



Fragmentation of the invasive, clonal plant *Alternanthera philoxeroides* decreases its growth but not its competitive effect



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ABSTRACT

Clonal integration and fragmentation are potentially competing advantages of clonal growth. Clonal fragmentation can increase the dispersal of ramets, but it prevents physiological integration, which can increase the growth of clones and may increase their competitive effect on other plant species. We tested whether fragmentation can reduce the competitive effect of invasive clonal plants within mixed communities and whether this effect of fragmentation is greater under conditions in which the competitive effect of a clonal plant is greater. We constructed wetland communities each consisting of four common, co-occurring, mainly aquatic plant species under flooded and unflooded conditions, and compared the growth of the species with and without intact or fragmented groups of ramets of the widespread, amphibious, invasive clonal plant *Alternanthera philoxeroides*. We measured the community-level competitive effect of *A. philoxeroides* on the four aquatic plant species. Fragmentation reduced mass accumulation of *A. philoxeroides*, but did not reduce its competitive effect, either under flooded or under unflooded conditions. One explanation is that *A. philoxeroides* was able to maintain production of new ramets when fragmented. Clonal plants may thus mitigate trade-offs between the potential ecological advantages of physiological integration and fragmentation by maintaining rates of vegetative reproduction after fragmentation, even when total growth is reduced.

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1. Introduction

Clonal growth, i.e. the production of new potentially physiologically independent units (ramets) that stay connected to the parent at least until establishment (De Kroon and van Groenendael, 2007), can serve potentially competing functions. Maintaining connections after establishment forms groups of ramets that are often physiologically integrated. In many clonal species, connected ramets can exchange signals and resources such as water, nutrients, and carbohydrates, and thereby increase their collective performance and survival (e.g., Roiloa et al., 2007; De Kroon et al., 2009; Kui et al., 2013; Song et al., 2013; Touchette et al., 2013; You et al., 2014a; Roiloa et al., 2014; Luo and Zhao, 2015; Johansen et al., 2016). On the other hand, fragmentation of groups by breakage or senescence of connections can form vegetative propagules that disperses more

readily and widely than intact groups of ramets (e.g., Boedeltje et al., 2008; Dong et al., 2012; Lin et al., 2012; Roiloa and Retuerto, 2016).

One important but little studied aspect of the potential trade-offs involved in the fragmentation of plant clones is the possible effect of fragmentation on the competitive ability of clonal plants within mixed communities of plant species (Li et al., 2015). If clonal integration promotes growth and if the promotion of growth increases competitive effect, then fragmentation should reduce the competitive effect of clones. Roiloa et al. (2010) observed that the negative effect of fragmentation on clonal performance was greater when clones experienced more intense competition, suggesting that loss of integration can decrease performance of clonal plants in response to competition. A number of studies have measured the effect of fragmentation, i.e., the severance of physical connections between ramets within clones, on the ability of clonal plants to grow from the open into stands of other plants (e.g., Wang et al., 2008; Yu et al., 2009; Xiao et al., 2011; You et al., 2014b, 2016). However, very few studies have directly tested whether fragmentation can decrease the competitive effect of clonal plants within plant communities (Li et al., 2015).

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Another area of uncertainty relates to how the effect of fragmentation on the competitive effect of clonal species may differ between habitats (Schooler et al., 2012). For example, many of clonal plant species is strongly amphibious and grow well in both aquatic and terrestrial habitats, that is, under flooded and unflooded conditions (Schooler et al., 2007; Rhazi et al., 2009; Lin et al., 2012). The competitive effects of these strongly amphibious species on co-occurring species that are mainly aquatic and only weakly amphibious seem likely to be greater in terrestrial than in aquatic habitats, because the fitness of the weakly amphibious species may be lower in terrestrial than in aquatic habitats whereas the fitness of the strongly amphibious species may be similar in the two types of habitats. Fragmentation of the strongly amphibious species and associated reduction of its competitive effect on weakly amphibious species could therefore have a greater effect in terrestrial than in aquatic habitats. More generally, fragmentation of a clonal plant species may reduce its competitive effect more in cases where its competitive effect when not fragmented is higher.

