



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



Jian Zhou<sup>a,b,1</sup>, Hong-Li Li<sup>a,1</sup>, Peter Alpert<sup>c</sup>, Ming-Xiang Zhang<sup>a</sup>, Fei-Hai Yu<sup>a,\*</sup>

<sup>a</sup> College of Nature Conservation, Beijing Forestry University, Beijing 100083, China

<sup>b</sup> Beijing Key Laboratory of Wetland Ecological Function and Restoration, Institute of Wetland Research, Chinese Academic of Forestry, Beijing, 100091, China

<sup>c</sup> Biology Department, University of Massachusetts, Amherst, MA 01003-9297, USA

## ARTICLE INFO

### Article history:

Received 13 October 2016

Received in revised form 10 January 2017

Accepted 17 January 2017

Edited by Hermann Heilmeyer

Available online 20 January 2017

### Keywords:

Clonal growth

Competition

Flooding

Physiological integration

Vegetative reproduction

Wetland communities

## 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).

\* Corresponding author.

E-mail address: [feihaiyu@bjfu.edu.cn](mailto:feihaiyu@bjfu.edu.cn) (F.-H. Yu).

<sup>1</sup> These authors contribute equally.

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](http://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<sup>-1</sup> dry mass of soil (mean [SD]; N = 3), 0.58 (0.07) mg total P g<sup>-1</sup>, 1.71 (0.05) mg K g<sup>-1</sup>, and 5.5 (1.38) mg organic matter g<sup>-1</sup>, 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

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