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## Phenotypic plasticity in resource allocation to sexual trait of alligatorweed in wetland and terrestrial habitats

Jialiang Zhang<sup>a</sup>, Wei Huang<sup>b,c,\*</sup>, Jianqing Ding<sup>d,\*\*</sup>

<sup>a</sup> Hubei Key Laboratory of Economic Forest Germplasm Improvement and Resources Comprehensive Utilization, Hubei Collaborative Innovation Center for the Characteristic Resources Exploitation of Dabie Mountains, Huanggang Normal University, Huanggang 438000, Hubei, China

<sup>b</sup> CAS Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, Hubei, China

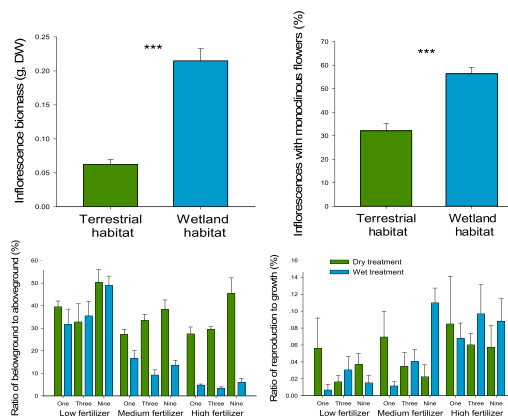
<sup>c</sup> Center of Conservation Biology, Core Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, Hubei, China

<sup>d</sup> State Key Laboratory of Crop Stress Adaptation and Improvement, School of Life Sciences, Henan University, Kaifeng 475004, Henan, China

### HIGHLIGHTS

- Environmental heterogeneity affected resource allocation of invasive alligatorweed.
- High resource availability increased resource allocation to sexual trait.
- Low resource availability increased resource allocation to clonal growth.
- Phenotypic plasticity in resource allocation may facilitate alligatorweed invasion.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Environmental heterogeneity in resource availability affects invasive plant reproductive strategies and resource allocation to reproduction. Here, we conducted two field surveys to examine the effect of wetland and terrestrial habitats on inflorescence production and resource allocation to inflorescence of the amphibious invasive plant *Alternanthera philoxeroides* in its invasive range (China). We also specifically examined the effects of water availability, fertilizer application, and plant density (space) in a greenhouse experiment. In field surveys, inflorescence biomass, normal monoclinal flowers and ratio of inflorescences to shoots of plants from wetlands were about 2.4-, 0.8- and 1.3-fold higher than those from terrestrial habitats, respectively. In greenhouse experiment, plants with higher fertilizer application and lower competition conditions produced more inflorescences, and had a lower ratio of roots to shoots and a comparable ratio of inflorescences to shoot and root. Furthermore, water availability had a significant interactive effect when combined with fertilizer level or plant density on inflorescence production and resource allocation. Together, our results indicate that high resources, such as those found in wetland habitats, favor both vegetative growth and sexual trait in *A. philoxeroides*. However, in terrestrial habitats where resources are relatively poor, the invader can adapt to the environment by allocating more resources to vegetative growth for clonal reproduction and less resources for sexual trait. This phenotypic plasticity in resource allocation likely facilitates the plant to invade heterogeneous wetlands and terrestrial environments.

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\* Correspondence to: W. Huang, CAS Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, Hubei, China.

\*\* Corresponding author.

E-mail addresses: [huangwei0519@wbgcas.cn](mailto:huangwei0519@wbgcas.cn) (W. Huang), [jding@henu.edu.cn](mailto:jding@henu.edu.cn) (J. Ding).

## 1. Introduction

The invasion success of exotic plants largely relies on resources availability and their reproductive capacity (Goldstein and Suding, 2014; Jaspers et al., 2018). During the initial invasion and long-term establishment in a novel invasive habitat, the environmental conditions can determine the relative success of competing reproductive strategies (Silva et al., 2020). Resource availability in heterogeneous environment not only influences the reproductive strategies (Giesel, 1976; Fu et al., 2010) but also affects the resource allocation to reproduction (Bloom et al., 1985; Müller et al., 2000).