To test the hypotheses (1) that fragmentation of a clonal plant species will decrease its community-level competitive effect on other plant species and (2) that fragmentation of a clonal plant species will reduce its competitive effect more in environments where its competitive effect when not fragmented is higher, we conducted a greenhouse experiment using the widespread, amphibious clonal species *Alternanthera philoxeroides* and a mixture of four common, mainly aquatic species that co-occur with *A. philoxeroides* in some wetlands in China. To test the first hypothesis, we predicted that (1) fragmentation would decrease the growth of *A. philoxeroides*; (2) the other four species would grow less in the presence than in the absence of *A. philoxeroides*; and (3) fragmenting *A. philoxeroides* would reduce this competitive effect. To test the second hypothesis, we predicted that (1) *A. philoxeroides* would grow equally well under flooded and unflooded conditions; (2) the other four species would grow better under flooded than under unflooded conditions; (3) the competitive effect of *A. philoxeroides* when not fragmented on the other four species would be smaller under flooded than under unflooded conditions; and (4) the negative effect of fragmentation on the competitive effect of *A. philoxeroides* on the other four species would be smaller under flooded than under unflooded conditions.

2. Materials and methods

2.1. Species and propagation

Alternanthera philoxeroides (Mart.) Griseb., or alligator weed, hereafter referred to as *Alternanthera*, is a herbaceous, perennial, amphibious, clonal plant in the Amaranthaceae native to South America (Geng et al., 2007; Xu et al., 2010). It is widespread in many countries where it has been introduced (Julien et al., 1995; Wang et al., 2008), including China, where it is highly invasive in both aquatic and terrestrial habitats (Ma and Wang, 2005; Pan et al., 2007). The prostrate to ascending stems of *Alternanthera* can produce leaves, side branches, and roots at each node, which thus corresponds to a ramet. Stems can grow up to 10 m long, and fragments as small as a single stem node can serve as vegetative propagules (Dong et al., 2012). Fragmentation of *Alternanthera* potentially occurs through senescence or disturbance caused by factors such as grazing, trampling, water movement, transportation vessels, and herbicides (Averill et al., 2010; Dong et al., 2012; Zhang et al., 2014).

Four emergent plant species were selected to measure the competitive effect of *Alternanthera* in wetland communities: *Acorus calamus* L., *Butomus umbellatus* L., *Iris wilsonii* C. H. Wright, and *Pontederia cordata* L. These are common, perennial herbs that

co-occur with *Alternanthera* in Xixi National Wetland Park and other semi-natural wetlands in China (Cao et al., 2011; Hong-Li Li, personal observation). Like *Alternanthera*, each of these species is a perennial, clonal herb. All four species are rhizomatous and can form a shallow, dense network of rhizomes (Hroudová et al., 1996; Vojtíšková et al., 2004; Lu and Huang, 2012). Plant height in natural populations is 50–80 cm in *A. calamus*, 30–120 cm in *B. umbellatus*, 50–60 cm in *I. wilsonii*, and 80–150 cm in *P. cordata* (www.efloras.org).

In early May 2011, ramets of *Alternanthera* were collected from six different sites in Xixi National Wetland Park in Hangzhou, Zhejiang Province, China; sites were at least 200 m away from each other. Ramets were brought to a greenhouse at the Forest Science Company, Beijing Forestry University, Beijing, China and propagated vegetatively. The substrate used for propagation was a mixture of sand and peat. Plants of the other four wetland species were purchased from Beijing Tianbei Waterscape Gardening, Ltd., and propagated vegetatively during May 2011 in the same greenhouse under ambient light and temperature. Single stem nodes of *Alternanthera* and single ramets of the other four species were grown in a 1:4 (v/v) mixture of soil collected from the shore of Yeya Lake near Beijing and river sand purchased from a construction company. The mixture contained 0.23 (0.02) mg total N g⁻¹ dry mass of soil (mean [SD; N = 3]), 0.58 (0.07) mg total P g⁻¹, 1.71 (0.05) mg K g⁻¹, and 5.5 (1.38) mg organic matter g⁻¹, based on analysis at the Institute of Agricultural Economics and Development of the Chinese Academy of Agricultural Sciences in Beijing.

