C. strigosus* and *X. strumarium* performed the best (greatest biomass) which is what we expected based on species’ tolerances. *X. strumarium* and *A. palmeri* were affected by disturbance as expected, both performing less under drought and flood disturbance. *X. strumarium* can tolerate flooding at all stages of growth and when grown under anaerobic conditions. *X. strumarium* has been shown to develop larger air spaces in the cortex when grown under aerobic conditions (Kaul 1968); they may also produce adventitious roots from the submerged portion of the stem that float and often become infested with oxygen-producing green algae which aids in aeration (Ambasht 1977) (Plate 1, this study). In a study in the southwestern U.S., *A. palmeri* was found to decrease in abundance as depth to water table increased (Wolden et al. 1995). Our data corroborate the intolerance of *A. palmeri* to drought.

Both annual species were more affected by disturbance; i.e., they were less tolerant than the perennial *C. strigosus*. The flooding treatment was the only factor that affected *C. strigosus* and it performed better. Evolution of tolerance would be expected for longer-lived species (Hegazy and Moser 1991, Heschel and Riginos 2005, Lambers et al. 2008).

Based on changes in interactions along gradients, we expected increased facilitation effects under disturbance. Based on the FAC-U status of *A. palmeri*, we hypothesized it would be the only species (if any) to show a facilitation response. Contrary to prediction, *A. palmeri* apparently was more negatively impacted by competition (specifically interspecific) in drained (control) conditions than *C. strigosus* or *X. strumarium* (least affected). However, *A. palmeri* grew better when with other individuals, especially conspecifics, than when grown independently in flooded conditions. *X. strumarium* had a similar response, growing significantly more when with conspecifics or hertospecifics in flood treatments than when growing alone. Some caution is required in this interpretation, as we did not replicate the single-grown pots, but the interaction deserves further scrutiny. Empirical studies have demonstrated that facilitation increases with environmental harshness (*sensu* stress-gradient hypothesis; Bertness and Callaway 1994, Callaway 1995).

Based on interaction switches along gradients, we expected decreased interspecific competitive effects in dis-
turbance-competition interaction. While altered competitive abilities along disturbance gradients have been suggested as one mechanism for species coexistence (Grace 1999), our data did not corroborate this concept. An interpretation of the response ratio data may suggest significantly less competition in drought conditions for *A. palmeri* and in flood conditions for *X. strumarium*, the latter to the point of a facilitation as noted above.

Because we found all three species coexisting on Mississippi River islands, we expected stronger intraspecific competition effects than interspecific competition effects. Classic competition theory predicts that under relatively stable environmental conditions (i.e., lack of disturbance) coexistence of species with similar requirements occurs when intraspecific competition is greater than interspecific competition (Goldberg and Barton 1992, Tilman and Pacala 1993). *A. palmeri* appeared to be more affected by heterospecifics than conspecifics, suggesting competitive dominance rather than coexistence. Contrarily for *X. strumarium*, biomass was greater under interspecific competition than intraspecific competition, supporting a niche-controlled coexistence. *X. strumarium* accumulated the greatest total biomass in this study regardless of disturbance or competition treatment suggesting that it was the superior competitor, or at least acquired resources and grew fastest (see Fig. 6). An important agriculture pest, *X. strumarium* competes vigorously with soybean and cotton (Weaver and Lechowicz 1982) and in the southern US soybean yield increased 6% for each 10% reduction in occurrence of *X. strumarium* (Anderson and McWhorter 1976). Unfortunately, these studies did not address *X. strumarium* growing with conspecifics, but it seems from this study and previous studies that *X. strumarium* competes better with others than with itself and this potentially leads to coexistence.

There is another potential explanation for *X. strumarium*’s greater ending biomass. *X. strumarium* had the greatest initial biomass (>10 times). In such dynamic systems, species-level priority effects may play a strong role in shaping plant community structure (Fukami et al. 2005). For our study, possible priority effects would be for rooting space as well as water uptake rates. The advantages for early germination and growth have been shown in numerous studies regarding woody species (see Streng et al. 1989, Jones and Sharitz 1989, Moore and Lacey 2009) and the same patterns likely hold true even for short-lived species as is the case in our study. *X. strumarium* likely benefited from greater exposure to light and less belowground competition that conferred an overall competitive advantage throughout this study.