Some invasive plants can reproduce sexually through seeds and clonally through vegetative propagules (Eckert and Barrett, 1993; Ortega-Baes and Gorostiague, 2013; Lin et al., 2016). Sexual reproduction is important for invasive plants to disperse over long distances or endure adverse environments in the long term (Dong et al., 2006; Grimsby et al., 2007; Albert et al., 2015), while clonal propagation is vital in the short term to maintain, survive, expand, and occupy ecological niches in changeable environments (Castro et al., 2016; Lin et al., 2016). In heterogeneous environments, plants change their resource allocation in response to resource availability, and resource allocation patterns largely determine the ability of plants to produce clonal and sexual offspring (Bloom et al., 1985; Schmid and Weiner, 1993). Under lower nutrition conditions, plants generally allocate more resources to roots and reduce sexual investment, while under higher nutrition conditions, plants often have more sexual reproductive organs and a lower root to shoot ratio (Müller et al., 2000; Wang et al., 2019). The shift between two reproduction strategies of an invasive plant can affect the processes and consequences of invasion (Barrett et al., 2008; Castro et al., 2016). Therefore, knowledge of the main reproductive strategies and resource allocation patterns to reproduction that invasive plants adopt in different environments is the key to understanding plant invasion success and management.

Many factors have the potential to affect plant reproductive strategies and resource allocation patterns to reproduction, such as space (light), temperature, water, and nutrition (Gleeson and Tilman, 1992; Tassin et al., 2007). For instance, under lower light and temperature as well as dry and windy conditions, *Trias verrucosa* maintains its population by shortening the period of florescence and shifting allocation from sexual to clonal reproduction (Liu et al., 2007). These factors can also affect invasive plant reproductive strategies and resource allocation patterns to reproduction. For example, water availability is an important factor that affects the reproductive mode of the invasive plant *Schinus terebenthifolius*, in that it expands and renews its population through clonality in arid areas, while in moist riparian zones, this is through seeds (Tassin et al., 2007). Other than environmental factors, plant traits (size and density) also influence the balance of sexual and clonal reproduction. For example, the invasive wetland plant *Pistia stratiotes* increases both sexual and clonal reproductive structures with increased density, and larger plants allocate more resources to sexual and clonal reproductive structures than smaller plants (Coelho et al., 2005). Invasive plants may face many kinds of heterogeneous environments during invasion, and hence, it is necessary to understand the reproduction of invasive plants under heterogeneous factors, such as water, nutrition, and competition, but few studies consider multiple environmental factors simultaneously.

Alligatorweed, *Alternanthera philoxeroides* (Mart.) Griseb, is native to South America and is widespread in a variety of terrestrial and wetland habitats globally. In its native range, *A. philoxeroides* reproduces by vegetative propagules and viable seeds (Sosa et al., 2004). In its invasive range, it mainly expands through clonal growth (Ye et al., 2003; Liu et al., 2011; Dong et al., 2019). However, in the invasive range of China, many studies showed that *A. philoxeroides* also produces seeds in the field (Zhang et al., 1993; Zhang et al., 2004) and a report from European and Mediterranean Plant Protection Organization (2016) indicated that *A. philoxeroides* can produce viable seeds. These studies

indicated that inflorescence is less like to be a vestigial or redundant organ in the invasive range. However, to date, there is little known about whether and how environmental heterogeneity between terrestrial and wetland habitats affects inflorescence production and resource allocation patterns to inflorescences. In the present study, we examined whether habitat type (wetland or terrestrial) affects *A. philoxeroides* inflorescence production and development of inflorescences. Furthermore, there are significant differences in the availability of water, nutrients, and *A. philoxeroides* density between wetland and terrestrial habitats (van der Valk et al., 1979; Jansson et al., 1994). We then tested the specific contributions of water, nutrients, and plant density to the observed patterns of inflorescence production and resource allocation to inflorescence of *A. philoxeroides* in the field.

## 2. Material and methods

### 2.1. Study species

*Alternanthera philoxeroides* was introduced into China in the 1930s and now occurs in 20 provinces (Ye et al., 2003), ranging from 18.30° to 36.62° N. In central China, *A. philoxeroides* flowers from May to September and can produce monoclinal and/or pistillate flowers (Liu et al., 2011). There are five stamens with yellow anthers around the pistil for monoclinal flowers, while there are five or fewer pistillody stamens without yellow anthers for pistillody flower (Liu et al., 2011; Zhang personal observation). Through observation of stamens and yellow anthers, the development of flowers (normal monoclinal or abnormal pistillate) can be determined easily by eye or with the aid of a magnifying glass (Fig. S1).