On 6 June 2011, once the axillary stem produced from each node of *Alternanthera* was about 20 cm long, plants of all five species were considered ready to transplant in a vertical position into 48 opaque plastic containers that were each 50 cm in diameter, 60 cm deep, and filled to 25 cm with the soil mixture described above. Each container received three single ramets of each of the four species other than *Alternanthera*, arranged such that each species occupied the same positions in each container (Fig. 1). A mixture of species was used in this study to focus on the community-level, competitive effects of *Alternanthera*; wetlands inhabited by *Alternanthera* in China generally include a mixture of other species. Two-thirds of the containers also received five plants of *Alternanthera* (Fig. 1). Each of these plants had 6–7 nodes and was planted with the two most basal nodes at least 2 cm below the soil surface. Containers were arranged in the greenhouse into eight blocks (replicates). There were six containers in each block, which were randomly assigned to six treatments (i.e. four treatments with and two treatments without *Alternanthera*) as described below.

2.2. Experimental design

After one week of establishment, on 13 June 2011, one container within each block was randomly assigned, within the constraint of already having or not having plants of *Alternanthera*, to each one of six treatment combinations, three *Alternanthera* treatments (absent, intact, or fragmented) crossed with two flooding treatments (not flooded or flooded). For the treatment with no flooding, containers were given enough tap water to just saturate the soil 2–3 times per week. Water was added slowly to the containers, and the soil was considered to be saturated when additional water would not drain into the soil. For the flooded treatment, containers were kept filled with tap water to a depth of 30 cm above the soil surface. For the fragmented treatment, each stem of *Alternanthera* that was at least 20 cm long was severed just distal to the fourth or fifth node at the start of the experiment. All stems that had newly reached at least 20 cm in length were similarly severed every two weeks thereafter. The detached, apical portion of the stem was allowed to fall on the soil in the unflooded treatment or to float in the flooded treatment to mimic the occurrence of this process in

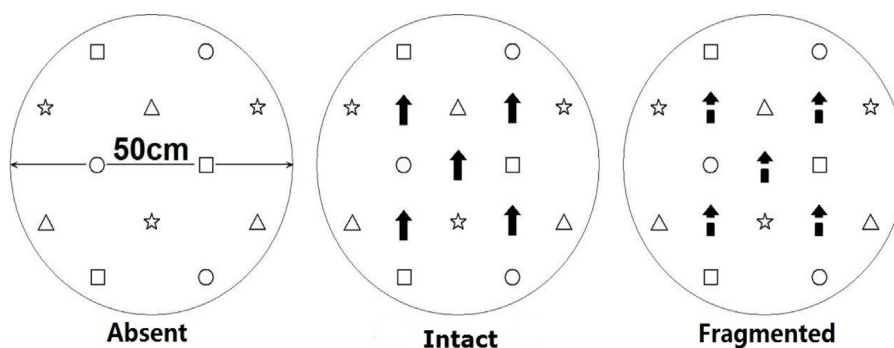


Fig. 1. Experimental design. Mixtures of three plants of each of four wetland species (open symbols: star – *Pontederia cordata*; circle – *Acorus calamus*; triangle – *Iris wilsonii*; square – *Butomus umbellatus*) were subjected to three treatments with *Alternanthera philoxeroides* (filled arrows: absent – no plants of *Alternanthera* added; intact – five plants of *Alternanthera* added; fragmented – five plants of *Alternanthera* added and periodically fragmented). These treatments were crossed with two flooding treatments (not shown; not flooded – 0 cm water depth; flooded – 30 cm water depth).

natural populations (Dong et al., 2012; Touchette et al., 2013). All containers were sprayed weekly with an insecticide (Hua Chong Yi Ci Jing, Zhenjiang Peilei Organic Fertilizer, Ltd.) prepared by dissolving 10 g of powder containing 10% imidacloprid in 3 L of water. The mean temperature and relative humidity in the greenhouse during the experiment were respectively 23.8 °C and 76%. Light intensity in the greenhouse was about 80% of the natural light outside the greenhouse; no additional light was provided.