Within such a stochastic system, chance colonizations are likely occurring. While our evidence suggests competitive effects and varying disturbance tolerance, all three species were found coexisting (at least in some combination with one another) throughout the disturbance gradient. At intermediate elevations on islands, the dominance of *A. palmeri* may be the result of greater propagule pressure since our evidence suggests it is not a great competitor or stress tolerator; *A. palmeri* is capable of producing many more seeds than *C. strigosus* or *X. strumarium*. Propagule pressure has been shown to be very important in assembly of species invading new areas due to the greater likelihood that the population will survive various stochasticities and be adapted to local conditions (sensu Lockwood et al. 2009). For herbaceous species, this would be equivocal to experiments that oversewed native species to prevent exotic invasion and showed a reduction in exotic productivity and seed set (Simmons 2005). The greater numbers of seeds produced may allow *A. palmeri* to exhibit greater propagule pressures on islands. In an effort to quantify the propagule numbers (i.e., seed bank), we took soil cores at different elevations on the islands and found no seed bank, suggesting no seed bank is formed, as seeds either germinate or are otherwise removed from the soil every year. The lack of growth under simulated flood and drought conditions suggests that dispersal and chance factors control the distribution of *A. palmeri* on Mississippi River islands and not its competitive abilities.

We attribute the lack of response to disturbance and competition by *C. strigosus* to its perennial life style and study design. In natural ‘optimal’ conditions, *C. strigosus* can attain dense monocultures and can reach 1 m in height (Moore pers. obs.). Our explanation of this would be that in potted conditions, *C. strigosus’* rhizomes cannot spread as they would in more natural conditions, thus greatly limiting its growth. Another possibility is that our experiment did not fully induce a ‘stressful’ situation which would have released *C. strigosus* from competition with *A. palmeri* and *X. strumarium* and showed increased biomass accumulation, especially in flooded treatments. *C. strigosus* was also the only perennial species in our experiment, and perhaps its tolerance is not based on differences in growth, but simply survivorship. Persistence is a major life history characteristic for many clonal plants (Eriksson and Jerling 1990).

In conclusion, it is apparent that flooding alters the competitive abilities of some plants, but that the effects of the disturbances themselves were stronger than species interactions. We found some evidence of facilitation, but the effect was not strong. We did see an increase in competition with decreased severity of environmental stress (i.e., drained conditions) for *A. palmeri* and *X. strumarium* (Fig. 6). Based on our results, we would predict that *X. strumarium* would dominate lower portions of the hydrologic gradient on islands due to its greater growth and sprouting adventitious roots to cope with anoxia. It is important to note, however, that these islands experience longer periods of drought than flooding and that could be limiting the natural distribution of *X. strumarium*. Our data suggest this may likely be the case, as *X. strumarium* accrued less biomass in all drought treatments. Coupled with this is the fact that during high water events *X. strumarium* seeds are distributed via water and during low water periods the seeds rely on allochthonous dispersal mechanisms (Weaver and Lechowicz 1982). During these low water periods seeds that remain near the ‘mother’ plant will be competing for the same resources as other conspeci-
tics and, as our data show, will limit their own growth. The other dominant we would expect is *C. strigosus*, due to its tolerance to both flooding and drought and its tolerance to competition. Despite this expectation based on niche constraints, *A. palmeri* dominates communities on these islands, and clearly suggests dispersal and chance play a major role in community assembly. Although this study is limited by the fact that it was conducted in a greenhouse, we do show evidence of the dynamic nature of these island systems and how disturbance affects species’ interactions. Our results indicate that factors other than competition, facilitation, and flood tolerance (e.g., priority effects) may be controlling island plant community dynamics.

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**References**


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