### 2.2. Effects of habitats on inflorescence and resource allocation to inflorescence of *A. philoxeroides*

In August 2017, we conducted a field survey across much of the invasive range of *A. philoxeroides* in central and southern China. There were 31 sites spanning 15° of latitude from 21.53° to 36.52° N (Table S1). At each site, we selected a monoculture of *A. philoxeroides* in both terrestrial and wetland habitats to eliminate the possible effect of interspecific competition on inflorescence production. Then, we established a 10-m transect along the roadside in a terrestrial habitat and a 10-m transect along a riverside in a wetland habitat, which were 200–500 m apart. In each transect, we randomly selected five sampling plots (0.5 × 0.5 m) that contained inflorescences of *A. philoxeroides*. We counted and collected all inflorescences. Then, we clipped the shoots at the soil surface within each plot. The inflorescences and shoots were kept separate and dried at 80 °C for 48 h and weighed in the laboratory. In this survey, we did not record the number of *A. philoxeroides* plants because high densities made it logistically impossible to discriminate individuals within each sampling plot.

### 2.3. Effects of habitats on the inflorescence development of *A. philoxeroides*

In August 2018, we conducted another field survey. In total, 43 sites, including 17 from 2017, were selected spanning 15° of latitude from 21.67° to 36.53° N (Table S1). At each site, we established transects in both habitats as described above. Along each transect, we randomly selected 100 inflorescences and determined monoclinal flowers or pistillody flowers.

### 2.4. Effects of water availability, fertilizer application, and plant density on inflorescences, growth and resource allocation of *A. philoxeroides*

We carried out a greenhouse experiment at the Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China, from May to September 2017. The experiment was established as a full factorial experiment with two levels of water availability (dry and wet treatments), three levels of

fertilizer application (low, medium, and high), and three levels of plant density (one, three, and nine plants per tub). There were five replicates for each combination and a total of 90 tubs. The greenhouse had a glass roof and a chain link fence. Thus, the conditions, including temperature and photoperiod, were the same as the surrounding environment, but the effect of precipitation was eliminated.

We collected *A. philoxeroides* plants from a natural population at the Wuhan Botanical Garden and cut stems into 4–5 cm lengths each with one node. Stem cuttings ( $N = 390$ ) were planted vertically in  $50 \times 40 \times 35$  cm plastic tubs filled with a mixture (1:1) of local topsoil and seedling substrate (Klasmann-Deilmann, Geeste, Germany). For low plant density, one stem cutting was planted in the center of the tub. For medium plant density, three stem cuttings were planted in a row along the middle of the tub separated by 10 cm from each other and the tub edge. For high plant density, nine stem cuttings were planted in three parallel rows, and the stem cuttings and rows were separated by 10 cm from each other and the tub edge. After 10 days, we randomly assigned half of the tubs of each plant density to the dry treatment with ~10% soil water content, and the remainder to the wet treatment with ~40–50% soil water content. During the experiment, we added water as needed to maintain the water treatments. Furthermore, we used a mixture of Hoagland nutrient solution and calcium nitrate at a ratio of 4:3 (Qingdao Hope Bio-Technology Co., Ltd. Qingdao, China) as fertilizer. For low, medium, and high fertilizer treatments, we added 0 g, 15 g, and 30 g/tub every month, respectively. After four months, we recorded the number of inflorescences, harvested inflorescences, shoots, and roots within each tub, and dried them separately at 80 °C for 48 h and then weighed them.

### 2.5. Data analysis

To examine the differences in inflorescences production and shoot biomass of *A. philoxeroides* between terrestrial and wetland habitats in the field survey, the number and biomass of inflorescences and the ratio of inflorescences to shoot biomass were analyzed using Wald tests with habitat type as a fixed factor and sample site nested within habitat as a random factor. To investigate the difference in inflorescence development of *A. philoxeroides* between terrestrial and wetland habitats, the percentage of normal inflorescences was analyzed using a paired sample *t*-test. Data analysis of field surveys was performed at the plot level.

To test the effects of treatments on inflorescences production, individual growth, and resource allocation of *A. philoxeroides* in a greenhouse experiment, the number of inflorescences, biomass of inflorescences, biomass of shoots and roots as well as the ratio of belowground (root) to aboveground (shoot) and ratio of reproduction (inflorescences) to growth (shoot + root) were analyzed using three-way ANOVAs with water availability (*W*), fertilizer application (*F*), and plant density (*D*) as fixed factors. Multiple comparisons were performed using least square mean post-hoc tests, and *P* values were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995) when there was a significant interactive effect. Data analysis of the greenhouse experiment was conducted at the individual level.