2.3. Measurements and data analysis

After 12 weeks, on 30 August 2011, the surviving plants of *Alternanthera* (including all fragments in each container) were harvested, measured for total number of ramets and total stem length, separated into leaves, stems and roots, dried at 70 °C for at least 48 h, and weighed. Specific stem length (cm g^{-1}) was calculated as total stem length divided by total stem dry mass, and root to shoot ratio as root dry mass divided by shoot dry mass. The surviving plants of each of the other species in each container were separated into shoots and roots, similarly dried and weighed. In one container, one native species (*B. umbellatus*) died completely. In the remaining 47 containers, all the four native species survived.

To measure the community-level competitive effect of *Alternanthera*, we calculated a log response ratio (Dibble et al., 2013), $\text{LnRR} = \ln(B_0/B_1)$, where B_0 is total dry mass of the four species (*A. calamus*, *B. umbellatus*, *I. wilsonii* and *P. cordata*) in the absence of *Alternanthera* in a block, and B_1 is that of the four species in the presence of intact or fragmented *Alternanthera* in that block. Log response ratios are widely used in ecology to quantify effects including those of competition, in part because they often meet assumptions for statistical analysis better than alternative measures (Hedges et al., 1999; Dibble et al., 2013).

Data were analyzed in SPSS 17.0 (SPSS, Chicago, Illinois, USA). To test effects of treatments on *Alternanthera*, ANOVAs were run with a block effect, fragmentation (intact or fragmented) and flooding (unflooded or flooded) as fixed effects, and total dry mass, leaf mass, stem mass, root mass, total stem length, total number of ramets, specific stem length, or root to shoot ratio by mass as the dependent variable. To test effects of treatments on the four wetland species other than *Alternanthera* combined and individually, ANOVAs were run with a block effect, flooding and *Alternanthera* (absent, intact, or fragmented) as fixed effects, and total mass as the dependent variable. An ANOVA was also run to test effects of block, fragmentation and flooding on the competitive effect (LnRR) of *Alternanthera* at the community level. All the data met the assumptions of ANOVA. Differences between individual means were tested with *post hoc* Tukey tests. Values of *P* from ANOVAs are presented without

adjustment for number of tests and should therefore be interpreted with caution.

3. Results

3.1. Effects of fragmentation and flooding on *Alternanthera*

Consistent with predictions, fragmentation of *Alternanthera* reduced its final dry total mass, stem mass, and root mass by about 40–50% (Fig. 2A–C and Table 1). However, fragmentation reduced leaf mass only when plants were flooded (Fig. 2D and Table 1) and had little effect on final total stem length or number of ramets (Fig. 2E and F and Table 1). As a result, specific stem length was much greater in fragmented than in intact plants (Fig. 2H and Table 1).

As expected, flooding did not alter total accumulation of mass of *Alternanthera* (Fig. 2A and Table 1). However, flooding increased final stem mass (Fig. 2B and Table 1) and decreased final root mass (Fig. 2C and Table 1), root to shoot ratio (Fig. 2G and Table 1) and specific stem length (Fig. 2H and Table 1).

3.2. Effects of *Alternanthera* and flooding on other species

Also consistent with predictions, the combined final total dry mass of the four species of plants other than *Alternanthera* was about 40–60% lower when *Alternanthera* was present than when it was absent (Fig. 3A and Table 2). As predicted, the combined mass of the other species was about 20–50% higher when they were flooded than when they were not (Fig. 3A), and the competitive effect of *Alternanthera* was lower in the flooded than in the unflooded treatment (Fig. 3B).

Contrary to predictions, fragmentation of *Alternanthera* did not affect the combined final mass of the other four species (Fig. 3A) nor the community-level competitive effect of *Alternanthera* (Fig. 3B). Accordingly, the effect of fragmentation on the competitive effect of *Alternanthera* did not differ between flooded and unflooded treatments (Fig. 3B).

Individually, the four species competing with *Alternanthera* generally showed qualitatively similar effects of *Alternanthera* and flooding (Fig. 4 and Table 2): most species accumulated much more total dry mass when *Alternanthera* was absent than when it was present, and more mass when flooded than when not flooded. The main exceptions were that the presence of *Alternanthera* did not significantly affect *A. calamus* and that flooding did not affect *I. wilsonii* (Fig. 4B and C and Table 2). The fragmentation of *Alternanthera* had no significant effect on total dry mass of any of the four species (Fig. 4).

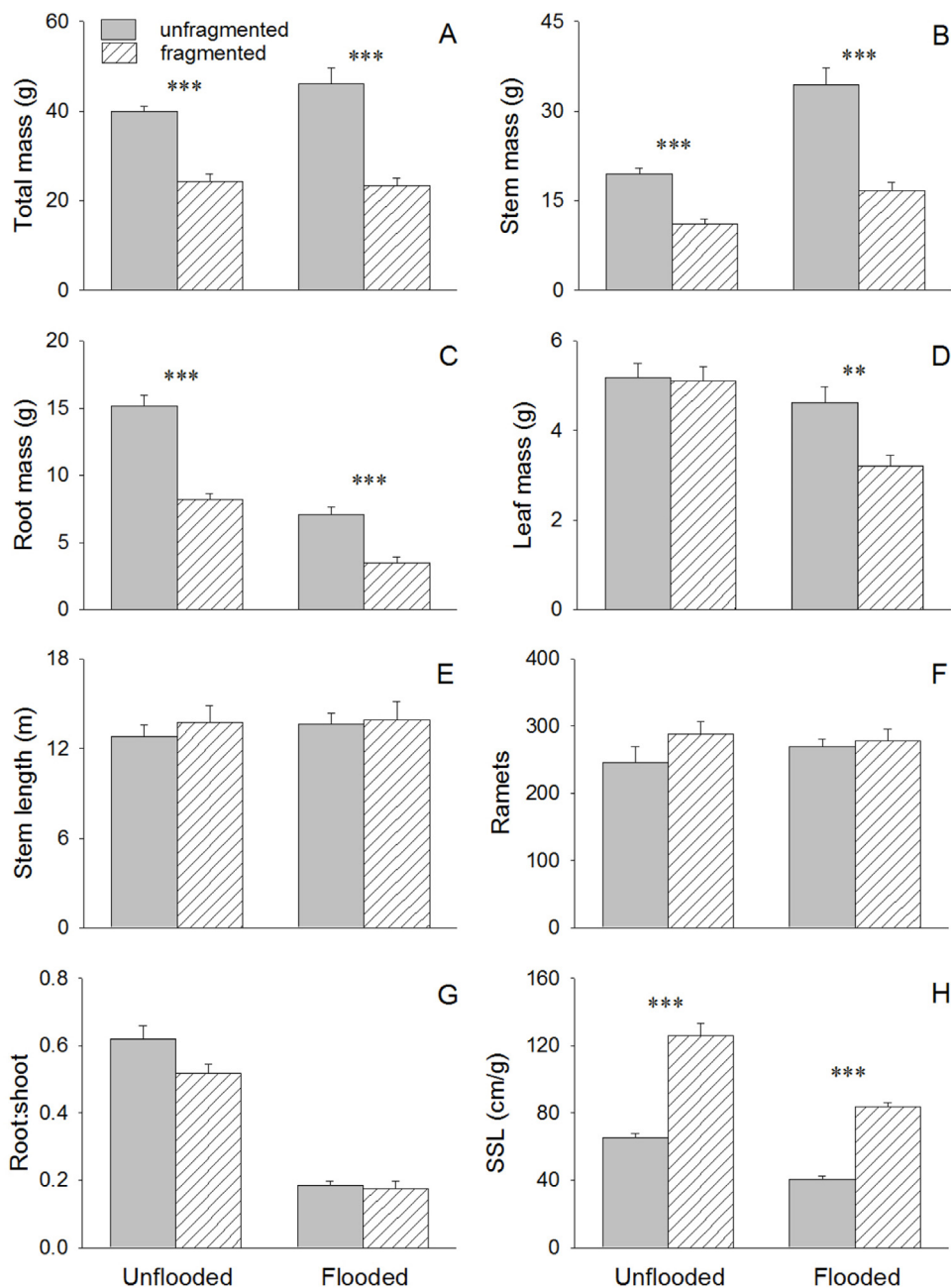


Fig. 2. Effects of fragmentation and flooding on dry mass and size (mean+SE, n=8) of *Alternanthera philoxeroides*: A – total mass; B – stem mass; C – root mass; D – leaf mass; E – total length of stems; F – number of ramets; G – root to shoot ratio; H – specific stem length (SSL, cm length g^{-1} mass). Symbols above pairs of bars give *P* (Tukey's tests: no symbol, $P>0.05$; **, $P=0.001-0.02$; ***, $P<0.001$) that means of fragmentation treatments did not differ within flooding treatments. See Table 1 for ANOVAs.

Table 1
ANOVAs of effects of fragmentation and flooding on final dry mass and size of *Alternanthera philoxeroides*. Values are in bold if $P<0.01$ and in italics if $P<0.05$. See Fig. 2 for data.