In all analyses, continuous and discrete variables were applied to linear mixed models and generalized linear mixed models with a Poisson distribution, respectively. All analyses were conducted using R 3.5.2 (R Foundation for Statistical Computing, Vienna, Austria) with 'CAR' (Fox and Weisberg, 2011), 'LME4' (Bates et al., 2015) and 'LSMEANS' (Lenth, 2016) packages.

## 3. Results

### 3.1. Field survey: habitats affect inflorescences and resource allocation to inflorescences of *A. philoxeroides*

Plots in the terrestrial habitat had fewer inflorescences ( $\chi^2 = 68.84$ ,  $P < 0.001$ , Fig. S2) and less biomass of inflorescences ( $\chi^2 = 19.40$ ,

$P < 0.001$ , Fig. 1A) than those in the wetland habitat. For 100 inflorescences, terrestrial habitats had less monoclinal flowers than wetland habitats ( $t_{1,42} = -11.00$ ,  $P < 0.001$ , Fig. 1B). Furthermore, plots in the terrestrial habitat had a lower ratio of inflorescence to shoot biomass than those in the wetland habitat ( $\chi^2 = 8.89$ ,  $P = 0.003$ , Fig. 1C).

### 3.2. Greenhouse experiment: water availability (*W*), fertilizer application (*F*), and plant density (*D*) affect inflorescences, growth, and resource allocation of *A. philoxeroides*

The number of inflorescences significantly increased with fertilizer application ( $\chi^2 = 72.62$ ,  $P < 0.001$ ), but significantly decreased with plant density ( $\chi^2 = 52.80$ ,  $P < 0.001$ , Table S2, Fig. S3). The combined effects of  $W \times F$  ( $\chi^2 = 10.91$ ,  $P = 0.004$ ) and  $W \times D$  ( $\chi^2 = 9.27$ ,  $P = 0.010$ ) also significantly affected the number of inflorescences (Table S2, Fig. S3). For the effect of  $W \times F$ , the number of inflorescences was the highest under combined wet and high nutrient conditions, while the fewest were found under combined wet and low nutrient conditions. For the effects of  $W \times D$ , plants produced more inflorescences under combined dry and low-density conditions than under conditions with other combinations of factors, which did not differ significantly. Similarly, the biomass of inflorescences was significantly enhanced by fertilizer application ( $F_{2,72} = 5.93$ ,  $P = 0.004$ ) and significantly decreased with increasing plant density ( $F_{2,72} = 4.04$ ,  $P = 0.022$ ), but were not affected by any combined effects (Table S2, Fig. 2A).

The biomass of shoots was also significantly enhanced by fertilizer application ( $F_{2,72} = 25.16$ ,  $P < 0.001$ ) and significantly decreased with plant density ( $F_{2,72} = 38.91$ ,  $P < 0.001$ , Table S2, Fig. 2B). Furthermore, the combined effects of  $W \times F$  ( $F_{2,72} = 6.42$ ,  $P = 0.003$ ) and  $F \times D$  ( $F_{4,72} = 3.59$ ,  $P = 0.010$ ) significantly affected the number of inflorescences (Table S2, Fig. S3). For the effect of  $W \times F$ , the biomass of shoots was the highest under the combined wet and high nutrient conditions, while the lowest was observed under the combined wet and low nutrient conditions. For the effect of  $F \times D$ , the biomass of shoots was the highest under the combined high nutrient and low density conditions, and the lowest was observed under the combined low fertilizer and high-density conditions. The biomass of roots was higher under dry conditions than under wet conditions ( $F_{1,72} = 152.30$ ,  $P < 0.001$ ), while it significantly decreased with increasing plant density ( $F_{2,72} = 46.97$ ,  $P < 0.001$ , Table S2, Fig. 2C). Analyses of combined effects showed that  $W \times D$  ( $F_{2,72} = 23.94$ ,  $P < 0.001$ , Table S2, Fig. 2C) also significantly affected root biomass. Plants produced more root biomass under combined dry and low-density conditions, while lower root biomass was observed under the combined wet and high-density conditions (Fig. 2C).