Measure	Block		Fragmentation (Fr)		Flooding (Fl)		Fr × Fl	
	<i>F</i> _{7,21}	<i>P</i>	<i>F</i> _{1,21}	<i>P</i>	<i>F</i> _{1,21}	<i>P</i>	<i>F</i> _{1,21}	<i>P</i>
Total mass	2.14	0.084	103.17	<0.001	1.94	0.178	3.75	0.066
Stem mass	1.55	0.204	71.45	<0.001	43.81	<0.001	8.98	0.007
Root mass	2.92	<i>0.027</i>	119.40	<0.001	175.47	<0.001	11.86	0.002
Leaf mass	2.40	0.057	7.73	<i>0.011</i>	21.29	<0.001	6.30	<i>0.020</i>
Ramet number	1.33	0.286	2.06	0.166	0.15	0.706	0.85	0.368
Stem length	1.07	0.417	0.39	0.541	0.27	0.607	0.12	0.732
Root:shoot ratio	2.15	0.082	1.51	0.232	139.31	<0.001	0.14	0.713
SSL ^a	1.50	0.221	183.80	<0.001	77.64	<0.001	5.13	<i>0.034</i>

^a Specific stem length.

Table 2

ANOVAs of effects of *Alternanthera* and flooding on final total dry mass of other wetland species. Values are in bold if $P < 0.01$ and in italics if $P < 0.05$. See Figs. 3 and 4 for data.

Species	Block		<i>Alternanthera</i> (A)		Flooding (F)		A × F	
	$F_{7,35}$	<i>P</i>	$F_{2,35}$	<i>P</i>	$F_{1,35}$	<i>P</i>	$F_{2,35}$	<i>P</i>
<i>Pontederia cordata</i>	1.81	0.117	35.99	<0.001	32.68	<0.001	0.84	0.440
<i>Acorus calamus</i>	0.69	0.681	0.54	0.590	12.04	<0.001	0.29	0.753
<i>Iris wilsonii</i>	1.25	0.302	18.92	<0.001	<0.01	0.999	0.88	0.422
<i>Butomus umbellatus</i>	2.29	<i>0.049</i>	23.98	<0.001	21.81	<0.001	0.63	0.539
Species combined	1.36	0.252	70.34	<0.001	45.24	<0.001	0.82	0.447