For resource allocation between above- and belowground, water availability ( $F_{1,72} = 72.22$ ,  $P < 0.001$ ) and fertilizer application ( $F_{2,72} = 38.79$ ,  $P < 0.001$ ) significantly decreased the ratio of roots to shoots, whereas plant density ( $F_{2,72} = 9.89$ ,  $P < 0.001$ ) significantly increased the ratio of roots to shoots (Table S2, Fig. 3A). The combined effects of  $W \times F$  ( $F_{2,72} = 15.71$ ,  $P < 0.001$ ) also significantly affected the ratio of inflorescence to shoot + root, with higher values under the combined dry and low fertilizer conditions, while lower values were observed under the combined wet and high fertilizer condition treatments (Fig. 3A). For resource allocation between inflorescence and growth, fertilizer application ( $F_{2,72} = 6.46$ ,  $P = 0.003$ ) significantly increased the ratio of inflorescence to shoot + root, while plant density ( $F_{2,72} = 0.20$ ,  $P = 0.822$ ) and water availability ( $F_{1,72} = 0.08$ ,  $P = 0.774$ ) had no effect (Table S2, Fig. 3B). The combined effects of  $W \times D$  ( $F_{2,72} = 4.15$ ,  $P = 0.020$ ) also significantly affected the ratio of inflorescence to shoot + root, but least square mean post-hoc tests did not show any difference between combinations (Fig. 3B).

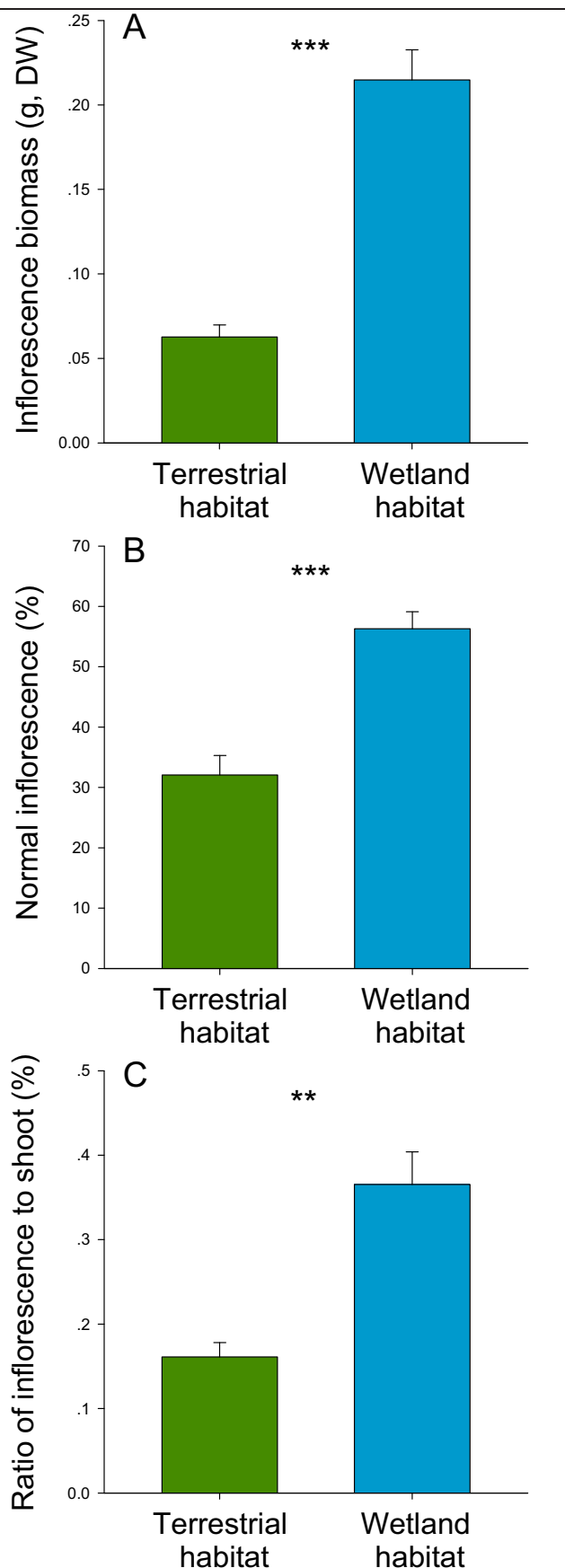
## 4. Discussions

The sexual trait and resource allocation to sexual trait of many amphibious invasive species are affected by water and nutrients (Robe and Griffiths, 1998; Ishii and Kadono, 2004; Liu et al., 2013) and understanding this across habitat types would improve our ability to manage invasions. The results of our study showed that *A. philoxeroides* can produce more inflorescences and more normal flowers in wetland habitats than in terrestrial habitats. Moreover, *A. philoxeroides* inflorescence production increased with increasing space availability (low plant density) and fertilizer application.

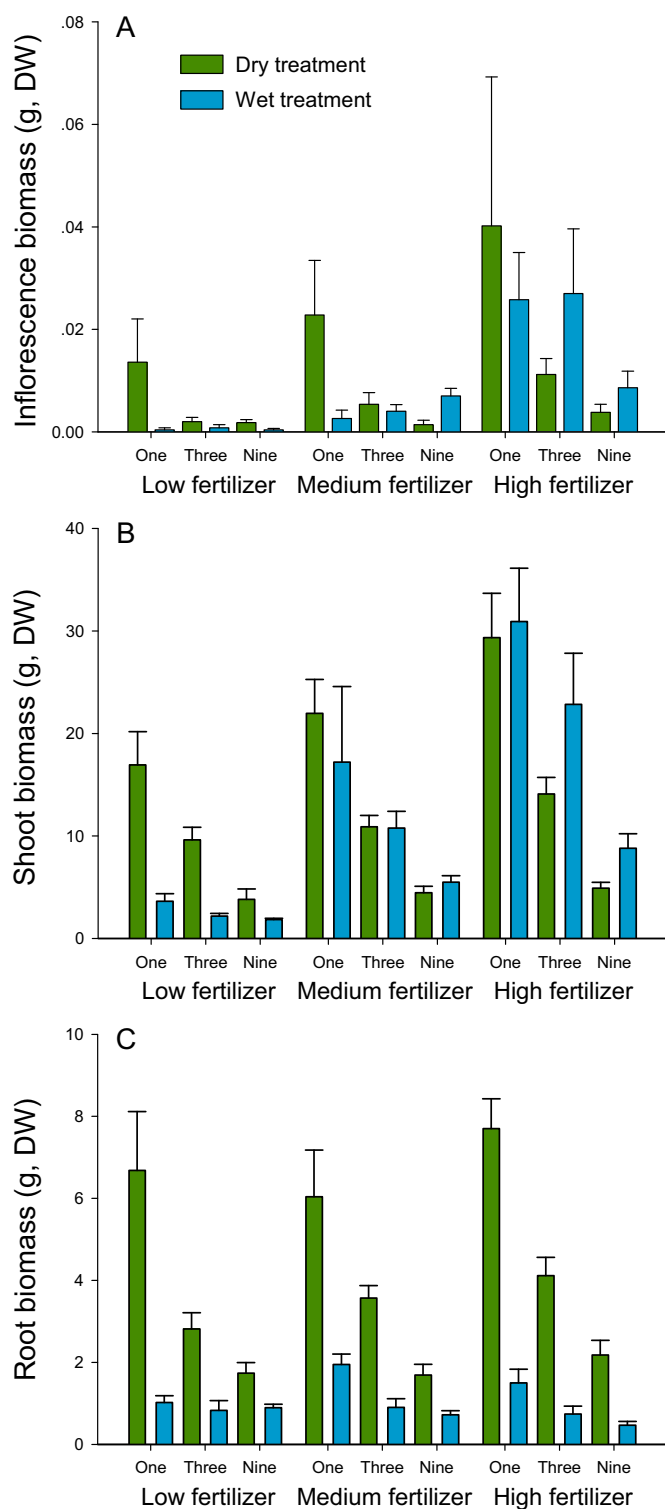
Water availability is an important limiting factor that can affect the sexual investment of plants. For example, *Caragana stenophylla* reduces sexual investment and enhances clonal reproduction with increasing arid gradients (Ma et al., 2013). In aquatic or wetland habitats, water has greater chemical and thermal stability than in terrestrial habitats and provides relatively stable growing environments (Philbrick and Les, 1996). The results of our field surveys revealed that *A. philoxeroides* plants in wetland habitats have a significantly higher output of inflorescences and ratio of inflorescences to shoots than those in terrestrial habitats. Similar results were obtained in our greenhouse experiment, in which *A. philoxeroides* produced more inflorescences in the wet treatment, especially under high nutrient and high-density conditions. This implies that *A. philoxeroides* grown under relatively favorable stable conditions will allocate more resources to shoots and inflorescences and enhance the ratio of sexual investment.

In our study, fertilizer significantly increased the output of *A. philoxeroides* inflorescences regardless of water treatment (habitat type), and there were significant interactions with water treatment or plant density. We found that *A. philoxeroides* produced fewer inflorescences under wet/low nutrient conditions than in the control (terrestrial), whereas more inflorescences were produced under wet/high nutrient conditions than in the control. These results highlight the complicated interactions between water availability and nutrition in generating inflorescences of *A. philoxeroides*.