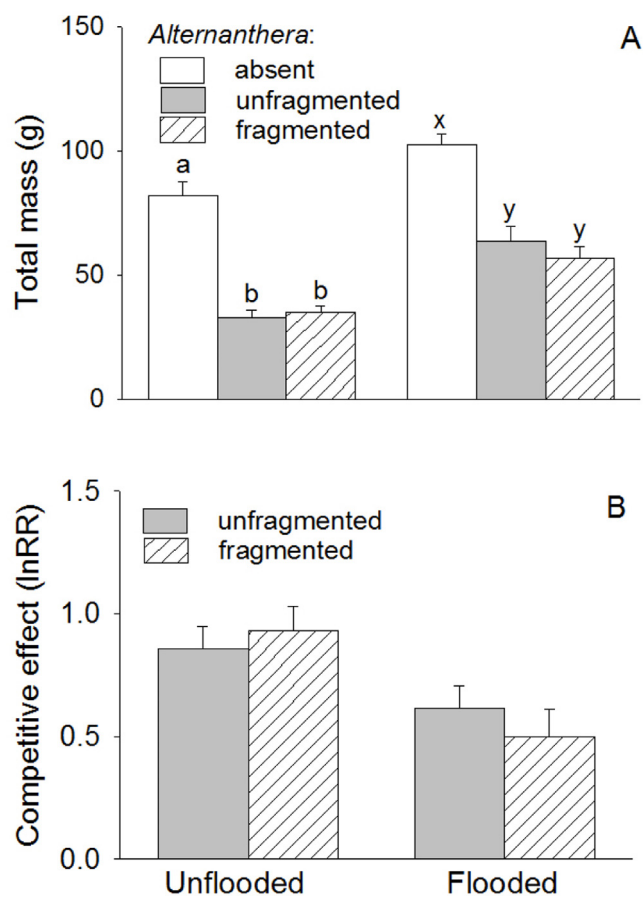


Fig. 3. Effects of *Alternanthera* and flooding on other species combined (mean + SE, $n = 8$): A) final total dry mass (See Table 2 for ANOVA); B) competitive effect (log response ratio of total mass; mean + SE, $n = 8$). Different letters above bars show which means differed within flooding treatments (Tukey tests; $P = 0.05$). Competitive effect differed between flooding treatments ($F_{1,28} = 11.93$; $P = 0.002$) but not between fragmentation treatments ($F_{1,28} = 0.06$; $P = 0.8$) or due to interaction between flooding and fragmentation ($F_{1,28} = 0.94$; $P = 0.3$).

4. Discussion

Results clearly failed to support either the hypothesis that fragmentation of a clonal plant species will decrease its competitive effect on other plant species or the hypothesis that the negative effect of fragmentation on competitive effect will be greater in environments where the competitive effect of unfragmented clones is greater. Since fragmentation prevents clonal integration, results did not suggest that physiological integration increases competitive ability in clonal plants.

This negative result cannot be explained by lack of an effect of fragmentation on the accumulation of mass by *Alternanthera*, of a competitive effect of *Alternanthera* on the other species, or of an effect of flooding on growth of these other species. On the contrary, results did meet each of the underlying predictions (1)

that fragmentation would reduce the accumulation of mass by *Alternanthera*, (2) that the presence of *Alternanthera* would reduce the accumulation of mass by the four other species with which it was grown, (3) that *Alternanthera* would accumulate similar mass under flooded and unflooded conditions, (4) that the other four species would accumulate more mass under flooded than under unflooded conditions, and (5) that the community-level competitive effect of *Alternanthera* would be smaller under flooded than unflooded conditions.

Instead, one explanation for the ability of *Alternanthera* to maintain the same competitive effect on other species despite fragmentation and associated reduction in growth in total mass may be its apparent ability to maintain vegetative reproduction regardless of fragmentation. There is considerable evidence that competition in plants can depend on factors other than size or mass (e.g., Goldberg and Landa, 1991; Warren et al., 2002; Weigelt et al., 2002; Cahill, 2003; Semchenko et al., 2013). It therefore seems plausible that the competitive effect in *Alternanthera* might depend upon number of ramets and spread of stems rather than just on total mass. If so, maintaining vegetative reproduction and spread despite fragmentation could avoid a trade-off between dispersal and competitive effect in clonal plants.