Furthermore, *A. philoxeroides* produced more inflorescences and a higher proportion of normal monoclinal flowers in wetland habitats than in terrestrial habitats. We expect that soil nutrition might vary between wetland and terrestrial habitats. Wetlands or waterbodies can act as nutrient traps (van der Valk et al., 1979; Jansson et al., 1994), and receive excessive nutrient loading from agricultural lands through surface runoff and groundwater in watersheds (Peterjohn and Correll, 1984; Wu et al., 2017). Our unpublished data on soil nutrition in terrestrial and wetland habitats for *A. philoxeroides* growth also showed that total nitrogen content in soil samples in wetland habitats was higher than that in terrestrial habitats. Therefore, wetlands stimulate *A. philoxeroides* to produce more inflorescences. Furthermore, nutrient and water availability also affect the development of flowers (Loehwing, 1940; Delesalle and Mazer, 1996; Su et al., 2013). Delesalle and Mazer (1996) found that abnormal anther numbers per flower of *Spergularia marina* Griseb. was affected by nutrient levels, and male reproductive traits were more sensitive to growing conditions than those related to female reproduction. Su et al. (2013) revealed that drought treatment of *Arabidopsis* during the reproductive stage could lead to abnormal anther production and reduced plant fertility. Together, nutrient and water availability in wetland habitats may generate more normal monoclinal flowers in *A. philoxeroides*.

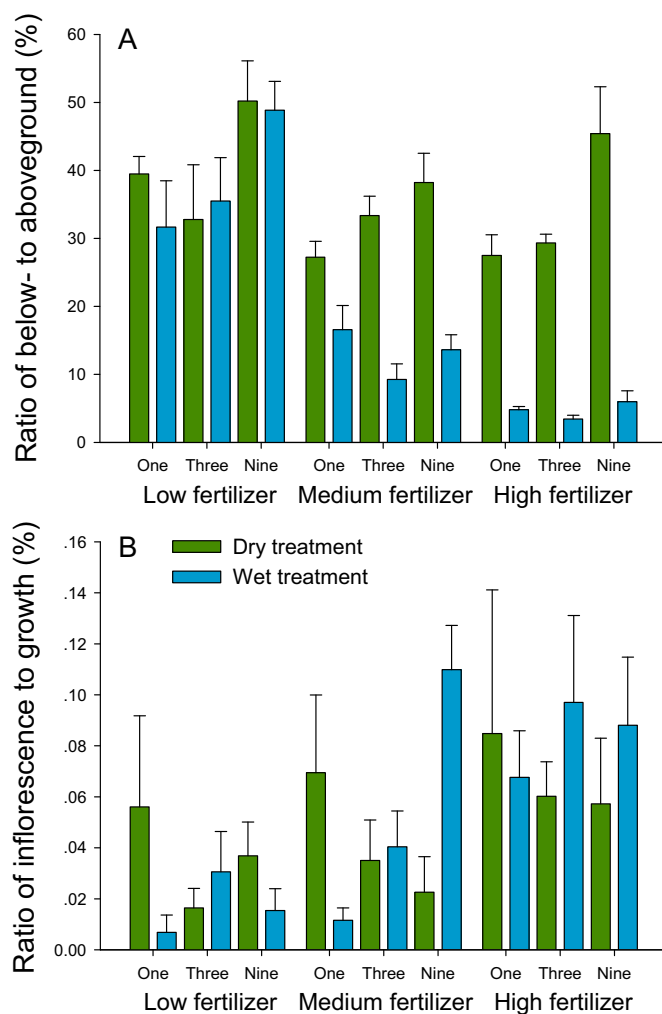


**Fig. 1.** The effect of habitats (terrestrial vs. wetland) on inflorescence of *Alternanthera philoxeroides* in the field surveys. (A) Inflorescence biomass, (B) Percentage of normal inflorescence, and (C) Ratio of inflorescence biomass to shoot biomass. Inflorescence biomass and ratio of inflorescence biomass to shoot biomass were obtained from survey in 2017 and are shown at plot level (31 sites  $\times$  2 habitats  $\times$  5 plots). Percentage of normal inflorescence was obtained from survey in 2018 with 100 inflorescences in each habitat at 43 sites. Values are mean  $\pm$  1 SE. Asterisks indicate a significant difference between habitats (\*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ).



**Fig. 2.** The effects of water availability, fertilizer application, and plant density on inflorescence output and growth of *Alternanthera philoxeroides* in greenhouse experiment. (A) Inflorescence biomass, (B) Shoot biomass, and (C) Root biomass. There were two levels of water availability (dry and wet), three levels of fertilizer application (low, medium, and high), and three levels of plant density (one, three, and nine plants per tub). Values are mean  $\pm$  1 SE.