To test the generality of this new hypothesis, future studies should address whether many other clonal plant species maintain ramet production when fragmented even in competitive environments and whether ramet number is a major factor in the competitive effect of many clonal species growing within mixed communities. Additional studies could also consider whether fragmentation and growth form interact to help determine the competitive effect of clonal plants; we tested only effect of a stoloniferous clonal species on rhizomatous ones. It is known that fragmentation in the absence of competition can induce production of more numerous, small ramets in *Alternanthera* (Dong et al., 2012) and *Eichhornia crassipes* (P. Alpert, unpublished data). There are several studies of the role of physiological integration in competition in clonal plants (e.g., Hartnett and Bazzaz, 1985; Schmid and Bazzaz, 1987; Hartnett, 1993; Pennings and Callaway, 2000; Peltzer, 2002). However, most recent studies have tested only ability to grow between areas with no and some competition (e.g., Wang et al., 2008; Yu et al., 2009; Xiao et al., 2011; You et al., 2014a), and only one has considered ramet number as a factor in competition (You et al., 2016).

One final caveat is that, although this study attempted to provide a relatively realistic test of the hypotheses through choice of conditions and species, fragments were not allowed to disperse out of experimental containers, as they might disperse away from a local area in a natural wetland subject to water flow. This would be expected to reduce the local, if not the global, competitive effect of clones. Given the results from this and other studies, a challenging, useful expansion of work on clonal growth and competition will be research that integrates the dispersal, fragmentation, and physiological integration of clones to advance understanding of how some clonal species achieve such remarkable dominance, especially in wetlands.

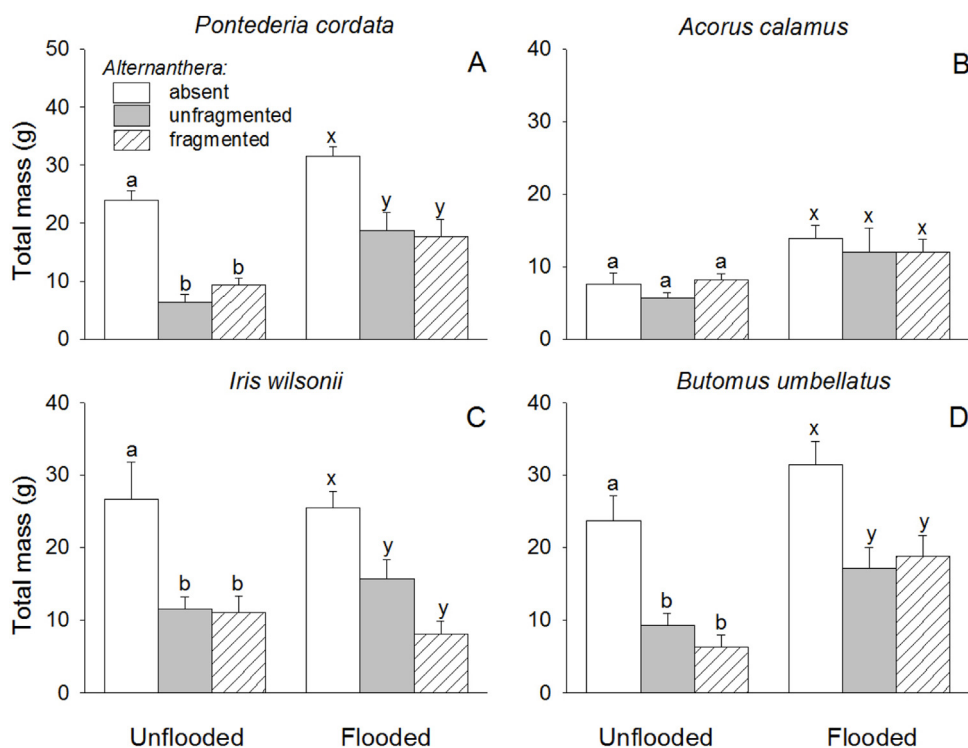


Fig. 4. Effects of *Alternanthera* and flooding on final total dry mass (mean + SE, n=8) of other wetland species individually. Different letters above bars show which means differed within flooding treatments (Tukey tests; $P=0.05$). See Table 2 for ANOVAs.

In conclusion, our results do not support the idea that physiological integration between connected ramets within clones necessarily increases their ability to compete with other plant species. Instead, clonal plants may mitigate loss of total growth due to loss of integration when fragmented by maintaining rates of vegetative reproduction.

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