We found that plants produced more inflorescences in each tub under high density; however, the number of inflorescences per individual plant decreased as density increased. This clearly shows that intraspecific competition can affect plant sexual reproduction, likely by limiting resources such as nutrients, space, and light (Xie et al., 2014).



**Fig. 3.** The effects of water availability, fertilizer application, and plant density on resource allocation of *Alternanthera philoxeroides* in greenhouse experiment. (A) Ratio of belowground (root) to aboveground (shoot), and (B) Ratio of reproduction (inflorescence) to growth (shoot + root). There were two levels of water availability (dry and wet), three levels of fertilizer application (low, medium, and high), and three levels of plant density (one, three, and nine plants per tub). Values are mean  $\pm$  1 SE.

There were significant combined effects between water and nutrients, water, and plant density on the inflorescence numbers of *A. philoxeroides* at the individual plant level. When plants are faced with heterogeneous resources, their performance is affected by multiple factors and their interactions. The efficiency of plants utilizing one resource is usually affected by the availability of another resource (Gleeson and Tilman, 1992) and allocating biomass to reproduction is size- or density-dependent (Zhang and Jiang, 2002; Coelho et al., 2005). Our results from the greenhouse experiment showed that water availability affected the ability of *A. philoxeroides* to utilize nutrients, and the interaction of water and higher nutrients induced *A. philoxeroides* to produce more inflorescences. Increasing plant density increased *A. philoxeroides* output of inflorescences per unit area but decreased output at the individual plant level. The interactions between density, nutrition, and water are complicated. At low or median nutrient levels, wet/low density conditions decreased *A. philoxeroides* inflorescence production, whereas production increased under wet/high nutrient conditions. In the field, there may be more factors that influence the output of *A. philoxeroides* inflorescences in wetland habitats, but water, at least, is important when combined with nutrient and plant density.

Many studies indicated that invasive plants can readily intrude into plant-pollinator networks in the introduced ranges and generally cause negative impacts on native plant reproduction through affecting

pollinator behavior, increasing pollinator distance to resources, and altering pollinator community. For example, Chittka and Schurkens (2001) simulated shifts in flower abundance between invasive plant *Impatiens glandulifera* and native plant *Stachys palustris* and found that the presence of *I. glandulifera* significantly decreased seed set of *S. palustris*. In the field experiment, Giejsztowt et al. (2020) also found similar results that seed mass of native plant *Dracophyllum subulatum* was lower in the patches with high proportion of invasive flowers than in ones with high proportion of native flowers. Thus, inflorescences have potential to promote plant invasion through disturbs native plant-pollinator networks. In our study, under high resource condition, such as aquatic habitat, more flower production may promote *A. philoxeroides* invasion by disturbance of native plant-pollinator relationship. In contrast, under low resource condition, such as terrestrial habitat, resource competition may be important for *A. philoxeroides* invasion and thus it allocates more resource to clonal growth and less to inflorescences. Future studies are needed to elucidate the effect of inflorescences in plant invasion, in particular for some species that is less likely to produce viable seeds.

In conclusion, our results revealed that *A. philoxeroides* can mediate resource allocation between shoots and roots depending on resource availability, and as a result, there was a significant difference in inflorescence output between terrestrial and wetland habitats. Our results also suggested that *A. philoxeroides* could tradeoff resources between sexual trait and clonal growth. These findings on phenotypic plasticity in resource allocation may also be relevant to other invasive clonal plants growing under rich- or poor-resource environments. For example, there was a significant tradeoff between seed output and clonal bulbil production in *Butomus umbellatus*, but it was not stronger under low nutrient conditions, which clearly restricts plant growth (Thompson and Eckert, 2004). Studies on resource allocation of clonal plants between sexual trait and clonal growth can reveal reproductive strategies in a changeable environment. This knowledge will be critical for future management of invasive clonal plants under global environmental changes (Wu and Ding, 2019).

### CRedit authorship contribution statement

**Jiali Zhang:** Investigation, Data collection, Formal analysis, Writing - original draft, Writing - review & editing. **Wei Huang:** Funding acquisition, Formal analysis, Visualization, Writing - review & editing. **Jianqing Ding:** Conceptualization, Methodology, Writing - original draft preparation, Writing - review & editing, Funding acquisition.

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### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.143819>.

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